4045c

National Library of Canada / Bibliothèque nationale du Canada

CANADIAN THESES ON MICROFICHE / THÈSES CANADIENNES SUR MICROFICHE

NAME OF AUTHOR/*NOM DE L'AUTEUR* David Henry Kavanaugh

TITLE OF THESIS/*TITRE DE LA THÈSE* THE NEARCTIC SPECIES OF NEBRIA LATREILLE (COLEOPTERA: CARABIDAE: NEBRIINI): CLASSIFICATION, PHYLOGENY, ZOOGEOGRAPHY, AND NATURAL HISTORY

UNIVERSITY/*UNIVERSITÉ* University of Alberta

DEGREE FOR WHICH THESIS WAS PRESENTED/ *GRADE POUR LEQUEL CETTE THÈSE FUT PRÉSENTÉE* Ph.D.

YEAR THIS DEGREE CONFERRED/*ANNÉE D'OBTENTION DE CE GRADE* 1978

NAME OF SUPERVISOR/*NOM DU DIRECTEUR DE THÈSE* George E. Ball, Ph.D.

Permission is hereby granted to the NATIONAL LIBRARY OF CANADA to microfilm this thesis and to lend or sell copies of the film.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

L'autorisation est, par la présente, accordée à la BIBLIOTHÈQUE NATIONALE DU CANADA de microfilmer cette thèse et de prêter ou de vendre des exemplaires du film.

L'auteur se réserve les autres droits de publication; ni la thèse ni de longs extraits de celle-ci ne doivent être imprimés ou autrement reproduits sans l'autorisation écrite de l'auteur.

DATED/*DATÉ* 25 Sept. 1978 SIGNED/*SIGNÉ* David H. Kavanaugh

PERMANENT ADDRESS/*RÉSIDENCE FIXÉ* 34 Carleton Drive
Petaluma, California 94952

National Library of Canada

Cataloguing Branch
Canadian Theses Division

Ottawa, Canada
K1A 0N4

Bibliothèque nationale du Canada

Direction du catalogage
Division des thèses canadiennes

NOTICE

The quality of this microfiche is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us a poor photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this film is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30. Please read the authorization forms which accompany this thesis.

THIS DISSERTATION
HAS BEEN MICROFILMED
EXACTLY AS RECEIVED

AVIS

La qualité de cette microfiche dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de mauvaise qualité.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, examens publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de ce microfilm est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30. Veuillez prendre connaissance des formules d'autorisation qui accompagnent cette thèse.

LA THÈSE A ÉTÉ
MICROFILMÉE TELLE QUE
NOUS L'AVONS REÇUE

THE UNIVERSITY OF ALBERTA

THE NEARCTIC SPECIES OF NEBRIA LATREILLE (COLEOPTERA: CARABIDAE: NEBRIINI): CLASSIFICATION, PHYLOGENY, ZOOGEOGRAPHY, AND NATURAL HISTORY

by

DAVID HENRY KAVANAUGH

©

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ENTOMOLOGY

EDMONTON, ALBERTA

FALL, 1978

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled "The Nearctic Species of Nebria Latreille (Coleoptera: Carabidae: Nebriini): Classification, Phylogeny, Zoogeography, and Natural History" submitted by David Henry Kavanaugh in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

Supervisor

Richard C. Fox

R. H. Goodin

D. E. H. Utt

J. A. Downes

External Examiner

Date Sept. 20, 1978

To Beverly, whose love and constant support

have been my most precious resource;

and to Mike, Jeff, Tom, Becky and Katie,

who have shared me with beetles and the mountains.

ABSTRACT

This study, based on examination of over 70,000 specimens, 26 months of field work, laboratory studies, and extensive literature review, brings together available information (through April 1978) on adult external and genitalic structure, geographical and habitat distributions, phylogenetic relationships, fossil record, and natural history of Nearctic members of the Holarctic genus Nebria Latreille.

Three hundred fifteen structural characters were used to compare representatives of Nearctic species, all nebriine subgenera and 50 other adephagan taxa. Structural characters of the female reproductive system (including genitalia), especially of the bursa copulatrix, spermatheca, and spermathecal duct, were found to be extremely useful for both discrimination and clustering purposes. Characters of male genitalia were also useful for discrimination among taxa, but less so for clustering of same. Intrapopulational dimorphism in hindwing size was not found among Nearctic Nebria taxa; but a complete spectrum of character states of hindwing size and shape (from full-sized/functional to short, scale-like/non-functional) is demonstrated by members of these taxa collectively.

Members of Nebria taxa are cool- or cold-adapted, nocturnal, general predator/scavengers. Taxa occupy more or less restricted life zone ranges (extremes for the genus include Arctic/Alpine and Upper Sonoran Life Zones, but highest diversity is in the Canadian Zone). Members of most taxa live at the margins of swift-flowing streams, but those of some occupy such extreme microhabitats as sea beaches and the margins of alpine glaciers. Members of most taxa characteristically

overwinter as adults, but those of a few taxa do so as larvae. Ambulation is the usual mode of locomotion for these beetles and the importance of flight for fully-winged individuals is yet unclear.

Forty-two native species are recognized for the Nearctic fauna, four of which are described as new: namely, Nebria gouleti (type locality--Rattlesnake Creek, Asotin County, Washington); N. darlingtoni (type locality--South Fork American River, El Dorado County, California); N. navajo (type locality--19 miles sw. of Kayenta, Navajo County, Arizona), and N. carri (type locality--Dollarhide Summit, Blaine County, Idaho). A total of 26 additional subspecies are recognized, 22 of which are described as new. A key for identification of adults is included. Only sample descriptions are provided; but a synonymy, bibliography, and complete list of known localities is presented for each species-group taxon.

Among Nearctic species, four main lineages are recognized (namely, the virescens, gyllenhali, gregaria, and metallica lineages), and each is also represented in the Palaearctic Nebria fauna. These comprise a total of 10 species groups, three of which (the hudsonica, mannerheimii, and trifaria groups) are endemic to the Nearctic Region, seven of which (the virescens, paradisi, gyllenhali, gregaria, obliqua, ovipennis, and metallica groups) are shared with the Palaearctic Region. The classification of taxa proposed is tentative, pending reclassification of the Holarctic nebriine fauna. It reflects a "systematization"--system of cladistic relationships suggested by analysis of 171 characters of external adult structure (including genitalia), comprising 670 character states. A "sequencing" convention was used in construction of the classification, to reduce the number of

categories required with no attendant loss of information on cladistic relationship. Determination of polarity and sequence in transformation series of characters was based on (1) "ex-group comparisons", (2) "character correlations", (3) "group trends", (4) "correlation with adaptive significance", and (5) "in-group comparisons" (in order of decreasing importance). These criteria, their application, and all other analytical procedures are discussed in detail. If phylogenetic relationships proposed actually reflect evolutionary history, a total of 1468 extra evolutionary steps (including both convergence and reversal steps) are required to account for the distribution of character states of characters analysed among members of Nearctic Nebria species. Seventy-two percent of characters studied have one or more character states reversed or acquired at least twice independently. Mean number of extra steps per character is 8.702; and some character states have evolved many times (one, for example, at least 36 times). Convergence appears to have been a more frequent evolutionary event than reversal in Nearctic Nebria evolution.

Present known distributions of Nearctic species and species groups are illustrated by dot and line maps, respectively. In North America, members of genus Nebria are restricted to areas north of 30°N latitude. Species and subspecies diversity is highest on the Pacific Coast, especially in Washington, and decreases in all directions from that area, except for secondary centers of diversity in the Sierra Nevada of California and the Rocky Mountains of Colorado and Utah. The fauna of eastern North America is unexpectedly low in diversity. Major centers of endemism include the Cascade Range north of the Columbia River (five endemic taxa), the Sierra Nevada (seven

endemic taxa), the southern Rocky Mountains of Colorado, northern New Mexico and southcentral Wyoming (four endemic taxa), and the southwestern portion of the Colorado Plateau (six endemic taxa). Several secondary centers and subcenters are also recognized and discussed. Distributions of taxa are correlated with mountain systems and not with drainage systems. Similarity in Nebria faunas between the Rocky Mountain system and West Coast systems is very low at southern latitudes and increases northward. The northern Rocky Mountain fauna is distinct from but clearly related to those of the central and southern Rocky Mountains, and Sierra Nevada and Cascade Range faunas share a similar relationship. Four groups of geographical range patterns are evident, based on concordance among distributions of species and subspecies. These are: (1) eastern (three patterns); (2) Rocky Mountain (seven patterns), (3) Pacific coastal (nine patterns); and northern and transamerican (four patterns). Vicariance patterns and "individual" and "generalized tracts" evident in the Nearctic Region are described and discussed in detail. Seven individual tracts link sister groups across the northern Pacific Basin and/or Bering Strait.

Striking altitudinal zonation patterns are apparent in montane areas with diverse Nebria faunas (e.g. Mountain Rainier, Washington; Yosemite, California; and the Front Range, Colorado). These are described and illustrated.

ACKNOWLEDGEMENTS

This manuscript is the result of an eight-year study, the initiation, execution and completion of which would have been all but impossible without the generous co-operation of the individuals and institutions mentioned below. For most of these, space limits prevent adequate description of their contributions, but I here extend sincere thanks to each for their essential part in this study.

G. E. Ball, my sponsor at the University of Alberta and chairman of my supervisory committee, provided constant encouragement, interest, enthusiasm and guidance throughout the study. The honesty, integrity and attention to detail which characterize both his relationships with colleagues and his scholarly work have served as constant inspiration for me. He also provided financial support for this study (including support from National Research Council of Canada Grant A-1399).

Additional financial support was obtained from the following: the Boreal Institute for Northern Studies (University of Alberta) through a Grant In Aid Of Research (1973-74), for field studies in Alaska; and the California Academy of Sciences, for field studies in the Pacific Northwest.

R. G. Fox, R. H. Gooding, and D. H. Vitt serving as members of my supervisory committe, read and criticized the manuscript and provided helpful suggestions for its improvement; and J. A. Downes provided further criticism and suggestions as external examiner on this committee.

Staff members at the California Academy of Sciences, in particular P. H. Arnaud, Jr. (Entomology Department chairman), provided continued

encouragement and a measure of freedom from some normal curatorial duties during the study. I am most grateful for their support.

Over half of the material used in the study was obtained through loans made possible by the individuals listed in section 2.11 below; and their considerable help is heartily acknowledged. In addition, the following made type material in their care available to me on loan or provided critical information on type specimens: T. L. Erwin (USNM [see section 2.11 for list of abbreviations]), P. M. Hammond (BMNH), H. Hippa (UMTF), S. Seleinikova (ZMUM), O. L. Kryzhanovskij and V. G. Shilenkov (ZIN), J. F. Lawrence and J. Scott (MCZ), H. B. Leech (CAS), O. Martin (ZMKD), T. Nyholm (NRSS), H. Perrin (MHNP), S. Rohwer (UWBM), W. Sauter (ETHZ), G. Scherer (ZSBS), and H. Silfverberg (UMHF).

The following individuals accompanied me at various times in field work on the project and contributed their physical labor and enthusiasm: R. T. Allen; T. C. Barr, Jr.; R. T. and J. R. Bell; E. Cronin; N. M. Downie; J. G. Edwards; T. L. and L. J. M. Erwin; H. Goulet; B. A., M. D., J. L., and T. W. Kavanaugh; R. D. Kavanaugh; A. Larochelle; W. Lazorko; E. A. Martinko; L. Russell; R. G. Thompson; and R. L. Westcott. Colleagues who collected material for this project during their own field studies include: M. Abrahams, R. T. Allen, J. Belicek, N. A. Bronstein, P. M. Choate, Jr., D. A Craig, L. R. Davis, Jr., H. Frania, D. Giuliani, R. H. Gooding, H. Goulet, R. L. Hoffman, H. J. Lee, D. Maddison, P. S. Miliotis, B. M. Rolseth, and J. R. Spence. R. P. Allen, T. C. Barr, Jr., P. J. Darlington, Jr., D. Durbin, P. Kushar, A. Larochelle, C. H. Lindroth, M. S. Mani, and R. P. Papp provided important data from field observations.

My field work was greatly facilitated by numerous individuals who provided directions, transportation, shelter or other assistance during my travels. Among these were: R. T. Allen, R. T. and J. R. Bell, M. Burroughs, J. M. Campbell, P. J. Darlington, Jr., N. M. Downie, A. R. Gittins, R. L. Hoffman and L. Knight, J. V. Matthews, Jr., and D. R. Whitehead. E. P. Bailey and R. D. Jones (Cold Bay), J. P. Cook (Fairbanks) and R. Tamberelli (Dutch Harbor) furnished transportation and lodging during my field work in Alaska; and without their help, I could not have completed my work there. I obtained collecting permits, information and considerable encouragement from the following members of the U. S. National Park Service: N. A. Bishop (Mount Rainier National Park), D. H. Huntzinger (Olympic National Park), P. F. McCrary and D. DeFoe (Great Smoky Mountains National Park), R. L. Vance (Lassen Volcanic National Park), and J. W. van Wagtendonk (Yosemite National Park). Permission to import live Nebria specimens was obtained from the Plant Protection Division, Production and Marketing Branch, Agriculture Canada through the efforts of J. R. Wetmore.

T. L. Erwin (USNM), M. H. Hatch (UWBM), J. F. Lawrence (MCZ), H. B. Leech (CAS), P. Oman (OSUO), L. L. Pechuman (CUIC), and A. Smetana (CNC) were helpful hosts during my visits to study material in their respective institutions.

I also note with appreciation the technical and clerical assistance of numerous co-workers. J. Belicek, L. J. Dempster, A. S. Loukashkin, J. Schonewald and S. E. Tatro provided translations of important passages from papers written in Russian, French and German. Portions of early drafts and the final version of this manuscript were typed by

R. Berlin, L. G. Freihofer and L. F. Toren. M. C. Giles, C. L. Mullinex and J. S. Scott provided many helpful suggestions on preparation and format of illustrative materials. Photographic work on the accompanying plates was done by M. C. Giles. Special thanks are due to R. Berlin, L. G. Freihofer, O. Frost, V. F. Lee and J. C. Shore, who handled a myriad of administrative problems and details on my behalf during this study.

I must thank all my colleagues at both the University of Alberta and the California Academy of Sciences who have been most generous with their time, interest and ideas in discussions on relevant topics. The opportunities they provided for me to voice, then re-evaluate, my own ideas in light of their comments were a great asset to me. D. A. Craig, R. C. Fox, H. Goulet, B. S. Heming, G. R. Noonan and D. R. Whitehead (University of Alberta) and P. H. Arnaud, Jr., R. C. Drewes, D. C. Rentz, E. S. Ross, E. L. Smith and D. D. Wilder (California Academy of Sciences) deserve special thanks for their frequent, perceptive dialogue and their patience with my inquiries. R. T. Bell, P. J. Darlington, Jr., C. H. Lindroth, and J. R. Spence have taken extraordinary interest in this study and provided continued comment and encouragement.

I thank W. E. and S. Ferguson, J. G. Edwards, T. L. and L. J. M. Erwin, G. E. Ball and H. Goulet for the very special contributions each has made to this project and to my career in entomology.

My wife, Beverly, has been my unfailing source of strength and renewal. She has patiently endured the frustrations and limitations of graduate student life for so many years, while providing for me and our

children an environment of sustenance and love. My accomplishments are hers as well.

TABLE OF CONTENTS

SECTION	PAGE
1.0 INTRODUCTION	1
1.1 Historical review of Nearctic Nebria systematics	3
2.0 MATERIALS AND METHODS	7
2.1 Materials	7
2.11 Materials received on loan	7
2.12 Materials collected for the study	14
2.13 Type material	14
2.14 Fossil material	15
2.2 Methods	15
2.21 Collection and preservation of specimens	15
2.22 Dissecting techniques	17
2.23 Sex determination and association	19
2.24 Measurements	19
2.25 Illustrations and maps	20
2.26 Descriptive format	21
2.27 Literature and synonymic lists	25
2.28 Procedural methods	26
2.29 Criteria for ranking taxa	27
3.0 SYSTEMATICS	33
3.1 Introduction	33
3.2 Comparative biology: character systems	34
3.21 Comparative morphology	36
3.211 General characteristics	37
3.212 Head	43

3.213 Prothorax 51
3.214 Pterothorax 57
3.215 Legs 69
3.216 Abdomen 74
3.217 Male genitalia 76
3.218 Female genitalia 84
3.22 Chorology 98
3.221 Characters of single localities 99
3.222 Known ranges of taxa 100
3.23 Natural history 166
3.231 Habitat distribution 167
3.2311 Macrohabitat 167
3.2312 Microhabitat 176
3.232 Life history 215
3.2321 Diel activity cycles 216
3.2322 Life cycle and seasonal activity 218
3.233 Other aspects of natural history 245
3.2331 Studies on *Nebria* populations 245
3.2332 Trophic relations 248
3.234 Locomotion and dispersal 253
3.2341 Locomotion 253
3.2342 Dispersal 261
3.24 Paleontology 273
3.3 Classification 278
3.31 Classification: a perspective 278
3.32 History of Nearctic *Nebria* classification 282
3.33 A reclassification of Nearctic *Nebria* 285

3.4 Nomenclature, description, and identification 294

3.41 Genus Nebria Latreille 294

3.42 Identification of Nearctic Nebria 312

3.421 Notes on the key and its use 312

3.422 A key for identification of adults of the Nearctic species and subspecies of Nebria 315

3.43 Species groups, species, and subspecies 340

3.431 Introduced species 341

3.432 The virescens lineage 342

3.4321 The virescens group 344

3.43211 N. virescens Horn 345

3.433 The gyllenhali lineage 352

3.4331 The paradisi group 353

3.43311 N. paradisi Darlington 354

3.4332 The hudsonica group 355

3.43321 N. gouleti new species 356

3.43322 N. hudsonica LeConte 357

3.43323 N. lacustris Casey 358

3.4333 The gyllenhali group 360

3.43331 The nivalis subgroup 362

3.433311 N. nivalis (Paykull) 362

3.43332 The gyllenhali subgroup 366

3.433321 N. crassicornis Van Dyke 366

3.433322 N. gyllenhali (Schonherr) 367

3.433323 N. frigida Sahlberg 375

3.434 The gregaria lineage 377

3.4341 The gregaria group 378

3.43411 The lyelli subgroup 379
3.434111 N. lyelli Van Dyke 379
3.434112 N. acuta Lindroth 379
3.43412 The sahlbergii subgroup 381
3.434121 N. sahlbergii Fischer von Waldheim 381
3.43413 The gregaria subgroup 385
3.434131 N. gregaria Fischer von Waldheim 385
3.434132 N. charlottae Lindroth 386
3.43414 The arkansana subgroup 386
3.434141 N. arkansana Casey 386
3.434142 N. fragilis Casey 389
3.434142 N. zioni Van Dyke 390
3.4342 The obliqua group 391
3.43421 The obliqua subgroup 392
3.434211 The obliqua infragroup 392
3.4342111 N. suturalis LeConte 392
3.4342112 N. obliqua LeConte 394
3.434212 The pallipes infragroup 396
3.4342121 N. appalachia Darlington 396
3.4342122 N. pallipes Say 397
3.4343 The mannerheimii group 398
3.43431 The mannerheimii subgroup 399
3.434311 N. darlingtoni new species 399
3.434312 N. mannerheimii Fischer von Waldheim 400
3.43432 The eschscholtzii subgroup 402
3.434321 The desolata infragroup 402
3.4343211 N. desolata Kavanaugh 402

3.4343212 N. navajo new species 402
3.434322 The eschscholtzii infragroup 403
3.4343221 N. eschscholtzii Ménétriés 403
3.4343222 N. diversa LeConte 405
3.435 The metallica lineage 407
3.4351 The ovipennis group 408
3.43511 The gebleri subgroup 408
3.435111 N. gebleri Dejean 408
3.43512 The ovipennis subgroup 413
3.435121 The kincaidi infragroup 413
3.4351211 N. carri new species 413
3.4351212 N. kincaidi Schwarz 414
3.435122 The ovipennis infragroup 416
3.4351221 N. spatulata Van Dyke 416
3.4351222 N. ovipennis LeConte 417
3.4352 The metallica group 418
3.43521 The meanyi subgroup 419
3.435211 N. meanyi Van Dyke 419
3.43522 The metallica subgroup 421
3.435221 The metallica infragroup 421
3.4352211 N. metallica Fischer von Waldheim 421
3.4353 The trifaria group 423
3.43531 The ingens subgroup 424
3.435311 N. ingens Horn 424
3.435312 N. vandykei Bänninger 425
3.43532 The schwarzi subgroup 427
3.435321 N. piperi Van Dyke 427

3.435322 *N. schwarzi* Van Dyke 428
3.43533 The *trifaria* subgroup 429
3.435331 The *purpurata* infragroup 429
3.4353311 *N. purpurata* LeConte 429
3.435332 The *trifaria* infragroup 430
3.4353321 *N. trifaria* LeConte 430
3.4353322 *N. coloradensis* Van Dyke 432
3.4353323 *N. piute* Erwin and Ball 433
4.0 ANALYSES OF THE NEARCTIC *NEBRIA* FAUNA 434
4.1 Phylogeny 434
4.11 Introduction 434
4.12 Cladistic analysis 444
4.13 Phylogeny of Nearctic *Nebria* 506
4.2 Zoogeography 522
4.21 Introduction 522
4.22 Contemporary zoogeography: present patterns of distribution 523
4.221 Generic, lineage, and species group patterns 523
4.222 Present distributions of Nearctic species and their relatives 526
4.223 *Nebria* fossils and past distributions 595
4.224 Habitat distributions; altitudinal zonation patterns 597
4.225 Range size, disjunction, and dispersal 602
4.226 Relationship between life cycle timing and distribution 605
4.23 Historical zoogeography 608

4.3 Compatibility between proposed phylogeny and historical zoogeography 610

4.4 Evolutionary trends 611

5.0 PROSPECTUS 612

5.1 Geographical distributions and undescribed taxa 612

5.2 Future directions in Nebria research 614

LITERATURE CITED 618

APPENDIX A. DISPOSITION OF PRIMARY TYPES OF NEARCTIC NEBRIA . . 661

APPENDIX B. MATERIAL EXAMINED 668

APPENDIX C. MATERIAL STUDIED FOR EX-GROUP COMPARISONS 838

AUTOBIOGRAPHY 842

FIGURES 844

LIST OF TABLES

Table 1. Mountain systems and ranges of North America 101

Table 2. Distribution of Nearctic Nebria taxa in relation to mountain systems and ranges 107

Table 3. Principal drainage systems of North America 128

Table 4. Distribution of Nearctic Nebria in relation to drainage systems 131

Table 5. Geographical relations of Nearctic Nebria taxa 144

Table 6. Maximum linear extent of geographical range of Nearctic Nebria taxa 159

Table 7. Size and orientation of significant disjunctions in the geographical ranges of Nearctic Nebria taxa . 162

Table 8. Life zone distributions of Nearctic Nebria taxa . . . 171

Table 9. Microhabitat distributions of Nearctic Nebria taxa . . 178

Table 10. Data on characteristics of microhabitats preferred by members of Nearctic Nebria taxa, I. Association with water bodies (including streams, lakes, oceans, snowfields, or glaciers) 182

Table 11. Data on characteristics of microhabitat preferred by members of Nearctic Nebria taxa, II. Substrate, cover type, and exposure 190

Table 12. Summary of data on nocturnal activity in members of Nearctic Nebria taxa 211

Table 13. Life cycle timing in Nearctic Nebria taxa 227

Table 13A. Data on field and laboratory observations on copulation in Nearctic Nebria 241

Table 14. Character states pleisiotypic for Nearctic Nebria species 446

Table 15. Phylogenetic classification of states of characters used in cladistic analysis of Nearctic Nebria species 450

Table 16. Total number of species and subspecies, "approximate landmass units" (LU), "average landmass 5° interval values" (ALIV), and "total interval values" (TIV) derived from Fig. 422 528

Table 17. Frequency distribution of maximum linear extent of geographical range in kilometers for Nearctic Nebria species and subspecies (based on data from Table 12 535

Table 18. Measure of Nebria faunal similarities among montane regions (as classified in Table 1): data matrix, Simpson coefficients 541

Table 19. Measure of Nebria faunal similarities among montane regions (as classified in Table 1): data matrix, Jaccard coefficients 544

Table 20. Measure of Nebria faunal similarities among mountain ranges of the central and southern Pacific Coast region: data matrix, Simpson coefficients 548

Table 21. Measure of Nebria faunal similarities among mountain ranges of the central and southern Pacific Coast region: data matrix, Jaccard coefficients 550

Table 22. Measure of Nebria faunal similarities among mountain ranges of the central and southern Rocky Mountain

regions: data matrix, Simpson coefficients 554

Table 23. Measure of Nebria faunal similarities among mountain ranges of the central and southern Rocky Mountain regions: data matrix, Jaccard coefficients 555

Table 24. Nebria species and subspecies shared between different Nearctic faunas and between Nearctic and Palaearctic faunas 574

Table 25. Data on vicariance relationships among Nearctic Nebria subspecies 579

Table 26. Data on vicariance relationships among Nearctic Nebria sister species 587

LIST OF FIGURES

Fig. 1. Components of "standardized body length" 846

Fig. 2. Habitus: general body form, type aile 846

Fig. 3. Habitus: general body form, type aptere 846

Fig. 4. Generalized head, with paired frontal red spots . . . 846

Fig. 5. Generalized head, with fused frontal red spots . . . 846

Fig. 6. Generalized head, with fused frontal red spots, M-shaped 846

Fig. 7. Elytral microsculpture, Nebria darlingtoni new species 848

Fig. 8. Elytral microsculpture, Nebria diversa LeConte 848

Fig. 9. Elytral microsculpture, Nebria appalachia Darlington . 848

Fig. 10. Elytral microsculpture, Nebria hudsonica LeConte . . . 848

Fig. 11. Elytral microsculpture, Nebria gregaria Fischer von Waldheim 848

Fig. 12. Elytral microsculpture, Nebria lacustris lacustris . . 848

Fig. 13. Head, Nebria crassicornis crassicornis Van Dyke . . . 850

Fig. 14. Head, Nebria crassicornis intermedia Van Dyke 850

Fig. 14A. Head, Nebria gyllenhali castanipes (Kirby) 850

Fig. 15. Head, Nebria gregaria Fischer von Waldheim 850

Fig. 16. Head, Nebria charlottae Lindroth 850

Fig. 17. Head, Nebria appalachia Darlington 850

Fig. 18. Head, Nebria gebleri gebleri Dejean 850

Fig. 19. Head, Nebria ovipennis LeConte 850

Fig. 20. Head, Nebria spatulata spatulata Van Dyke 850

Fig. 21. Head, Nebria metallica Fischer von Waldheim 850

Fig. 22. Head, Nebria ingens ingens Horn 852
Fig. 23. Relative measure of antenna length 852
Fig. 24. Antennal scape, Nebria gouleti new species 852
Fig. 25. Antennal scape, Nebria hudsonica LeConte 852
Fig. 26. Antennal scape, Nebria gyllenhali castanipes (Kirby) . 852
Fig. 27. Antennal scape, Nebria gyllenhali lassenensis new subspecies 852
Fig. 28. Antennal scape, Nebria gyllenhali lindrothi new subspecies 852
Fig. 29. Antennal scape, Nebria lyelli Van Dyke 852
Fig. 30. Antennal scape, Nebria arkansana uinta new subspecies 852
Fig. 31. Antennal scape, Nebria zioni zioni Van Dyke 852
Fig. 32. Antennal scape, Nebria zioni oasis new subspecies . . 852
Fig. 33. Antennal scape, Nebria ovipennis LeConte 852
Fig. 34. Antennal scape, Nebria spatulata spatulata Van Dyke . 852
Fig. 35. Antennal scape, Nebria spatulata sierrae new subspecies 852
Fig. 36. Antennal scape, Nebria vandykei vandykei Bänninger . . 852
Fig. 37. Antennal scape, Nebria vandykei wyeast new subspecies 852
Fig. 38. Antennal scape, Nebria trifaria trifaria LeConte . . . 852
Fig. 39. Antennal scape, Nebria trifaria catenata Casey 854
Fig. 40. Antennal scape, Nebria coloradensis Van Dyke 854
Fig. 41. Antennal scape, Nebria piute Erwin and Ball 854
Fig. 42. Basal antennomeres, Nebria purpurata LeConte 854
Fig. - Basal antennomeres, Nebria ingens ingens Horn 854

Fig. 44. Basal antennomeres, Nebria virescens Horn 854
Fig. 45. Antennal pedicel, Nebria virescens Horn 854
Fig. 46. Antennal pedicel, Nebria nivalis nivalis (Paykull) . . 854
Fig. 47. Antennal pedicel, Nebria nivalis nivalis (Paykull) . . 854
Fig. 48. Clypeus, Nebria desolata Kavanaugh 854
Fig. 49. Clypeus, Nebria hudsonica LeConte 854
Fig. 50. Labrum, Nebria pallipes Say 854
Fig. 51. Labrum, Nebria hudsonica LeConte 854
Fig. 52. Labrum, Nebria ingens ingens Horn 854
Fig. 53. Labrum, Nebria gregaria Fischer von Waldheim 854
Fig. 54. Left mandible, Nebria virescens Horne 856
Fig. 55. Left mandible, Nebria vandykei vandykei Banninger . . 856
Fig. 56. Left mandible, Nebria nitidula (Fabricius) 856
Fig. 57. Right mandible, Nebria virescens Horn 856
Fig. 58. Right mandible, Nebria nitidula (Fabricius) 856
Fig. 59. Right mandible, Nebria appalachia Darlington 858
Fig. 60. Right maxilla, Nebria brevicollis (Fabricius) 858
Fig. 61. Labium, Nebria virescens Horn 858
Fig. 62. Labium, Nebria hudsonica LeConte 858
Fig. 63. Labium, Nebria ingens ingens Horn 858
Fig. 64. Mentum, general form and position of setae 858
Fig. 65. Mentum, Nebria hudsonica LeConte 858
Fig. 66. Mentum, Nebria lyelli Van Dyke 860
Fig. 67. Mentum, Nebria gregaria Fischer von Waldheim 860
Fig. 68. Mentum, Nebria charlottae Lindroth 860
Fig. 69. Mentum, Nebria obliqua LeConte 860
Fig. 70. Mentum, Nebria mannerheimii Fischer von Waldheim . . . 860

Fig. 71. Mentum, Nebria desolata Kavanaugh 860
Fig. 72. Mentum, Nebria carri new species 860
Fig. 73. Mentum, Nebria kincaidi kincaidi Schwarz 860
Fig. 74. Mentum, Nebria spatulata spatulata Van Dyke 860
Fig. 75. Mentum, Nebria ovipennis LeConte 860
Fig. 76. Mentum, Nebria ingens ingens Horn 862
Fig. 77. Mentum, Nebria trifaria trifaria LeConte 862
Fig. 78. Mentum, Nebria trifaria catenata Casey 862
Fig. 79. Gula, general form and position of setae 862
Fig. 80. Gula, Nebria zioni zioni Van Dyke 862
Fig. 81. Gula, Nebria purpurata LeConte 862
Fig. 82. Pronotum, general form and associated terms 864
Fig. 83. Pronotum, general form and associated terms 864
Fig. 84. Pronotum, Nebria virescens Horn 864
Fig. 85. Pronotum, Nebria chalceola Bates 864
Fig. 86. Pronotum, Nebria paradisi Darlington 864
Fig. 87. Pronotum, Nebria lacustris lacustris Casey 866
Fig. 88. Pronotum, Nebria lacustris bellorum new subspecies . . 866
Fig. 89. Pronotum, Nebria nivalis nivalis (Paykull) 866
Fig. 90. Pronotum, Nebria nivalis gaspesiana new subspecies . . 866
Fig. 91. Pronotum, fossil specimen, nivalis subgroup 866
Fig. 92. Pronotum, Nebria crassicornis crassicornis Van Dyke . 866
Fig. 93. Pronotum, Nebria crassicornis intermedia Van Dyke . . 866
Fig. 93A. Pronotum, Nebria gyllenhali castanipes (Kirby) 868
Fig. 93B. Pronotum, Nebria gyllenhali lindrothi new subspecies . 868
Fig. 94. Pronotum, Nebria lyelli Van Dyke 868
Fig. 95. Pronotum, Nebria acuta acuta Lindroth 868

Fig. 96. Pronotum, Nebria acuta quileute new subspecies 868
Fig. 97. Pronotum, Nebria sahlbergii modoc new subspecies . . . 868
Fig. 98. Pronotum, Nebria sahlbergii triad new subspecies . . 868
Fig. 99. Pronotum, Nebria zioni zioni Van Dyke 868
Fig. 100. Pronotum, Nebria suturalis LeConte 868
Fig. 101. Pronotum, Nebria obliqua LeConte 870
Fig. 102. Pronotum, Nebria appalachia Darlington 870
Fig. 103. Pronotum, Nebria pallipes Say 870
Fig. 104. Pronotum, Nebria darlingtoni new species 870
Fig. 105. Pronotum, Nebria mannerheimii 870
Fig. 106. Pronotum, Nebria desolata Kavanaugh 870
Fig. 107. Pronotum, Nebria gebleri gebleri Dejean 870
Fig. 108. Pronotum, Nebria gebleri cascadensis new subspecies . 872
Fig. 109 Pronotum, Nebria gebleri rathvoni LeConte 872
Fig. 110. Pronotum, Nebria gebleri siskiyouensis new subspecies 872
Fig. 110A. Pronotum, Nebria gebleri strawberriensis new subspecies 872
Fig. 111. Pronotum, Nebria carri new species 872
Fig. 112. Pronotum, Nebria kincaidi kincaidi Schwarz 872
Fig. 113. Pronotum, Nebria meanyi meanyi Van Dyke 872
. 114. Pronotum, Nebria meanyi lamarckensis new subspecies . 872
Fig. 115. Pronotum, Nebria meanyi sylvatica new subspecies . . . 874
Fig. 116. Pronotum, Nebria metallica Fischer von Waldheim . . . 874
Fig. 117. Pronotum, Nebria ingens ingens Horn 874
Fig. 118. Pronotum, Nebria piperi Van Dyke 874
Fig. 119. Pronotum, Nebria schwarzi schwarzi Van Dyke 876

Fig. 120. Pronotum, Nebria schwarzi beverlianna new subspecies . 876
Fig. 120A. Pronotum, Nebria purpurata LeConte 876
Fig. 121. Pronotum, Nebria trifaria trifaria LeConte 876
Fig. 121A. Pronotum, Nebria trifaria utahensis new subspecies . . 876
Fig. 122. Pronotum, Nebria coloradensis Van Dyke 878
Fig. 123. Prothoracic venter, Nebria gouleti new species 878
Fig. 124. Prothoracic venter, Nebria sahlbergii modoc new subspecies 878
Fig. 125. Prosternal intercoxal process, Nebria brevicollis (Fabricius) 878
Fig. 125A. Prosternal intercoxal process, Nebria piperi Van Dyke 878
Fig. 126. Prosternal intercoxal process, Nebria fragilis fragilis Casey 878
Fig. 127. Prosternal intercoxal process, Nebria appalachia Darlington 878
Fig. 128. Prosternal intercoxal process, Nebria charlottae Lindroth 878
Fig. 129. Prosternal intercoxal process, Nebria gregaria Fischer von Waldheim 878
Fig. 130. Prosternal intercoxal process, Nebria ingens riversi Van Dyke 878
Fig. 131. Prosternal intercoxal process, Nebria purpurata LeConte 878
Fig. 132. Prosternal intercoxal process, Nebria arkansana uinta new subspecies 878
Fig. 133. Front coxal cavities, Nebria brevicollis (Fabricius) . 880

Fig. 134. Front coxal cavities, Nebria brevicollis (Fabricius) . 880
Fig. 135. Elytral silhouette, generalized rectangular 880
Fig. 136. Elytral silhouette, generalized subrectangular 880
Fig. 137. Elytral silhouette, generalized subovoid 880
Fig. 138. Elytral silhouette, generalized subovoid-narrowed . . 880
Fig. 139. Elytral silhouette, generalized ovoid 880
Fig. 140. Elytral silhouette, generalized tear-shaped 880
Fig. 141. Elytral silhouette, Nebria gregaria Fischer von Waldheim 880
Fig. 142. Elytral silhouette, Nebria charlottae Lindroth 880
Fig. 143. Elytral silhouette, Nebria desolata Kavanaugh 880
Fig. 144. Elytral silhouette, Nebria piperi Van Dyke 880
Fig. 145. Elytral silhouette, Nebria paradisi Darlington 880
Fig. 146. Elytra, general form and associated terms 882
Fig. 147. Elytral base, Nebria arkansana edwardsi 882
Fig. 148. Elytral base, Nebria altaica Gebler 882
Fig. 149. Elytral base, Nebria kincaidi kincaidi Schwarz 882
Fig. 150. Elytral base, Nebria kincaidi balli new subspecies . . 882
Fig. 151. Elytral base, Nebria meanyi meanyi Van Dyke 882
Fig. 152. Elytral base, Nebria meanyi lamarckensis new subspecies 882
Fig. 153. Elytral base, Nebria piperi Van Dyke 882
Fig. 154. Elytral base, Nebria ingens ingens 882
Fig. 155. Left elytron, Nebria virescens Horn 884
Fig. 156. Left elytron, Nebria frigida Sahlberg 884
Fig. 157. Left elytron, Nebria acuta acuta Lindroth 884
Fig. 158. Left elytron, Nebria sahlbergii sahlbergii Fischer

von Waldheim 884
Fig. 159. Left elytron, Nebria suturalis LeConte 886
Fig. 160. Left elytron, Nebria vandykei vandykei Banninger . . . 886
Fig. 161. Left elytron, Nebria schwarzi schwarzi Van Dyke. . . . 886
Fig. 162. Elytral apices, Nebria virescens Horn 888
Fig. 163. Elytral apices, Nebria chalceola Bates 888
Fig. 164. Elytral apices, Nebria paradisi Darlington 888
Fig. 165. Elytral apices, Nebria lacustris lacustris Casey . . . 888
Fig. 166. Elytral apices, Nebria pallipes Say 888
Fig. 167. Elytral apices, Nebria meanyi meanyi Van Dyke 888
Fig. 168. Elytral apices, Nebria schwarzi schwarzi Van Dyke . . 888
Fig. 169. Internal plica, Nebria hudsonica LeConte 890
Fig. 170. Internal plica, Nebria hudsonica LeConte 890
Fig. 171. Elytral base, Nebria gouleti new species 890
Fig. 172. Elytral base, Nebria metallica Fischer von Waldheim . 890
Fig. 173. Elytral base, Nebria trifaria trifaria LeConte . . . 890
Fig. 174. Elytral base, Pterostichus adstrictus Eschscholtz . . 890
Fig. 175. Elytral base, Amara insignis Dejean 890
Fig. 176. Elytral base, Agonum maculicolle Dejean 890
Fig. 177. Elytral base, Patrobus longicornis Say 890
Fig. 178. Elytral fragments, fossil specimens, Nebria nivalis (Paykull) 892
Fig. 179. Elytral fragments, fossil specimens, Nebria lacustris Casey or Nebria pallipes Say 892
Fig. 180. Elytral fragments, fossil specimens, Nebria suturalis LeConte 894
Fig. 181. Hindwing (metathoracic wing), general form and

associated terms 896
Fig. 182. Hindwing, Nebria virescens Horn 896
Fig. 183. Hindwing, Nebria appalachia Darlington 896
Fig. 184. Hindwing, Nebria coloradensis Van Dyke 896
Fig. 185. Hindwing, Nebria charlottae Lindroth 896
Fig. 186. Hindwing, Nebria gregaria Fischer von Waldheim 898
Fig. 187. Hindwing, Nebria purpurata LeConte 898
Fig. 188. Hindwing, Nebria fragilis fragilis Casey 898
Fig. 189. Hindwing, Nebria lyelli Van Dyke 898
Fig. 190. Hindwing, Nebria spatulata sierrae new subspecies . . 898
Fig. 191. Hindwing, Nebria gyllenhali castanipes (Kirby) 898
Fig. 192. Hindwing, Nebria gyllenhali lindrothi new subspecies . 898
Fig. 193. Hindwing, Nebria arkansana arkansana Casey 900
Fig. 194. Hindwing, Nebria arkansana uinta new subspecies . . . 900
Fig. 195. Hindwing, Nebria navajo new species 900
Fig. 196. Hindwing, Nebria trifaria utahensis new subspecies . 900
Fig. 197. Oblongum cell, Nebria frigida Sahlberg 902
Fig. 198. Oblongum cell, Nebria trifaria catenata Casey 902
Fig. 199. Oblongum cell, Nebria hudsonica LeConte 902
Fig. 200. Oblongum cell, Nebria obliqua LeConte, ... 902
Fig. 201. Wedge cell, Nebria pallipes Say 902
Fig. 202. Wedge cell, Nebria darlingtoni new species 902
Fig. 203. Wedge cell, Nebria sahlbergii modoc new subspecies . . 902
Fig. 204. Wedge cell, Nebria piperi Van Dyke 902
Fig. 205. Wedge cell, Nebria schwarzi schwarzi Van Dyke 902
Fig. 206. Hindwing, Trachypachus gibbsi LeConte 904
Fig. 207. Relative measure of metasternum length 904

Fig. 208. Metasternum, Nebria piperi Van Dyke 904
Fig. 209. Metasternum, Nebria fragilis teewinot new subspecies . 904
Fig. 210. Metasternum, Nebria kincaidi bal[illegible] new subspecies . . 904
Fig. 211. Anterior intercoxal process of metasternum, Nebria meanyi lamarckensis new subspecies 906
Fig. 212. Anterior intercoxal process of metasternum, Nebria zioni oasis new subspecies 906
Fig. 213. Anterior intercoxal process of metasternum, Nebria brevicollis (Fabricius) 906
Fig. 214. Anterior intercoxal process of metasternum, Nebria virescens Horn 906
Fig. 215. Metepisternum, Nebria brevicollis (Fabricius) 906
Fig. 216. Metepisternum, Nebria obliqua LeConte 906
Fig. 217. Hindleg, Nebria crassicornis crassicornis Van Dyke . . 906
Fig. 218. Hindleg, Nebria vandykei wyeast new subspecies 906
Fig. 219. Hindleg, Nebria gouleti new species 906
Fig. 220. Front coxa, Nebria obliqua LeConte 906
Fig. 221. Middle coxa, Nebria obliqua LeConte 906
Fig. 222. Middle coxa, Nebria metallica Fischer von Waldheim . . 906
Fig. 223. Hind coxa, Pelophila borealis (Paykull) 908
Fig. 224. Hind coxa, Nebria fragilis fragilis Casey 908
Fig. 225. Hind coxa, Nebria virescens Horn 908
Fig. 226. Hind coxa, Nebria schwarzi schwarzi Van Dyke 908
Fig. 227. Hind coxa, Nebria schwarzi beverlianna new subspecies 908
Fig. 228. Hind coxa, Nebria appalachia Darlington 908
Fig. 229. Hind coxa, Nebria desolata Kavanaugh 908

Fig. 230. Front trochanter, Nebria diversa LeConte 908
Fig. 231. Middle trochanter, Nebria diversa LeConte 908
Fig. 232. Hind trochanter, Nebria diversa LeConte 908
Fig. 233. Front femur, Nebria brevicollis (Fabricius) 910
Fig. 234. Middle femur, Nebria brevicollis (Fabricius) 910
Fig. 235. Hind femur, Nebria brevicollis (Fabricius) 910
Fig. 236. Anterior tibia, Nebria brevicollis (Fabricius) 912
Fig. 237. Middle tibia, Nebria pallipes Say 914
Fig. 238. Middle tibia, Nebria gouleti new species 914
Fig. 239. Middle tibia, Nebria carri new species 914
Fig. 240. Middle tibia, Nebria virescens Horn 914
Fig. 241. Front tarsus, Nebria purpurata LeConte, male 916
Fig. 242. Front tarsus, Nebria ingens ingens Horn, male 916
Fig. 243. Front tarsus, Nebria ovipennis LeConte, male 916
Fig. 244. Hind tarsus, Nebria purpurata LeConte 918
Fig. 245. Hind tarsus, Nebria ingens ingens Horn 918
Fig. 246. Hind tarsus, Nebria ovipennis LeConte 918
Fig. 247. Hind tarsus, Nebria brevicollis (Fabricius) 918
Fig. 248. Hind tarsus, Nebria eschscholtzii Menetries 918
Fig. 249. Fourth tarsomere, hind tarsus, Nebria virescens Horn . 920
Fig. 250. Fourth tarsomere, hind tarsus, Nebria arkansana edwardsi new subspecies 920
Fig. 251. Fourth tarsomere, hind tarsus, Nebria nivalis gaspesiana new subspecies 920
Fig. 252. Fourth tarsomere, hind tarsus, Nebria paradisi Darlington 920
Fig. 253. Abdominal sterna, Nebria frigida Sahlberg, ... 922

Fig. 254. Abdominal sterna, Nebria frigida Sahlberg 922
Fig. 255. Abdominal sterna, Nebria hudsonica LeConte, male . . . 922
Fig. 256. Anal sternum, Nebria hudsonica LeConte, female 922
Fig. 257. Abdominal sterna, Nebria appalachia Darlington 922
Fig. 258. Abdominal sterna, Nebria vandykei wyeast new subspecies, male 924
Fig. 259. Anal sternum, Nebria vandykei wyeast new subspecies, female 924
Fig. 260. Male genitalia, general form and associated terms . . 924
Fig. 261. Orientation of male genitalic structures in in copulatory position 926
Fig. 262. Median lobe, Nebria virescens Horn 926
Fig. 263. Median lobe, Nebria brevicollis (Fabricius) 926
Fig. 264. Median lobe, Nebria paradisi Darlington 926
Fig. 265. Median lobe, Nebria acuta acuta Lindroth 926
Fig. 266. Median lobe, Nebria acuta quileute new subspecies . . 926
Fig. 267. Median lobe, Nebria sahlbergii sahlbergii Fischer von Waldheim 928
Fig. 268. Median lobe, Nebria arkansana edwardsi new subspecies 928
Fig. 269. Median lobe, Nebria arkansana oowah new subspecies . . 928
Fig. 270. Median lobe, Nebria arkansana uinta new subspecies . . 928
Fig. 271. Median lobe, Nebria fragilis fragilis Casey 928
Fig. 272. Median lobe, Nebria desolata Kavanaugh 928
Fig. 273. Median lobe, Nebria navajo new species 930
Fig. 274. Median lobe, Nebria eschscholtzii Menetries 930
Fig. 275. Median lobe, Nebria gebleri gebleri Dejean 930

Fig. 276. Median lobe, Nebria gebleri strawberriensis new subspecies 930
Fig. 277. Median lobe, Nebria carri new species 930
Fig. 278. Median lobe, Nebria kincaidi kincaidi Schwarz 932
Fig. 279. Median lobe, Nebria spatulata sierrae new subspecies . 932
Fig. 280. Median lobe, Nebria ovipennis LeConte 932
Fig. 281. Median lobe, Nebria trifaria trifaria LeConte 932
Fig. 282. Median lobe, Nebria trifaria catenata Casey 934
Fig. 283. Median lobe, Nebria trifaria utahensis new subspecies 934
Fig. 284. Median lobe, Nebria coloradensis Van Dyke 934
Fig. 285. Median lobe, Nebria piute Erwin and Ball 934
Fig. 286. Median lobe, Nebria gouleti new species 936
Fig. 287. Median lobe, Nebria zioni oasis new subspecies 936
Fig. 288. Internal sac of median lobe, Nebria vandykei vandykei Banninger 936
Fig. 289. Internal sac of median lobe, Nebria gyllenhali castanipes (Kirby) 936
Fig. 290. Right paramere, Nebria virescens Horn 938
Fig. 291. Left paramere, Nebria virescens Horn 938
Fig. 291A. Left paramere, Nebria paradisi Darlington 938
Fig. 292. Right paramere, Nebria gouleti new species 938
Fig. 293. Left paramere, Nebria gouleti new species 938
Fig. 294. Parameres, Nebria brevicollis (Fabricius) 938
Fig. 295. Left paramere, Nebria ovipennis LeConte 938
Fig. 296. Right paramere, Nebria schwarzi beverlianna new subspecies 938

Fig. 297. Ring sclerite in relation to median lobe 938
Fig. 298. Ring sclerite in Nebria, generalized 938
Fig. 299. Ring sclerite in Amphizoa lecontei Matthew 938
Fig. 300. Eighth sternum, Nebria virescens Horn, female 940
Fig. 301. Eighth sternum, Nebria metallica Fischer von Waldheim, female 940
Fig. 302. Eighth sternum, Nebria gouleti new species, female . . 940
Fig. 303. Eighth sternum, Nebria paradisi Darlington, female . . 940
Fig. 304. Eighth sternum, Nebria carri new species, female . . . 940
Fig. 304A. Eighth sternum, Trachypachus gibbsi LeConte 940
Fig. 305. Proctiger and paraprocts, Nebria virescens Horn . . . 940
Fig. 306. Proctiger and paraprocts, Nebria diversa LeConte . . . 940
Fig. 307. Paraproct and valvifer, Nebria arkansana edwardsi new subspecies 940
Fig. 308. Paraproct and valvifer, Nebria virescens Horn 940
Fig. 309. Valvifer, Nebria lacustris bellorum new subspecies . . 940
Fig. 310. Valvifer, Nebria lyelli Van Dyke 940
Fig. 311. Valvifer, Nebria gregaria Fischer von Waldheim 940
Fig. 312. Tenth sternum, Nebria paradisi Darlington 942
Fig. 313. Tenth sternum, Nebria suturalis LeConte 942
Fig. 314. Tenth sternum, Amphizoa lecontei Matthew 942
Fig. 315. Coxostylus, Nebria virescens Horn 944
Fig. 316. Coxostylus, Nebria darlingtoni new species 944
Fig. 317. Coxostylus, Nebria piperi Van Dyke 944
Fig. 318. Coxostylus, Nebria gebleri gebleri Dejean 944
Fig. 319. Coxostylus, Nebria gyllenhali castanipes (Kirby) . . . 944
Fig. 320. Coxostylus, Nebria nivalis nivalis (Paykull) 944

Fig. 321. Coxostylus, Nebria zioni zioni Van Dyke 944
Fig. 322. Bursa copulatrix, general form and associated terms . 946
Fig. 323. Bursa copulatrix, general form and associated terms . 946
Fig. 324. Bursa copulatrix, Nebria virescens Horn 946
Fig. 325. Bursa copulatrix, Nebria hudsonica LeConte 946
Fig. 326. Bursa copulatrix, Nebria crassicornis crassicornis Van Dyke 946
Fig. 327. Bursa copulatrix, Nebria frigida Sahlberg 948
Fig. 328. Bursa copulatrix, Nebria acuta acuta Lindroth 948
Fig. 329. Bursa copulatrix, Nebria acuta quileute new subspecies 948
Fig. 329A. Bursa copulatrix, Nebria sahlbergii sahlbergii Fischer von Waldheim 948
Fig. 330. Bursa copulatrix, Nebria sahlbergii modoc new subspecies 948
Fig. 331. Bursa copulatrix, Nebria arkansana edwardsi new subspecies 950
Fig. 332. Bursa copulatrix, Nebria arkansana oowah new subspecies 950
Fig. 333. Bursa copulatrix, Nebria gebleri gebleri Dejean . . . 952
Fig. 334. Bursa copulatrix, Nebria gebleri strawberriensis . . . 952
Fig. 335. Bursa copulatrix, Nebria kincaidi kincaidi Schwarz . . 952
Fig. 336. Bursa copulatrix, Nebria coloradensis Van Dyke 952
Fig. 336A. Bursa copulatrix, Nebria piute Erwin and Ball 954
Fig. 337. Bursa copulatrix, Nebria trifaria trifaria LeConte . . 954
Fig. 338. Bursa copulatrix, Nebria trifaria catenata Casey . . . 954
Fig. 339. Bursa copulatrix, Nebria trifaria utahensis new

subspecies 954

Fig. 340. Bursa copulatrix, Nebria paradisi Darlington 954

Fig. 341. Bursa copulatrix, Nebria darlingtoni new species . . . 954

Fig. 342. Bursa copulatrix, Nebria desolata Kavanaugh 956

Fig. 343. Bursa copulatrix, Nebria obliqua LeConte 956

Fig. 344. Bursa copulatrix, Nebria nivalis nivalis (Paykull) . . 956

Fig. 345. Spermatheca and duct, Nebria virescens Horn 956

Fig. 346. Spermatheca and duct, Nebria hudsonica LeConte 956

Fig. 347. Spermatheca and duct, Nebria frigida Sahlberg 958

Fig. 348. Spermatheca, Nebria subdilatata Motschulsky 958

Fig. 349. Spermetheca and allied structures, Notiophilus sp . . 958

Fig. 350. Spermatheca and duct, Nebria piperi Van Dyke 958

Fig. 351. Spermatheca and duct, Nebria pallipes Say 958

Fig. 352. Spermatheca and duct, Nebria crassicornis intermedia Van Dyke 960

Fig. 353. Oviduct and bursa copulatrix, Nebria brevicollis (Fabricius) 960

Fig. 354. Oviduct and bursa copulatrix, Nebria virescens Horn . 960

Fig. 355. Altitude and latitude components of distribution: Nebria hudsonica LeConte 962

Fig. 356. Altitude and latitude components of distribution: Nebria gyllenhali (Schonherr) 962

Fig. 357. Altitude and latitude components of distribution: Nebria obliqua LeConte 964

Fig. 358. Altitude and latitude components of distribution: Nebria purpurata LeConte 964

Fig. 359. Relationship between proximity to water and altitude

among Nebria, Front Range, Colorado 966
Fig. 360. Cell of Nebria diversa LeConte larva 968
Fig. 361. Life cycle timing: schematic representation 968
Fig. 362. Thoracic venter, Nebria eschscholtzii Menetries, bearing mites 970
Fig. 363. Histiosoma maritimus (Oudemans) (Acarina: Anoetidae) immature 970
Fig. 364. Floating posture, Nebria piperi Van Dyke 972
Fig. 365. Comparison in species group composition between Lindroth's (1961a) classification a two proposed earlier 974
Fig. 366. Comparison in species group composition between Lindroth's (1961a) classification of Nearctic taxa and three proposed later 976
Fig. 367. Sample cladogram reflecting relationships among extant taxa 978
Fig. 368. Hypothetical reconstruction of transformation series . 978
Fig. 369. Cladogram illustrating hypothetical set of relationships among Nebria and allied genera 978
Fig. 370. An example of use of "character correlation" in cladistic analysis 978
Fig. 371. A hypothetical evolutionary sequence 978
Fig. 372. Distribution of character states among Nearctic Nebria species and their Palaearctic relatives 980
Fig. 373. Cladogram illustrating proposed phylogenetic relationships among Nearctic Nebria species and their Palaearctic relatives 991

Fig. 374. Frequency distribution of characters and total number of extra evolutionary steps 993
Fig. 375. Frequency distribution of characters and intrinsic extra steps 993
Fig. 376. Frequency distribution of characters and convergent, intrinsic steps 993
Fig. 377. Frequency distribution of characters and reversed, intrinsic steps 993
Fig. 378. Frequency distribution of character states and convergent, extrinsic steps 993
Fig. 379. Frequency distribution of character states and reversed, extrinsic steps 993
Fig. 380. Geographical distribution map for Nebria brevicollis (Fabricius) records in North America 995
Fig. 381. Geographical distribution map for Nebria virescens Horn 995
Fig. 382. Geographical distribution map for Nebria paradisi Darlington 995
Fig. 383. Geographical distribution map for Nebria gouleti new species 995
Fig. 384. Geographical distribution map for Nebria hudsonica LeConte and Nebria lacustris Casey 995
Fig. 385. Geographical distribution map for Nebria nivalis (Paykull) 997
Fig. 386. Geographical distribution map for Nebria nivalis (Paykull) 997
Fig. 387. Geographical distribution map for Nebria crassicornis

Van Dyke 997

Fig. 388. Geographical distribution map for Nebria gyllenhali (Schonherr) 999

Fig. 389. Geographical distribution map for Nebria frigida Sahlberg 999

Fig. 390. Geographical distribution map for Nebria acuta Lindroth and Nebria lyelli Van Dyke 1001

Fig. 391. Geographical distribution map for Nebria sahlbergii Fischer von Waldheim 1001

Fig. 392. Geographical distribution map for Nebria arkansana Casey 1001

Fig. 393. Geographical distribution map for Nebria gregaria Fischer von Waldheim and Nebria charlottae Lindroth 1001

Fig. 394. Geographical distribution map for Nebria fragilis Casey and Nebria zioni Van Dyke 1001

Fig. 395. Geographical distribution map for Nebria obliqua LeConte 1003

Fig. 396. Geographical distribution map for Nebria pallipes Say 1003

Fig. 397. Geographical distribution map for Nebria appalachia Darlington 1003

Fig. 398. Geographical distribution map for Nebria suturalis LeConte 1003

Fig. 399. Geographical distribution map for Nebria manherheimii Fischer von Waldheim and Nebria darlingtoni new species 1005

Fig. 400. Geographical distribution map for Nebria eschscholtzii Menetries, Nebria desolata Kavanaugh, and Nebria navajo 1005

Fig. 401. Geographical distribution map for Nebria diversa LeConte 1005

Fig. 402. Geographical distribution map for Nebria gebleri Dejean 1005

Fig. 403. Geographical distribution map for Nebria spatulata Van Dyke 1005

Fig. 404. Geographical distribution map for Nebria ovipennis LeConte 1005

Fig. 405. Geographical distribution map for Nebria kincaidi Schwarz and Nebria carri new species 1005

Fig. 406. Geographical distribution map for Nebria meanyi Van Dyke 1007

Fig. 407. Geographical distribution map for Nebria metallica Fischer von Waldheim 1007

Fig. 408. Geographical distribution map for Nebria vandykei Banninger and Nebria ingens Horn 1007

Fig. 409. Geographical distribution map for Nebria piperi Van Dyke, Nebria schwarzi Van Dyke, and Nebria purpurata LeConte 1007

Fig. 410. Geographical distribution map for Nebria coloradensis Van Dyke and Nebria piute Erwin and Ball 1007

Fig. 411. Geographical distribution map for Nebria trifaria LeConte 1007

Fig. 412. Geographical distribution map for the virescens species

group 1009
Fig. 413. Geographical distribution map for the paradisi species group 1009
Fig. 414. Geographical distribution map for the gregaria species group 1009
Fig. 415. Geographical distribution map for the hudsonica species group 1009
Fig. 416. Geographical distribution map for the gyllenhali species group 1009
Fig. 417. Geographical distribution map for the mannerheimii species group 1011
Fig. 418. Geographical distribution map for the trifaria species group 1011
Fig. 419. Geographical distribution map for the ovipennis species group 1011
Fig. 420. Geographical distribution map for the obliqua species group 1011
Fig. 421. Geographical distribution map for the metallica species group 1011
Fig. 422. Numbers of Nebria species and subspecies represented in 5° latitude and longitude intervals 1013
Fig. 423. Histogram for Nebria diversity in relation to latitude 1013
Fig. 424. Histogram for Nebria diversity in relation to longitude 1013
Fig. 425. Centers of endemism among Nearctic species and subspecies of Nebria 1015

Fig. 426. Diagrammatic representation of Nebria faunal similarities, based on Simpson coefficients, for mountain ranges of central and southern Rocky Mountain regions and for ranges of central and southern Pacific Coast regions 1015

Fig. 427. Diagrammatic representation of Nebria faunal similarities, based on Jaccard coefficients, for mountain ranges of central and southern Rocky Mountain regions and for ranges of central and southern Pacific Coast regions 1015

Fig. 428. Mountain systems and ranges of North America 1017

Fig. 429. Principal drainage systems of North America 1017

Fig. 430. Diagrammatic representation of Nebria faunal similarities, based on Simpson coefficients, among major montane regions 1019

Fig. 431. Diagrammatic representation of Nebria faunal similarities, based on Jaccard coefficients, among major montane regions 1019

Fig. 432. Eastern geographical range patterns 1021

Fig. 433. Rocky Mountain geographical range patterns 1023

Fig. 434. Pacific coastal geographical range patterns 1025

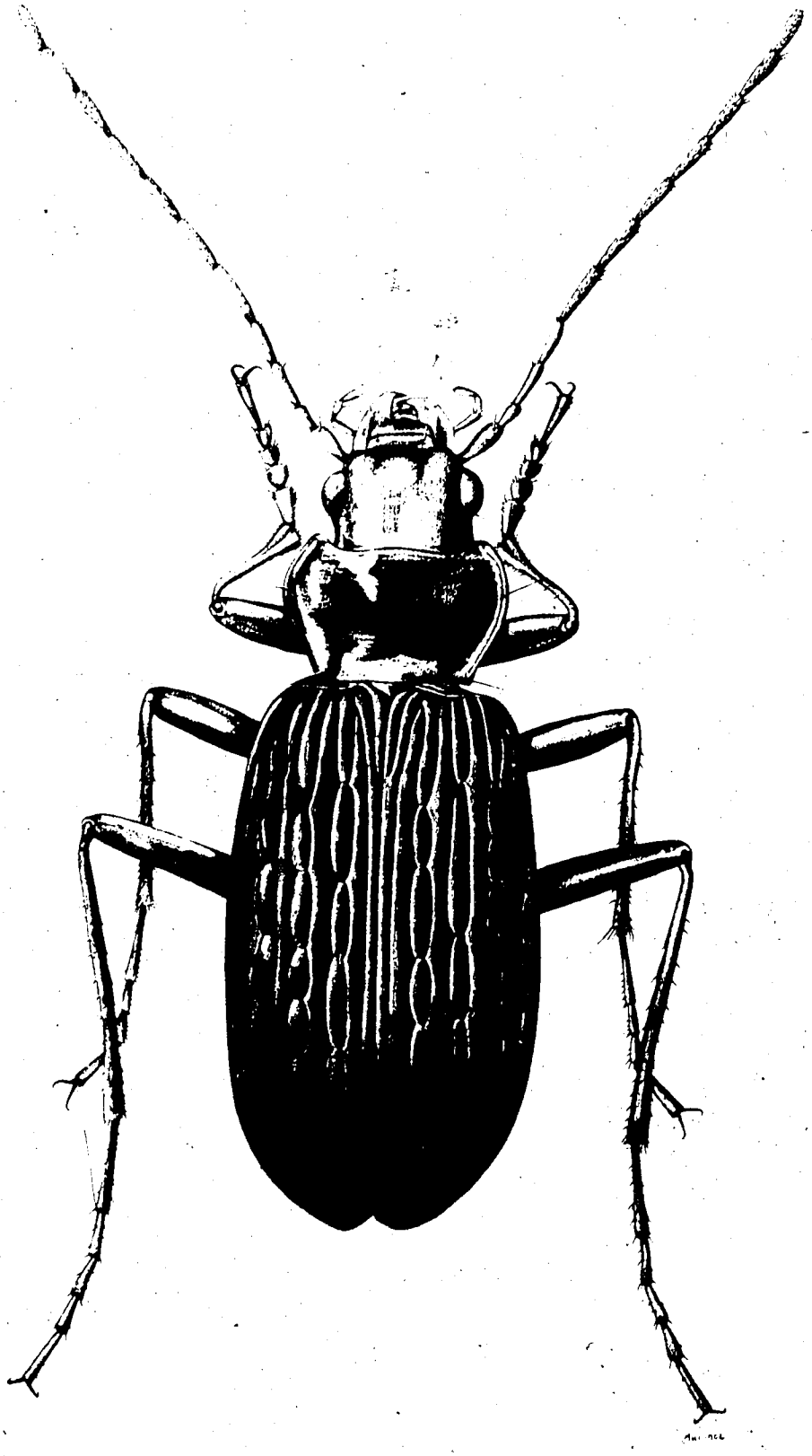
Fig. 435. Northern and transamerican geographical range patterns 1027

Fig. 436. Scattergram relating lower limit of microhabitat range to southern limit of geographical range . . . 1029

Fig. 437. Vicariance patterns among Nearctic Nebria subspecies . 1031

Fig. 438. Vicariance patterns among Nearctic Nebria sister

species or other closely related species 1031
Fig. 439. Vicariance patterns within Nearctic Nebria species groups 1031
Fig. 440. Relationship between geographical range patterns and vicariance in Nebria subspecies 1033
Fig. 441. Relationship between geographical range patterns and vicariance in Nebria species 1035
Fig. 442. Patterns of altitudinal zonation among Nebria taxa: Cascade Range (Mount Rainier) and Sierra Nevada (Yosemite) 1037
Fig. 443 Patterns of altitudinal zonation among Nebria taxa: Rocky Mountains (Front Range, Colorado; and Sangre de Cristo Range, New Mexico) 1039
Fig. 444 The author conferring with his major professor on a point critical to the project 1041



Frontispiece. Nebria schwarzi beverlianna new subspecies: adult male in dorsal aspect (approximately 8X actual size). [Illustration by C. L. Mullinex].

1.0 INTRODUCTION

My interest in beetles of the genus Nebria Latreille began in 1967. While collecting carabid beetles in the Rocky Mountains of Colorado, I concentrated on my own preferred haunts, namely, riparian, nival and peri-nival habitats. This specialization provided frequent encounters with members of various Nebria species because, in these habitats, few insect groups approach Nebria in abundance. With the aid of Lindroth's (1961) treatment of the genus for Canada and Alaska, I was able to identify most of my material. It soon became evident that Nebria species formed a biologically important and interesting element of the montane carabid fauna. Species diversity and population densities in suitable habitats were impressively high; and I began to recognize patterns of altitudinal zonation among the resident species. Observations made on collecting trips in Utah and California suggested that similar patterns of diversity and habitat distribution existed in these and other areas of western North America.

The opportunity to begin serious study of Nearctic Nebria appeared in July, 1970, when I enrolled at the University of Alberta. Although Nearctic Nebria were, at the time, among the taxonomically better-known carabid groups, I hoped to build on my previous experience through additional studies which seemed both feasible and potentially rewarding scientifically. I planned to obtain data with which to further define the structural and distributional limits of Nearctic species and explore the evolutionary relationships among them. My initial goals were the formulation of an improved infrageneric classification of the New World species and attainment of some basic understanding of the

historical development of diversity and distributional patterns observed in our fauna.

Genus Nebria, in the broadest sense, comprises a group of over 500 nominal taxa which, in aggregate, demonstrate holarctic distribution. The Palaearctic component of the genus is much more diverse, in both species and major lineages, than the Nearctic. Consequently, as discussed below (see sections 3.31 and 5.1), conclusions on the relationships among the New World species and historical development of the fauna would be considered tentative, pending study of the genus in the Old World. Fortunately, as work toward the initial project goals progressed, new sources of taxonomic data became available as by-products of field work and efforts to obtain comparative material on loan. These additional resources permitted expansion of the project to include coverage of the Palaearctic Nebria fauna and the use of additional character systems in coverage of the Nearctic fauna. The latter included external structure of immature stages, life history features (especially life cycle timing) and adult internal structure.

Various facets of the expanded project have progressed at different rates and many studies are yet incomplete or barely begun. This paper represents a first report on the Nearctic fauna. I present here a comprehensive taxonomic treatment of the species, based on characters of adult external and (some) internal structure, distribution and life history features. Phylogenetic and contemporary and historical zoogeographic hypotheses are provided and discussed, and evolutionary trends in the fauna are recognized. Also included are an interim infrageneric classification of the species, reflecting the proposed

phylogeny but pending reclassification of the World fauna, and a preliminary comparative morphology, chorology and natural history of the genus in the New World.

1.1 Historical review of Nearctic Nebria systematics

Study of the Nearctic Nebria fauna has slowly progressed from a purely descriptive phase (alpha-level systematics) toward a more analytical phase (beta- and gamma-level systematics), a progression characteristic of systematic work in general. However, the second phase has broadly overlapped with rather than simply replaced the first, as illustrated by some early analytical work (see below) and the descriptions of new species-group taxa presented here.

First members of the Nearctic fauna named were those with holarctic distributions, N. nivalis (Paykull) (1790) and N. gyllenhali (Schönherr) (1806), both described from the Palaearctic Region and originally assigned to genus Carabus Linnaeus. Say (1823) was the first North American entomologist to describe an endemic American species, N. pallipes. Representatives of many common Nebria species were among specimens collected by Eschscholtz [expeditions in 1815 to 1818 and 1823 to 1826] and Vosnesensky [various expeditions during 1839 through 1845] in the Russian New World colonies. Their material was studied, named and described by Dejean (1831), Fischer von Waldheim (1821 and 1828), Mannerheim (1853), Ménétriés (1844) and Motschoulsky (1850, 1859, 1865). Other early descriptions were those of Horn (1870), Kirby (1837), J. Sahlberg (1885) and R. F. Sahlberg (1844). LeConte (1850, 1853, 1859a, 1863a, 1863b, 1866 and 1878) named 11 species, including

the first known from the Sierra Nevada (California) and the Rocky Mountains. Schwarz (1900), Bänninger (1928), Darlington (1930, 1931a, and 1931b), Lindroth (1961), Kavanaugh (1971) and Erwin and Ball (1972) each recognized one or more new and relatively localized species. Casey (1913, 1920 and 1924) provided 26 new names, four (15%) of which I recognize here as valid. Probably the most significant descriptive work on the Nearctic fauna was that by Van Dyke (1924, 1925, 1943, 1949 and 1953). He maintained a life-long interest in the genus, described 12 new species (mainly from material he collected) and amassed the finest Nebria collection in North America. His field notes, preserved at the California Academy of Sciences, are both enjoyable to read and a source of supplemental data on his specimens.

Horn (1870) provided the first key to Nearctic species. LeConte (1878) proposed additions to Horn's key and presented new keys to species groups he recognized. Schaupp (1878) repeated Horn's key, incorporating LeConte's additions. Bänninger (1925) included known Nearctic forms in his descriptive keys to subgenera and groups in the World fauna. Hatch (1939a and 1953) provided keys for the northwestern North American species. The most complete and useful key to date has been Lindroth's (1961), nominally for Canada and Alaska but also useful for more southern areas. Erwin and Ball (1972) and Kavanaugh (1971) suggested additions to Lindroth's key.

Efforts at clarification of nomenclatural problems, including designation of lectotypes (or neotypes), were those of Lindroth (1954b, 1961 and 1975 [lectotypes for Casey species]) and Lindroth and Freitag (1969 [neotype for N. pallipes Say]).

Discussion of the history of classification of and other studies of relationship among Nearctic Nebria is presented separately, in section 3.3 on classification (see section 3.32).

Zoogeographic analysis of the fauna has been minimal. LeConte (1878 and 1879) and Van Dyke (1919, 1926 and 1940) discussed distributions of Nebria species or species groups and made limited use of these as examples for defining generalized distributional patterns in North American biota. Errors in recognition of relationships among the species, however, reduced the effectiveness of these generalizations. More contemporary and sound zoogeographic treatments of (or including) Nebria are those of Lindroth (1963a and 1963b), Ball (1970) and Erwin and Ball (1972).

LeConte (1878 and 1879) and Van Dyke (1919 and 1926), as usual, were among the first to show interest in the altitudinal distributions of Nebria species. Subsequent studies by Darlington (1943), in the Presidential Range of New Hampshire, Haubold (1951) and Armin (1963), in the Front Range of the Colorado Rocky Mountains, and Spence (1974), in the Green Mountains of Vermont, provided information on the altitudinal ranges of several species.

Comparative studies of Nearctic species have, until recently, dealt only with adult structure. Even isolated descriptions of immatures are few (see Schiødte, 1867 and Larsson and Gigja, 1959). Recent comparative work on larval structure is encouraging. Andersen (1970) described and distinguished the larvae of N. gyllenhali (Schönherr) and N. nivalis (Paykull) in Scandinavia. Luff (1972) provided descriptions of and a key to larvae of the British Nebria

species, including the species named above. Spence (1974) and Spence and Bell (1976) were the first to describe and compare the larvae of American species. Larochelle (1972 and 1976a) and Spence (1974) have presented comparative natural history data on Nearctic species.

2.0 MATERIALS AND METHODS

2.1 Materials

This study is based on the examination of 65,690 Nearctic and 5,818 Palaearctic adult Nebria specimens, 2,374 specimens representing other nebriine genera, and an additional 470 specimens representing an array of more distinctly related or unrelated caraboid taxa (see Appendix C for a list of taxa sampled).

2.11 Materials received on loan

Approximately 35,000 specimens were borrowed for study from various institutional and private collections in North America, Europe and Asia. An effort was made to examine all available material in order to obtain a maximum number of geographical and temporal samples. The following is a list of abbreviations used throughout the text and in Appendices A. and B. which refer to the various collections from which specimens were received. Most, but not all, abbreviations correspond to those proposed by Arnett and Samuelson (1969).

AHab A. Habu, National Institute of Agricultural Sciences, Tokyo, Japan.

ALar A. Larochelle, College Bourget, Rigaud, Quebec JOP 1PO.

AMor A. Morgan, University of Waterloo, Waterloo, Ontario N2L 3G1.

AMNH American Museum of Natural History, New York New York 10 ; L. H. Herman, Jr.

ANSP Academy of Natural Sciences, Philadelphia, Pen ivania 19103; W. W. Moss.

BFCa B. F. Carr, 5208 32nd Avenue, Calgary, Alberta T3B OJ6.

BMNH British Museum (Natural Hist), London, England; P. M. Hammond, H. K. Kenward, M. E. Bacchus.

BRot B. Rotger, CR., Immaculate Heart of Mary Church, P. O. Box 451, Pagosa Springs, Colorado 81147.

CArm C. Armin, 191 West Palm Avenue, Reedley, California 93654.

CAS California Academy of Sciences, San Francisco, California 94118; H. B. Leech.

CDA California State Department of Food and Agriculture, Sacramento, California 95814; F. G. Andrews.

CNC Canadian National Collection of Insects, Biosystematics Research Institute, Ottawa, Ontario K1A OC6; R. de Ruette, A. Smetana.

CSU Colorado State University, Fort Collins, Colorado 80521; T. O. Thatcher.

CUB University of Colorado, Boulder, Colorado 80302; H. Rodeck.

CUIC Cornell University, Ithaca, New York 14850; L. L. Pechuman.

DBUM Université de Montreal, Montreal, Québec; M. Coulloudon.

DENH University of New Hampshire, Durham, New Hampshire 03824; W. J. Morse.

DEUN University of Nebraska, Lincoln, Nebraska 68503; B. C. Ratcliffe.

DHKa D. H. Kavanaugh, California Academy of Sciences, San Francisco, California 94118.

DJLa D. J. Larson, Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland A1C 5S7.

DRWh D. R. Whitehead, United States National Museum, Washington, D. C. 20560.

DZEC Montana State University, Bozeman, Montana 59715; N. L. Anderson.

EAMa E. A. Martinko, University of Kansas, Lawrence, Kansas 66044.

EDNC North Carolina Department of Agriculture, Raleigh, North Carolina 27602; J. F. Greene.

EMUS Utah State University, Logan, Utah 84332; W. J. Hanson.

ETHZ Eidgenössische Technische Hochschule Entomologisches Institut, Zürich, Switzerland; W. Sauter.

FMNH Field Museum of Natural History, Chicago, Illinois 60605; H. Dybas.

GRNo G. R. Noonan, Milwaukee Public Museum, Milwaukee, Wisconsin 53233.

HGou H. Goulet, Biosystematics Research Institute, Ottawa, Ontario K1A OC6.

HoKn R. L. Hoffman and L. Knight, Radford College, Radford, Virginia 24141.

HNHM Hungarian Natural History Museum, Budapest, Hungary; S. Horvatovich.

ICCM Carnegie Museum, Pittsburg, Pennsylvania 15213; G. E. Wallace.

INHS Illinois Natural History Survey, Urbana, Illinois 61803; M. W. Sanderson.

ILar I. La Rivers, University of Nevada, Reno, Nevada 89507.

ISUI Iowa State University, Ames, Iowa 50010; R. Miller.

IUIC Indiana University, Bloomington, Indiana 47401; F. N. Young.

JBel J. Belicek, University of Alberta, Edmonton, Alberta T6G 2E3.

JKus J. Kuster, University of Alberta, Edmonton, Alberta T6G 2E3.

JNeg J. Nègre, 9 Boulevard de Lesseps, Versailles, France.

JSch J. Schuh, 4039 Shasta Way, Klamath Falls, Oregon 97601.

JSpe J. Spence, University of British Columbia, Vancouver, British Columbia V6T 1W5.

JVMa J. V. Matthews, Jr., Geological Survey of Canada, Ottawa, Ontario K1A OE8.

KMFe K. [illegible] Fender, 911 Ashwood Avenue, McMinnville, Oregon 97128.

KSUC [illegible] State University, Manhattan, Kansas 66502; H. D. Blocker.

KUSM University of Kansas, Snow Museum, Lawrence, Kansas 66044; G. Byers.

LACM Los Angeles County Museum of Natural History, Los Angeles, California 90007; C. L. Hougue.

LECM Macdonald College, Lyman Entomological Museum, Ste. Anne de Bellevue, Quebec J7V 3N8; V. R. Vickery.

LRus L. Russell, 828 NW 27th Street, Corvallis, Oregon 97330.

MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138; J. F. Lawrence.

MGF Museum G. Frey, Entomologisches Institut, Tutzing bei München, West Germany; M. Würmli.

MHNG Museum d'Histoire Naturelle, Geneva, Switzerland; C. Besuchet.

MHNP Museum National d'Histoire Naturelle, Paris, France; A. Bons, H. Perrin.

MLLu M. L. Luff, University of Newcastle, Newcastle-upon-Tyne, England.

MSU Michigan State University, East Lansing, Michigan 48823; R. L. Fischer.

NBM Naturhistorisches Museum Basel, Basel, Switzerland; W. Wittmer.

NMDo N. M. Downie, 505 Lingle Terrace, Lafayette, Indiana 47901.

NMPC National Museum in Prague, Prague, Czechoslovakia; Z. Mlynar.

NRSS Naturhistoriska Riksmuseet, Stockholm, Sweden; T. Nyholm.

NSDA Nevada State Department of Agriculture, Reno, Nevada 89504; R. C. Bechtel.

ODA Oregon State Department of Agriculture, Salem, Oregon 97310; R. L. Westcott.

OSEC Oklahoma State University, Stillwater, Oklahoma 74074; W. A. Drew.

OSUC Ohio State University, Columbus, Ohio 43210; C. A. Triplehorn.

OSUO Oregon State University, Corvallis, Oregon 97331; P. Oman.

PADA Pennsylvania State Department of Agriculture, Harrisburg, Pennsylvania 17120; T. J. Henry.

PMCh P. M. Choate, Jr., University of Florida, Gainesville, Florida 32601.

PMNH Peabody Museum of Natural History, Yale University, New Haven, Connecticut 06520; C. L. Remington, K. W. Brown.

PSMi P. S. Miliotis, Depot Street Dunstable, Massachusetts 01827.

PSUC Pennsylvania State University, University Park, Pennsylvania 16802; K. C. Kim.

PUCA Pacific Union College, Angwin, California 94508; L. E. Eighme.

PURC Purdue University, Lafayette, Indiana 47907; A. Provonsha.

RCGr R. C. Graves, 627 Crestview, Bowling Green, Ohio 43402.

RCra R. Crawford, University of Washington, Seattle, Washington 98195.

RDav R. Davidson, University of Vermont, Burlington, Vermont 05401.

RFre R. Freitag, Lakehead University, Thunder Bay, Ontario P7B 5E1.

ROM Royal Ontario Museum, Toronto, Ontario M5S 2C6; G. B. Wiggins.

RPPa R. P. Papp, University of California, Berkeley, California 94720.

RTBe R. T. Bell, University of Vermont, Burlington, Vermont 05401.

SFVS California State University, Northridge, California 91324; P. F. Bellinger.

SDSU South Dakota State University, Brookings, South Dakota 57006; E. U. Balsbaugh, Jr.

SJSU San Jose State University, San Jose, California 95114; J. G. Edwards.

TCBa T. C. Barr, Jr., University of Kentucky, Lexington, Kentucky 40506.

TNak T. Nakane, National Science Museum, Tokyo, Japan.

TMZN Tromsø Museum, Tromsø, Norway; J. H. Andersen.

UAFA University of Arkansas, Fayetteville, Arkansas 72701; R. T. Allen.

UASM University of Alberta, Strickland Museum, Edmonton, Alberta T6G 2E3; G. E. Ball.

UBC University of British Columbia, Spencer Museum, Vancouver, British Columbia V6T 1W5; G. G. E. Scudder.

UCB University of California, Berkeley, California 94720; J. A. Chemsak.

UCD University of California, Davis, California 95616; R. O. Schuster.

UCR University of California, Riverside, California 92502; S. Frommer.

UIMI University of Idaho, Moscow, Idaho 83843; W. F. Barr.

UMHF Universitetets Zoologiska Museum Entomologiska Avdelningen, Helsingfors, Finland; H. Silfverberg.

UMMZ University of Michigan, Ann Arbor, Michigan 48104; R. D. Alexander.

UMRM University of Missouri, Columbia, Missouri 65201; W. R. Enns.

UMTF University of Turku, Turku (Abo), Finland; H. Hippa.

USNM United States National Museum, Smithsonian Institution, Washington, D. C. 20560; T. L. Erwin.

UWBM University of Washington, Burke Museum, Seattle, Washington 98105; M. H. Hatch, S. Rohwer.

UWEM University of Wisconsin, Madison, Wisconsin 53706; L. J. Bayer.

UWLW University of Wyoming, Laramie, Wyoming 83070; R. J. Lavigne.

VMKi V. M. Kirk, Northern Grain Insects Research Laboratories, Brookings, South Dakota 57006.

WSU Washington State University, Pullman, Washington 99163; W. J. Turner.

ZILR Zoological Institute, Academy of Science, Leningrad, U. S. S. R.; O. L. Kryzhanovskij, V. G. Shilenkov.

ZMKD Universitetets Zoologiske Museum, København, Denmark; O. Martin.

ZMLS Zoological Institute, University of Lund, Lund, Sweden; C. H. Lindroth.

ZMUM Zoological Museum Moscow University, Moscow, U. S. S. R.; S. Keleinikova.

ZSBS Zoologische Sammlung des Bayerischen Staates, München 19, West Germany; G. Scherer.

2.12 Materials collected for the study

During the period 1969-1975, I collected over 30,000 adult Nebria specimens for the study (see section 2.21 for details). Several hundred additional specimens were collected for me by various companions on field trips or by colleagues working elsewhere (see Acknowledgements for a listing of individuals). Their contributions of specimens and field notes added substantially to my own geographical coverage. Of particular importance were collections from the following areas: Queen Charlotte Islands, British Columbia (J. Belicek and M. Pitman); Swan Hills, Alberta (H. Frania and H. Goulet); Appalachian Mountains, eastern United States (R. L. Hoffman); Sierra Nevada, California (D. Giuliani); and Siberia, eastern U. S. S. R. (V. G. Shilenkov).

2.13 Type material

I have been able to study the type specimens of all 85 previously-described Nearctic nominal taxa, through the co-operation of the curators listed above (see Acknowledgements), who provided either work space and access to specimens during my visits to their institutions or loans of specimens. Three minor nomenclatural problems remain unsolved, but none, I think, will require further attention. Nebria eschscholtzii Sturm (1826:173) and Nebria eschscholtzii Sturm (1826:173) (not of Ménétriés) must be considered nomina nuda because these names appear only in Sturm's catalog to his collection, unaccompanied by either description or statement of locality; and no type specimens exist. The problem with and current status of the name Nebria elias Motschulsky is discussed with treatment of Nebria gyllenhali

(Schönherr) (section 3.43 below).

Where necessary, lectotypes have been chosen and so labelled; and their formal designations appear here (see nomenclature sections under appropriate species headings in section 3.43). For a listing of the status and place of deposit of primary type specimens for the Nearctic nominal taxa, consult Appendix A. Holotypes designated for taxa described as new in this study (with the exception of the holotype of N. trifaria utahensis n. ssp.) have been deposited in the collection of the California Academy of Sciences with the Van Dyke Nebria types.

2.14 Fossil Material

A total of 12 fragmentary fossil specimens representing Nebria species were received on loan from A. Morgan and J. V. Matthews, Jr. Together, these specimens constitute the fossil record (to date) for Nebria in the Nearctic Region. In spite of their paucity and relatively low diversity, certain valuable inferences can be drawn from their consideration (see sections 3.24, 3.43 and 4.23 for discussions).

2.2 Methods

2.21 Collection and preservation of specimens

Most of the specimens and natural history data collected for use in this study were obtained on several long expeditions taken each year (1970 to 1974) from May to September. Areas sampled extensively included the Coast Ranges (1971, 1974), the Cascade Range (1971, 1972, 1974), and the Rocky Mountain and Intermountain Regions (1970 to 1973) of western North America. The Sierra Nevada (California) and

Appalachian Mountains, eastern North America in general, and Alaska (interior, Alaskan Peninsula and inner Aleutian Islands) were partially sampled during these expeditions. In July and August, 1972, I spent five weeks in Mount Rainier National Park collecting specimens of and comparative field data on the 14 Nebria species inhabiting the Park. Previous field work in the Rocky Mountains of Colorado (1967 to 1969) provided specimens of and similar comparative field data on the eight species in that area.

For specific information on collecting specimens of particular taxa, consult headings entitled "Habitat distribution" and "Natural History" in the description of each taxon (see section 3.43). In general, individuals are usually found hiding under suitable cover during the day. Typically, they are abundant under small to large stones at the edges of glaciers, snowfields or streams of various size. Because large numbers of specimens can be collected by hand during the day, the use of pitfall traps is unnecessary and usually less effective. Collecting at night with the aid of flashlight or headlamp generally produces fewer specimens but a great deal more natural history data on these nocturnal beetles. Individuals of species which inhabit glacial margins and crevasses or talus slopes can be efficiently collected only at night (when they are active on the surface) because of their inaccessibility to hand collecting during the day.

Adult specimens were generally incapacitated by ethyl acetate fumes, then transferred to and stored in vials containing sawdust or tissue paper and fresh ethyl acetate to await preparation. When adults were sufficiently abundant, specimens were also collected in Weaver's

Fixative (see Ekis and Gupta, 1972) or 70% ethyl alcohol for future studies on internal structures. Other individuals were kept alive for breeding purposes. Results of the breeding program and a study of the immature stages of Nearctic Nebria will be presented in a subsequent paper.

Prior to pinning and labelling, all specimens were relaxed and cleaned in soapy boiling water, then rinsed. Genitalia (median lobe and parameres of males, coxostyli of females) were routinely everted (see section 2.22) at this time but not detached. This procedure permitted the subsequent examination of these structures in thousands of specimens without subsequent relaxation and dissection. When possible, specimens collected in Weaver's Fixative were used for the study of internal genitalic structures (eg. bursa copulatrix, spermatheca).

Older pinned specimens (such as those received on loan) were easily and effectively cleaned of dirt and grease by careful application of a mixture of ammonia, water and a surface tension reducer ("Tergitol") with a fine paint brush. This mixture also relaxed individual body joints and thereby permitted limited [illegible]gement of appendages as needed.

2.22 Dissecting techniques

Successful examination of the hindwings and genitalia of Nebria specimens usually requires some dissection. Specimens were prepared for dissection by soaking them for five to 10 minutes in boiling water. Additio[illegible] a very small amount of detergent (such as "Mr. Clean")

hastened the relaxation process. Specimens collected in ethyl acetate fumes became relaxed easily, but material collected in potassium cyanide fumes or ethyl alcohol sometimes required a brief (two to five minute) treatment in warm potassium hydroxide (10% solution).

A general impression of the size (but not shape) of the hindwings was obtained by simply lifting the left elytron to expose the wing. For a study of venation and wing shape, the left hindwing was torn free at wing base using fine forceps, then spread and mounted in alcohol on a slide. Permanent mounts (in Euparal medium) were made for all taxa studied; however, most hindwings examined were later dried, glued to cards and pinned with the specimens.

The apex and shaft of the median lobe and the parameres in male specimens or the coxostyli in female specimens were quickly examined in relaxed specimens by simple eversion of these structures using fine forceps. For study of the base of the median lobe in males or the spermatheca, bursa copulatrix and other internal structures in females, the genitalia were extracted as a unit by tearing the membraneous connections between eighth tergum and sternum and the "ring sclerite" (in males) or the valvifers, paraprocts and proctiger (in females). Genitalia were next treated for five to 10 minutes in hot 10% potassium hydroxide solution to remove non-sclerotized tissue, rinsed, further dissected as needed, then transferred to and examined in glycerine. After genitalia were studied and drawn, they were placed in polyethylene microvials in a drop of glycerine and pinned with the specimen.

2.23 Sex determination and association

Determination of the sex of an individual was very simple, requiring only examination of the front tarsi. With some experience, this was done with the unaided eye. Refer to the first couplet (i) in the key to species and subspecies (section 3.422) for characters. No other external structural characters exhibit sex-specific character states throughout Nebria; but sexual dimorphism is present in one or more other characters in some species or species groups (refer to sections 3.41 and 3.43 under "Sexual dimorphism" heading descriptions of taxa).

Males and females of almost all taxa were easily associated by reference to characters of external structure and/or distribution. In those few instances where individuals of two taxa are externally almost indistinguishable and the geographical ranges of the taxa overlap, dissection of the hindwings or genitalia were required to confirm identification and, therefore, association. Fortunately, no two externally similar taxa have perfectly congruous geographical ranges. This permitted the study of internal structures in individuals of each taxon from some locality outside the area of range overlap and subsequent use of observed differences in identifying individuals from the area of sympatry.

2.24 Measurements

The only mensural character used in this study is "standardized body length". This expression appears in descriptions and the key and refers to the sum of three measurements (Fig. 1): length of head,

measured along midline from apical margin of clypeus to a point opposite posterior margin of eye; length of pronotum, measured along midline from apical to basal margin; length of longer elytron measured along midline from apex of scutellum to a point opposite elytral apex. While this measure of relative size avoids error due to variation in extension or retraction of body parts among specimens, it consistently underestimates the apparent total body length of specimens (such as could be measured from the most anterior to the most posterior point) by from 12 to 18 percent.

Range in standardized body length in my sample for each taxon was established by visual selection of smallest and largest specimens for each sex. All measurements were made with a Leitz stereoscopic dissecting microscope at a magnification of 16 diameters, using a calibrated ocular grid with a scale interval of 0.1 mm.

2.25 Illustrations and maps

Line drawings illustrating structural characters were made with the aid of an ocular grid mounted in a Leitz stereoscopic dissecting microscope. Preliminary drawings were penciled on tracing paper placed over a grid of one cm squares. Final inked drawings were then made on heavy weight natural vellum by tracing directly over the preliminary drawings. Unless otherwise noted, scale lines accompanying illustrations equal 1.0 mm. All drawings of homologous structures are consistent in scale and aspect to facilitate comparisons. In some drawings, uniform sparse stippling is used to indicate membranous areas and broken lines represent vague boundaries of sclerotized areas. When

only part of a structure is illustrated (such as the basal region of an elytron), a wavy line serves as the artificial margin.

Scanning electron photomicrographs, used to illustrate various shapes and patterns in microsculpture, were obtained by use of the Cambridge Mark IV "Stereoscan" scanning electron microscope (SEM) in the Department of Entomology, University of Alberta. Specimens were gold-coated prior to examination with the microscope.

Maps are presented to illustrate the distributions of taxa and various geographical (including climatic and physiographic) features, patterns of geographical variation and aspects of zoogeographic reconstruction and analyses. Symbols used on species distribution maps represent approximate locations of samples (refer to Appendix B for listing of sample localities for each taxon).

Wriiten permission was obtained for use of the following maps (or parts of same): Goode Base Map No. 202 (Copyright by the University of Chicago Department of Geography); Landform Map No. 3 (United States) (Copyright by Erwin Raisz).

2.26 Descriptive format

Information about each species is presented in the following sequence: a synonymy (including data on type specimens) and species bibliography; notes on nomenclature and types; derivation of taxon name; diagnostic combination; description of form and structure; sexual dimorphism; geographical distribution; geographical variation; geographical relations with allied taxa; habitat distribution; ecophenotypic variation; taxonomic notes; phylogenetic relationships; dispersal potential; natural history; and fossil record. Presentation

of information on supraspecific taxa (species groups and the genus) follows the same format but with some sections omitted.

The composition, organization and completeness of synonymies and lists of references are discussed below (see section 2.27). Data on the type specimens for all species-group names are ordered as follows: status (as holotype, lectotype or neotype); sex; repository; label data; and type locality. Type localities considered either erroneous or too general (such as a state or provincial record) were emended or restricted respectively. Comments on synonymies, lectotype designations, selection or restriction of type localities and related topics appear under notes on nomenclature and types. Derivations of species-group names are presented only for taxa described as new.

The diagnostic combination is a brief listing of structural and/or distributional character states which, in combination, distinguish members of the taxon from members of other taxa.

Descriptions presented in this study have been arranged so that, by reference to genus, species group or species and subspecies descriptions, the range of character states for any structural character exhibited by members of any taxon can be ascertained by the reader. To this end, the genus description is inclusive, covering the range of character states observed in all characters used for all members of the genus examined. Those characters represented by a single character state or a consistent range of states throughout the genus are omitted from descriptions of lower ranking taxa. Species group descriptions are both inclusive, covering the range of character states for all characters which vary among and within the groups, and

exclusive of characters constant for the genus. Similarly, descriptions of species and subspecies cover the range of character states for all characters (and only those) which vary among members of a species group.

Species and subspecies descriptions presented refer to my concepts of the taxa so ranked rather than to type specimens. The selection and formal designation of holotypes for species-group names is essential to a stable nomenclature. The type serves as the voucher specimen for the name and its application and provides a link between a species name and a certain population or group of populations. Once designated, the type specimen fulfills its role, even if not or only poorly described, because the specimen and the name are permanently associated. Left unassociated, however, are the name and the taxonomist's concept of the taxon of which the type is a member. What requires description, then, is this concept and its limits recognized through the study of variation among taxon members. The extent to which the concepts of taxa reflect their actual properties and limits is dependent on the fidelity of their representation in study samples. Fortunately, my material has been, with few exceptions, quite representative as evidenced by the low incidence of novel variation among new samples received of previously-studied taxa.

For convenience, characters of color and size are treated throughout this study as structural characters although they are really non-structural in the strict sense. Sexual dimorphism, where evident, is treated in a separate section following the description.

The section on geographical distribution provides a brief

statement on the range of the species or subspecies with respect to both political units and boundaries and physiographic features. Maps of distributions and listings of localities for material examined (see Appendix B) provide visualization of and greater detail on distributions respectively. Locality records from the literature which I could not verify with actual specimens are not considered. Consideration of variation associated with geographical distribution presupposes familiarity with distribution and therefore follows treatment of the latter. Sympatry, parapatry and allopatry with respect to related species or subspecies are discussed in the section on geographical relations.

In the section on habitat distribution, the range of microhabitats and altitudinal range occupied by the taxon are discussed and classified according to broad life zone concepts (see also section 3.231). Apparent examples of ecophenotypic variation among members of some taxa are treated in the following section.

Information on the recognition of members of the taxon and/or their separation from members of similar taxa or comments on taxonomic relationship or classification are included under taxonomic notes. Brief comments on proposed phylogenetic relationships are presented under that heading, with more comprehensive treatment deferred to section 4.1 (phylogeny of the Nearctic taxa).

Discussions of the dispersal potential of the taxa are attempts to integrate information on locomotory capabilities with notes on habitat restriction and isolation of populations from other environmentally suitable but unoccupied areas. The section on natural history provides

information on life cycle timing and behavior and notes to aid in collecting members of the taxon.

For those few taxa with a fossil record, data on location and age of deposits yielding specimens are presented together with discussions of past geographical and habitat distributions suggested by the fossil specimens and their respective assemblages.

2.27 Literature and synonymic lists

The results of an extensive review of the literature on Nearctic Nebria appear in the synonymies presented. Each synonymy is a chronological listing of all names which have been applied, correctly or not, wholly or in part, to a species or subspecies here recognized. A history of the status and/or generic placement of these names is not provided. An attempt is made to present a complete bibliography for each species with references listed alphabetically by author after the name which the author used for the taxon. I have probably overlooked some references to Nearctic species, but none have been consciously omitted from the lists. References to both taxonomic and non-taxonomic works (including catalogs, faunal lists, and ecological, physiological, morphological and behavioral studies) have been included.

Although many species-group names have been repeatedly misapplied to various Nearctic taxa, I have been able to re-examine virtually all the specimens involved or otherwise reinterpret literature records. Reference to information provided for each taxon should, therefore, permit accurate interpretation of records of previous works.

2.28 Procedural methods

Specimens obtained by preliminary collecting or on loan were assembled and sorted into clusters based on similarity in characters of size, color and external structure. This rough sorting was facilitated by reference to characters used and clusters recognized by Lindroth (1961). Similarity between males and females of a species-group taxon was generally sufficient to permit inclusion of members of both sexes in the same cluster at this point. Individuals in each cluster were next sorted by locality; and through comparisons of presumptive geographical samples, cluster limits were further defined.

Study of the distributions of samples in all clusters suggested areas in which additional field work might provide taxonomically important data. As time permitted, many of these areas were subsequently visited for the collection of field data and specimens. New material obtained was sorted as described above. Dissections were then made of male and female genitalia and hindwings; and data on habitat distribution for clusters in general and individual geographical samples in particular were examined. Similarities and differences apparent from these studies permitted final adjustments to the limits of clusters. A decision on the status of each cluster and its relationships to other clusters was based on my criteria for recognizing species and subspecies as outlined in section 2.29.

Application of names to clusters ranked as species or subspecies was based on the study of type specimens for species-group names and a review of the literature. Lectotypes were designated and new names provided as required. I examined type specimens for all published

names (see data on types in synonymies, section 3.43).

Species thought to share close phylogenetic relationship, as suggested by analyses using the methods of phylogenetic systematics (cladistics) outlined by Hennig (1966), were grouped in clusters ranked informally as "lineages", species "groups", "subgroups", or "infragroups". Successively more inclusive supraspecific groupings were formed by uniting groups thought to share most recent common ancestry (sister group relationship). This procedure generated a nested hierarchy of strictly monophyletic (Hennig, 1966) [holophyletic (Ashlock, 1974)] groups which served as the basis for the classification presented (section 3.33). Discussions of cladistic theory and analytical methods used and of the relationship between phylogeny and classification are presented in section 3.1 (and 3.31) on classification and in section 4.1 on phylogeny. Additional comments on these and related topics appear in section 3.1.

2.29 Criteria for ranking taxa

Taxonomic categories used in this study and in the tentative classification proposed include the formal ones of subspecies, species and genus and the informal ones of lineage, group, subgroup, and infragroup. Refer to section 3.33 on classification for the rationale behind my choices of particular supraspecific categories.

All available evidence suggests the universality of sexual reproduction among nebriine species. Because apparently all Nebria species are bisexual, I accept as appropriate Mayr's (1969:26) proposed definition of the biological species (as amended by Whitehead, 1972:

139); namely, that species are populations or groups of populations through which gene flow actually or potentially exists, but which are reproductively [intrinsically] isolated from all other such populations [or groups of populations]. As noted by Whitehead (1972:139) and Larson (1975:251-252), the species so defined is a category with a nonarbitrary, objective basis; but this applies only to the extent that interspecific hybridization is excluded or non-introgressive. Success in application of this species definition to the recognition of contemporary species and, therefore, the "objective" bases of taxa recognized depend on the degree to which actual reproductive isolation can be demonstrated or inferred where it exists and excluded where it does not. Direct, unequivocal evidence for this intrinsic isolation or lack of same can seldom, if ever, be provided, even from breeding tests. Only criteria by which indirect evidence can be evaluated are generally useful.

The following working criteria were used in recognizing species. Two sympatric or parapatric forms were considered separate species if all individuals (of one or both sexes) of one differ from all members (of the same or both sexes) of the other in one or more structural characters (other than color or size). In practice, members of sympatric or parapatric Nebria species generally differ in several characters and therefore easily fulfill this criterion. Two allopatric forms were considered separate species if differences between members of each were roughly equivalent to differences between members of two closely related sympatric species, AND if members of geographically intermediate populations of either failed to exhibit intermediate

character states for the differentiating characters. Use of the above criteria requires the following assumption: that continuity or discontinuity in characters of external structure, internal genitalic structure, geographical and habitat distribution, and life history provided by study of population samples (individuals) are evidence of reproductive continuity or isolation, respectively, among natural populations. Clearly, recognition of allopatric species is more arbitrary than distinguishing sympatric or parapatric species; but hypotheses about relationships must be drawn from available evidence, and some estimate about these relationships is preferable to none.

I accept the subspecies definition of Edwards (1959b:230) in slightly altered form: subspecies are populations or groups of populations whose members are recognizably different from members of other conspecific populations and would interbreed with the latter IF they occurred sympatrically and synchronously (under natural conditions) BUT are distinctly isolated from them during their mating periods. The subspecies category was frequently used in ranking allopatric Nebria populations and population groups because patterns of geographical variation are often such that discontinuities in structural and other characters correlate well with discontinuities in habitat or physiography (see also Ball, 1966; and Ball and Negre, 1972). Other workers (Erwin, 1970; Madge, 1967; Noonan, 1973; and Whitehead, 1976) have avoided use of the subspecies category in their studies of lowland, mainland groups. Recognition of the usefulness of a subspecies concept appears to depend on one's particular perspective, more specifically on the distribution of habitats or areas occupied by the organisms one studies. Where gaps between areas of suitable habitat are broad and

clear, such as with predominantly montane groups like Nebria, correlated discontinuity in variation is more confidently recognized and suggestive of active, effective barriers to gene flow.

Because names for subspecies are accorded the same right and strictures as species names and compete with the latter for priority under the present International Code of Zoological Nomenclature, the description of new subspecies (and resultant introduction of new names into the literature) must be justified. I suggest that recognition of subspecies as defined above is justified because they represent incipient species. They are at present independent evolutionary units whose members are differentiated from members of other conspecific populations. Because these units are generally of zoogeographic significance, the formal subspecies trinomen is as welcome a "shorthand notation" (Larson. 1975:252) as the species binomen or other formal names.

In addition to the question of usefulness is one of practicality, recognizing inherent difficulties in the formulation and application of a subspecies concept. The use of the subspecies category has been warmly debated for decades (see for example Brown and Wilson, 1954; Edwards, 1954, 1956a and 1956b; Ingër, 1961; and Wilson and Brown, 1953). Without question, great variation in subspecies concepts has existed among taxonomists, such that taxa recognized by various workers are seldom equivalent or comparable units. The inability of taxonomists to formulate and apply a common subspecies concept to their studies is unfortunate but understandable in light of evolutionary theory which predicts a spectrum of intermediate stages in the process of speciation.

Assignment of formal subspecific rank to populations at one particular stage in the process is complicated by the potential for almost infinite variety in evolutionary rate and direction of change.

I agree with Edwards (1954, 1956a and 1956b) that the subspecies as defined above is a relatively objective ("comparatively but not absolutely nonarbitrary" [Simpson, 1961:116]) category. Extensive barriers to gene flow between subspecies can, as suggested earlier, be recognized in some instances through detailed studies of habitat and geographical distribution and life histories. These may in fact be easier to demonstrate than intrinsic isolating mechanisms between distinct species. Arbitrariness arises in decisions on how "different" allopatric or allochronous populations must be for recognition as either distinct species or conspecific subspecies.

Working criteria used for recognizing subspecies were as follows. Two populations or groups of populations were considered separate subspecies if (1) their respective geographical ranges are allopatric and separated by recognizable environmental barriers AND (2) differences between members of each are constant but less distinctive than differences between two closely related sympatric species in one or more characters of structure, color or size AND (3) the geographical pattern of variation in distinguishing characters is non-clinal or distinctly step-clinal. In general, all members of a subspecies can be recognized on structural characters. However, in some instances, where two subspecies were recognized as distinct by a step-clinal pattern of variation, all members of one subspecies may be distinguished only from all members of the most proximate populations of the other (see for

example the subspecies of Nebria lacustris Casey). The following assumption is required with use of the above criteria: that the amount of phenotypic divergence between two allopatric populations is a measure not only of the completeness and duration of their extrinsic isolation but also of the probability that reproductive (intrinsic) isolation has evolved between them. Where this assumption is invalid, the resultant error in ranking (i.e. recognizing as subspecies taxa which in fact conform to the biological species definition) is less objectionable than its opposite. If ranked as subspecies, close relationship between the taxa is emphasized, and species-group names are provided and protected by priority, requiring only change in status should actual relationships be determined later.

The informal categories of infragroup, subgroup, group, and lineage were used respectively in ranking successively more inclusive monophyletic groups. Monophyly and sister group relationships were suggested by phylogenetic analyses (see section 4.1 on phylogeny); and the method I used for representing these relationships in the formal classification is discussed in sections 3.31 and 3.33 below. Formal ranking required subjective assessment of the distinctiveness and breadth (internal divergence) of supraspecific taxa (without regard to taxon size) in the absence of more objective data on the timing of the proposed branching sequence (cladogram, section 4.13). Hennig's (1966) minimum age criterion for formal ranking is non-arbitrary, but at present generally inapplicable, especially for infrageneric classification.

3.0 SYSTEMATICS

3.1 Introduction

Systematics, as defined by Simpson (1961), is "the scientific study of the kinds and diversity of organisms and of any and all relationships among them". So defined, systematics is a master discipline which embraces taxonomy and all comparative aspects of biology. Included in this section is a diverse group of topics, all of which are clearly within the province of systematics.

The results of various comparative studies (morphology, chorology, etc.) presented represent preliminary attempts toward a broad comparative biology of Nebria. Data generated by these studies have also served as the bases for the key, descriptions, classification and analyses presented here.

Simpson (1961) defines taxonomy as "the theoretical study of classification, including its bases, principles, procedures, and rules". This definition, with which I agree in principle, depicts taxonomy as a purely theoretical discipline, while Mayr's (1969) definition (that, "taxonomy is the theory and practice of classifying organisms") comes closer to the more widely held concept of the term. In practice, taxonomy embraces not only classification ("the ordering of [organisms] into groups (or sets)...." (Simpson, 1961)), but also naming of taxa (i.e. nomenclature) and description and identification (including construction of keys) of individuals.

A preliminary classification of Nearctic Nebria is presented in this section, followed by a key for the identification of members of included taxa and a nomenclatural, bibliographic and descriptive

treatment of same. As discussed below (see sections 3.31 and 4.11), the classification is based on the results of cladistic and zoogeographic analyses (section 4.0). The analyses, although prerequisite to the classification and properly included under systematics, are presented separately (with discussion of evolutionary trends in the fauna) for ease of access, in anticipation of interest in these topics among biologists with little or no interest in Nebria classification per se.

3.2 Comparative Biology: Character Systems

Because the essence of systematics is in comparison, its data must be strictly comparable. Hennig (1966) introduced the term semaphoront, defined as "an individual at some specific, given point in the developmental sequence" (Kavanaugh,1972), to emphasize the importance of restricting comparisons not only to equivalent (homologous) traits of different organisms but also to equivalent developmental stages among them.

The bases of comparison used by systematists are traditionally called characters; and the particular manifestation of a given character in any individual is one character state of that character. The recognition and use of particular characters depends on the kinds of comparative studies made (e.g. morphology, embryology, etc.). Each different study results in the generation of a different set of characters, a character system. Use of combinations of character systems in taxonomic and evolutionary studies has increased in recent years (see for example the works of Brothers (1975) on mutillid wasps

and Goulet (1974) on the species of subgenus Bothriopterus (Carabidae, genus Pterostichus)), a most welcome and potentially fruitful trend away from classical "single character" or 'single system' taxonomy.

In this section, I present results of the following comparative studies on Nearctic Nebria: morphology (study of form and structure); chorology (study of geographical distribution); natural history (study of life style); and paleontology (study of fossils and their temporal and spatial distribution). These studies permitted either widespread or limited (as noted) use of characters from the following character systems: adult external form and structure; adult internal form and structure (limited); contemporary geographical distribution; historical geographical distribution (limited); contemporary habitat distribution; historical habitat distribution (limited); life history; mating behavior (limited); feeding behavior (limited); and locomotion (including dispersal capabilities) (limited). I have tried to make appropriate use of the diverse data available from these studies in the analyses and construction of the classification by first recognizing their respective limits. Data on form, structure and date and locality of capture of adults were available for almost all specimens examined. Natural history data were available for approximately half of the material studied (i.e. that material collected specifically for the project) and were, therefore, representative of fewer and/or smaller samples. Fossil specimens (see section 3.24) are limited in both quantity and their temporal and spatial representation; and, consequently, data resulting from their study were generally of limited use.

3.21 Comparative morphology

It follows from the discussion in section 3.1 that, for systematists, comparative morphology is the study of characters of form and structure. A total of 315 adult structural (including color and size) characters were recognized and used in this study. Sixty-six of these are represented by a single character state among Nearctic Nebria species. My coverage of external structure was broad and, generally, in detail; but study of mandibular and maxillary structure was superficial. Careful comparative study of these mouthparts will undoubtedly yield additional useful characters, especially if an effort is made to relate structural with functional differences [For example, Evans (1965a, 1965b, 1965c) has related mouthpart structure to feeding behavior in N. brevicollis (Fabricius) adults].

Study of internal structure was limited to the genitalia and associated structures: median lobe and parameres of males; ovipositor, bursa copulatrix, common oviduct, spermatheca and spermathecal duct of females. Shape of the internal sac of the male median lobe was not routinely examined, although potentially useful characters were recognized in this structure. Meaningful interpretation of inter- and intraspecific variation in both internal sac shape and shape of the bursa copulatrix in females must wait in copulo studies to ascertain correspondence of parts. Previous studies of internal structure in Nebria have been limited to the digestive system (Carleton, 1936; and Erwin and Ball, 1972), pygidial defense glands (Forsyth, 1972), parts of the female reproductive system (Erwin and Ball, 1972), and the neuro-endocrine complex (Ganagarajah, 1965), all (except the work of

Erwin and Ball) on members of N. brevicollis (Fabricius).

3.211 General characters

Size

Among the Carabidae, members of Nebria species are medium-small to medium-large in size. Within the genus, size range is considerable and frequently a useful taxonomic and/or key character. Range in size (standardized body length) of Nearctic species is from 6.7 to 14.9 mm; but species with small or larger members are found in the Palaearctic fauna.

With few exceptions, body size class (i.e. small, medium or large size) is relatively constant within species groups and subgroups. For example, most Nearctic species whose members are large belong to the same species group. Females are usually larger than males of the same species; but the reverse is true for members of both subspecies of N. ingens Horn. Intraspecific size variation is considerable in some species, but intrapopulational variation is great in only a few species. Examples of geographical and suspected ecophenotypic variation in size are discussed under descriptions of taxa involved and in section 4.4 on Evolutionary Trends.

In general, proportions of adult individuals remain constant regardless of body size. In some species (see for example descriptions of N. lacustris Casey and N. nivalis gaspesiana n. ssp.), pronotal shape appears to change with increased size; but other examples of apparent allometry were not found.

General form

These beetles are generally slender in form and delicately structured, most markedly resembling the Agonini in habitus. Variation in general form among Nearctic species is slight compared to that in the Nebria fauna world-wide. The head and pronotum are generally short in relation to elytra, but the relative sizes (lengths or widths) of these parts are extremely useful characters (see also below). Sex-associated variation in relative head size or relative elytral length is apparent in several species. With few exceptions, appendages are slender and elongate.

Of the four general types of body form recognized by Jeannel (1926; see also Erwin, 1970), two are found among members of the Nearctic Nebria fauna. These are:

1. Type ailé (long-winged type) (Fig. 2)-- eyes large, pronotum short, elytra rectangular with base broad and humeri prominent, metasternum long.
2. Type aptère (short-winged type) (Fig. 3)-- eyes large or small, pronotum long, elytra ovoid with base narrow and humeri flattened, metasternum short.

A complete spectrum of intermediates between these two types of body form is also found among members of the fauna. Pigmentation does not appear to be correlated with body form in Nearctic Nebria as it does in some other groups (see Erwin, 1970; Jeannel, 1926). For additional discussion on the suite of characters associated with evolution of brachyptery in Nebria, see section 4.4.

Color

Color (pigmentation) characters are extremely useful in working with Nearctic Nebria. Range in body color is from pale yellow to black. Head, pronotum, elytra, venter and appendages are most often concolorous, although shading varies among parts in some taxa (for example, more proximal articles of all appendages usually grade to a darker shade of the same color than more distal ones). However, marked contrast in colors of different parts is evident in members of some species. Most commonly, the elytra and other appendages (most noticeably the legs and antennae) are involved in these contrasting patterns. A number of species have all members with contrasting pale appendages, while others are dimorphic for appendage color (i.e. members of the same population have all appendages either pale or dark). Still others are polymorphic for this character (members are either concolorous, or the pattern is strongly contrasting, or some intermediate condition is exhibited); and this variation is either random (intrapopulational) or geographically correlated. Members of fewer species exhibit the contrasting pale elytra pattern. Species dimorphic or polymorphic for this character are known, but no Nearctic species has all members with contrasting pale elytra. The pattern is usually correlated with geography and habitat (see also section 4.4 on Evolutionary Trends).

An important taxonomic character is the presence or absence of "red spots" on the frons. These spots are actually faintly- or non-pigmented areas and their presence can only be recognized in species whose members have dark head color. The spots, if present, are small,

paired and paramedial (Fig. 4) in most members of most species; but they are broadly fused as a single, larger median spot (Fig. 5) or incompletely fused (anteriorly only) forming a vaguely M-shaped spot (Fig. 6) in a few members of some species and all members of a few taxa.

For up to seven weeks following eclosion, adults are teneral (i.e. soft and not fully pigmented). This provides a source of error in evaluating color in individuals. In general, hardening of the cuticle and deposition of pigment are roughly synchronous, and most suspected teneral adults are distinguished from pale matures by their softness and pliability.

Reflection

I use the term 'reflection' for the apparent metallic coloration seen in members of many Nearctic species. This visual effect (metallic color) is produced as light passes into and is reflected by various layers of the cuticle (Gilmour, 1970). The particular spatial relations among cuticular layers and the nature and content of intervening spaces account for absence of the effect or its presence, intensity and hue. I reserve the simple term 'color' (as discussed above) for pigmentation. Color and reflection are quite independent characters, the only apparent correlation between them being that metallic reflection is always associated with dark color (rufous to black).

When present, reflection is metallic blue, or violet, or red, or green, or suggested as brassy or copper highlights. It is most commonly seen and intense on the elytra, less common and intense on the pronotum and head, rarely present on the venter, and absent from the appendages.

Reflection is frequently very faint and difficult to recognize. Differences in lighting and condition of specimens may alter its perception. For consistent results, clean, dry specimens should be viewed under natural or fluorescent light. Maturity of the specimens can also affect reflection. Some teneral adults exhibit faint metallic reflection even if mature adults of the same species are brilliantly metallic or totally non-metallic.

Luster and microsculpture

The luster (shininess, dullness or iridescence) of dorsal body surfaces is useful on its own for distinguishing members of some species, although it is merely a visual effect dependent on the so-called microsculpture of that surface. Range in luster among Nearctic Nebria is from very dull to faintly iridescent. In general, individuals exhibit a slight increase in dullness (or decrease in shininess) from head to pronotum to elytra. In comparisons among individuals and taxa, therefore, luster of the same respective body regions must be examined. Iridescence is quite rare and faint in Nebria and, when present, restricted to the elytra or abdominal venter.

Microsculpture (Figs. 7 - 12) refers to the surface pattern of microlines and areas delimited by them. The patterns of lines are called meshes, probably because they resemble wire mesh patterns. The meshes vary in continuity (whether broken or unbroken), depth of impression (from absent to deeply impressed) and shape (from 'isodiametric' (Fig. 7) to slightly to markedly transverse (Figs. 9 - 11) to present only as transverse lines and interspaces with little or no mesh-like appearance (Fig. 12)). In fact, areas

delimited by meshes, the alveolae, rather than the meshes themselves, actually have shape; but the tradition of referring to mesh shape is followed here for conformity with other recent studies. Convexity of alveolae, however, is described, ranging within the genus from flat (Fig. 8) to slightly convex (Fig. 7).

A transition is generally evident within individuals in microsculpture (just as in luster) from head to pronotum to elytra. In general, depth of impression of the meshes increases from head to elytra. In addition, meshes, if present, are isodiametric on the head, and of most individuals on the pronotum, independent of mesh shape on the elytra. Comparisons of mesh shape are, therefore, meaningful only for the elytra. For consistency, observations of microsculptural characters were made in the following areas: frons, vertex, clypeus and labrum (at longitudinal center of each, just left of midline); pronotum (at longitudinal center of disc, midway between midline and left lateral margin); and elytra (at a point one-fourth the elytral length distant from the basal margin and centered on the third, fourth, or fifth interval.

Pubescence

Members of Nearctic Nebria are without pubescence except on the fifth through eleventh (flagellar) antennomeres (also on apex of fourth antennomere in a few individuals of N. virescens) and on the ventral surfaces of the basal two or three tarsomeres of anterior tarsi in males. Setae, relatively abundant and taxonomically important, are discussed with the parts which bear them.

3.212 Head

Frons and vertex

Frontal characters, useful in studying many other carabid groups, are of little importance among Nebria. Within the genus, convexity varies slightly (frons is moderately convex in members of most species, almost flat in those of a few) and macrosculpture (frons is completely smooth in most members of all species but faintly rugulose laterally in some individuals). A single pair of supraorbital setae is present in members of all species, one positioned medial to the posterior margin of each eye (Fig. 13). The frontal furrows are evident (Fig. 13), although shallow, broad and vague in many individuals. In all members of some species (e.g. N. ingens) and some members of many other species, the furrows are present only as short, moderately deep foveae (Fig. 22).

The vertex in members of all species is smooth and moderately convex. In at least some individuals in all species, a faint median foveate or transverse impression is seen.

Genae

Among carabids, relative enlargement (swelling and broadening) of the genae is often associated with decrease in eye size in many species. This inverse relationship maintains among Nearctic Nebria also. In all species, the head width across the genae is greater than across the frons anterior to the eyes (Fig. 18). With even moderate reduction in eye size (see below), broadening of the head behind the eyes is evident, reaching an extreme in males of N. ingens (Fig. 22) where the post-orbital maximum head width is

greater than the width across the eyes.

Sex-associated variation in head width across the genae is present in several species. In these taxa, females are relatively broader than males, except in N. ingens (where the opposite pertains).

Occiput

Among Nearctic Nebria, the occipital region is not constricted to form a "neck" as in members of some Leistus species and a few Palaearctic Nebria species. In general, variation in width across the occiput mirrors variation in head width across the genae; and sex-associated variation is the same as with the latter (see above).

Eyes

No nebriine species is known to have eyeless members, although those of Nebria nudicollis Peyerimhoff (from the Djurdjura Mountains, Algeria) have very small (yet still multifaceted) eyes. Members of most Nearctic Nebria species have medium-sized (in diameter) eyes (Fig. 18), but those of a few species have eyes slightly to moderately reduced in size (Fig. 19). In members of all Nearctic species, eyes are convex, protuberant; but interspecific variation in this character is evident. The most markedly convex eyes are seen in members of N. appalachia Darlington (Fig. 17) and the least convex members of N. ingens (Fig. 22).

Antennae

In general, the antennae of members of Nearctic Nebria are elongate and filiform. Interspecific variation is evident, however, in relative antennal length and in the shape, number of setae and (in one instance) pubescence of various antennomeres.

In assessing relative antennal length, a standard comparative measure was needed. I chose to relate antennal length to body size in a manner illustrated in Fig. 23. If the antennae are relaxed, bent at right angles distal to the scape and stretched posteriorly along the dorsum, their length is estimated by reference to the points of insertion for the middle and hind coxae. Length classes and grades of each were recognized. In members of most Nearctic species, antennae are medium-length or long, slightly shortened or very long in members of only a few species. Males of all species have relatively longer antennae than conspecific females, although the difference is slight in most species.

Shape of the antennal scape is an extremely useful character (Figs. 24 - 41). Members of some closely related species or different subspecies differ greatly in scape shape. Three aspects of shape are important: relative length, symmetry (whether straight [Fig. 32], arcuate [Fig. 41] or bisinuate [Fig. 25]), and diameter (whether cylindrical [Fig. 34], oval [Fig. 24], apically [Fig. 30] or basally [Fig. 28] narrowed or anteriorly swollen [Fig. 27]). Among members of Nearctic species, antennomeres are approximately round in cross-section (except in members of N. ingens, in which the second through fourth antennomeres are laterally compressed basally [Fig. 43]). Flagellar antennomeres (i.e. fifth to eleventh) vary slightly but consistently in shape (relative length) even among members of some closely related species or different subspecies.

Pubescence is restricted to the fifth through eleventh antennomeres in all members of Nearctic species, except for a few individuals of

N. virescens which have scattered pubescence also on the apex of the fourth antennomere (Fig. 44). The scape bears a single subapical, anterodorsal seta (Fig. 24) in members of all species, and the pedicel a single ventroapical seta (Fig. 45) in those of all but a few species. In the latter, members have instead two to four apical setae (Figs. 46 - 47).

Clypeus

The clypeus is similarly-shaped in members of all Nearctic species, with the anterior margin approximately truncate (Fig. 48) or weakly concave (Fig. 49). In all specimens examined, a single pair of paralateral setae was present, and the fronto-clypeal suture was clearly evident and complete (Fig. 48).

Labrum

The labrum is rectangular, with three pairs of setae across its anterior margin (Fig. 50) in members of all species. The medial pair is short and fine, the lateral pair longest, and the middle pair more varied in length and thickness. Variation in shape of the anterior margin is considerable within and between taxa, but of little systematic importance. The margin is approximately truncate (Fig. 50) or weakly convex (Fig. 51), concave (Fig. 52) or bisinuate (Fig. 53), with all possible combinations found among members of one species or another.

Mandibles

All Nearctic Nebria have mandibles which are basally trigonal, apically subfalciform and slightly asymmetrical (Figs. 54 - 59). Each mandible bears a large, sharply defined unisetose scrobe. The

apex of the terebral blade of the left mandible is moderately (Fig. 54) to markedly (Fig. 55) angulate medially (i.e. hooked), while that of the right mandible (Fig. 57) is evenly arcuate (not hooked). In members of most species, the basilateral area is narrowly explanate (Fig. 57); but in members of a few species (e.g. N. hudsonica LeConte, N. pallipes, this area is moderately broad (Fig. 59) and vaguely reminiscent of such development in members of Leistus species.

As noted above, detailed comparative study of the medial (cutting) margins and associated structures of the mandibles has not been made. A general survey of structure in Nearctic Nebria compared with members of related genera and tribes permits, however, the following synopsis. [Terms are those of Ball, 1959.] The terebral margin of each mandible is long and weakly concave, terminating basally in a moderately (Fig. 57) to strongly (Fig. 58) developed tooth. In general, this and all other teeth are more strongly developed on the right mandible than on the left (Figs. 54 - 59). The retinacular ridge is short, not or only slightly extended distal to the retinacular tooth and ventral to the terebral margin. The retinacular tooth is present as a vague, broad marginal swelling (Fig. 54) or well defined and dentiform (Fig. 56); and on the right mandible, it is very long and projected (Fig. 58) or moderate in length. In the molar region, a premolar tooth is evident (Fig. 56) or not (Fig. 54) on the left mandible; but this tooth is not developed on the right mandible. At the base of the molar region, a markedly developed tooth (of unknown homology) is present on each mandible (Figs. 57 - 58). A setiferous ventral groove

is present on each mandible, extended longitudinally, parallel to the cutting edge and teeth and separated from these by a trough which is sharply delimited laterally and medially continuous with the horizontal plane of the edge (Figs. 57 - 58). The medial (oral) basal margin of each mandible is excavate; and the connecting membranes bear patches of fine setae (Figs. 57 - 58). Erwin (1970) illustrated mandibles (see his figure "5.") with setae in a similar area in certain Brachinida; but his representation suggests that, in those beetles, the setae are on the mandible itself rather than on a connecting membrane.

Maxillae

Among Nearctic species, the maxilla (Fig. 60) exhibits little variation. Although detailed interspecific comparisons have not been made, a general survey of selected taxa indicates that slight differences in number and/or arrangement of spines and setae on the cardo, stipes, lacinia, palpiger and palpus may characterize some species or species groups. Differences in relative lengths of different maxillary palpomeres may also prove useful.

The setiferous subuniform ventral processes characteristic of members of Leistus species are entirely lacking from all Nebria.

Labium

Structural characters in the labium are extremely useful in distinguishing and grouping nebriine and related genera; but interspecific differences are usually slight and often inconsistent. Several characters are, however, useful in defining species groups and in distinguishing members of certain species.

The ligula (Figs. 61 - 62) is roughly quadrate or faintly

trapezoidal in outline, longitudinally keeled ventrally, the keel terminated apically in an anteroventrally projected tooth in members of most species. Two apico-medial setae are found in members of all species, usually associated with the tooth. The anterior margin is truncate (Fig. 63) or anteriorly projected medially in association with development of the keel tooth (Fig. 62) The paraglossae are indistinct, completely fused with the ligula (fused glossae) (Fig. 62) except in N. virescens, members of which have minute but distinct dentiform lobes at the apicolateral angles of the ligula (Fig. 61).

The palpi (Fig. 61), comprised of three filiform palpomeres, articulate basally with the palpigers, the latter connected by membranes to the base of the ligula and the anterodorsal margin of the mentum. The penultimate labial palpomere is equal to or slightly less than the terminal palpomere in length and, in members of most species, bears three setae on its anterior surface (Fig. 62). Members of a few species have only two anterior setae (Fig. 61).

The shape of the mentum (Figs. 64 - 78) is similar in all species. The anterior margin is deeply emarginate and toothed medially. Depth of the emargination varies within and between species, occupying from one-third (Fig. 65) to one half (Fig. 71) the total length of the mentum. The medial tooth is bifid in members of most species, although tooth length and depth of the apical notch vary within or between certain taxa. It is roundly truncate, however, in members of N. ingens (Fig. 76) and only slightly emarginate apically in members of N. ovipennis LeConte (Fig. 75) and related species. The epilobes are broad, smoothly rounded laterally and anteriorly, each terminated

apicomedially in a sharp tooth. Interspecific variation in development of the tooth is considerable, ranging from a minute projection (Fig. 70) to a long, stout spike (Fig. 74). A maximum of four pairs of setae, each with characteristic position are seen on the mentum in members of nebriine genera. All four pairs are in members of genus Leistus, but no more than three among those of Nebria species. Chaetotaxy of the mentum is illustrated in Fig. 64. Members of all Nearctic Nebria lack the M4 setae (Figs. 65 - 78). The occurrence and position of M1 and M3 setae are constant in all members (except those of N. carri n. sp. in which the M3 setae are absent [Fig. 72]). M2 setae are present in all members of all taxa, but variation in their position is a useful character. In members of most species, M2 setae are positioned about two-thirds the distance from the base of the mental tooth to the base of the mentum (Fig. 77). Variant positions are: (1) more apically, at about half the distance from the tooth base to the base of the mentum; or (2) basally, adjacent to the basal margin (Fig. 65).

The gula (Fig. 79) is T-shaped, smooth, without the setiferous spiniform processes or ridges characteristic of members of genus Leistus. A row of setae traverses the broad anterior region. Inter- and intraspecif[illegible]n observed in both number and position of these setae was s[illegible]s to preclude formulation of a chaetotaxic scheme as was done [illegible]e mentum. A rough distinction is made, however, between 'medial' and 'lateral' pairs of setae (Fig. 79). Among members of Nearctic species, number of medial pairs ranges from zero to two and of lateral pairs from one to seven. Number and position

of these setae are quite constant among members of a few species; and in N. ingens, sex-associated differences in the numbers of both lateral and medial setae were apparent. In general, however, characters based on gular setae are unreliable.

3.213 Prothorax

Pronotum

Shape of the pronotum (Figs. 82 - 122) is an extremely useful character. Seemingly strong differences in habitus among individuals of a single species or those of different species are often found to involve only slight differences in pronotal shape. In members of N. virescens, the pronotum (Fig. 84) is semiovoid, not noticeably narrowed basilaterally. In members of all other Nearctic species, the pronotum is basically cordate, with interspecific variation in shape (ranging from faintly[Fig. 120] to very markedly [Fig. 111] cordate) common. Terms used in reference to the pronotum are illustrated in Figs. 82 - 83 . The pronotal disc is convex (but in members of some species more weakly or strongly so) and smooth, except in a few species in which some individuals have the disc very faintly punctulate (e.g. N. vandykei Bᵾnninger).

Intraspecific variation in shape of the apical (anterior) margin is considerable, ranging among members of some species from truncate to convex or weakly concave medially. Interspecific variation in the anterior margin is too inconsistent to permit use of this character in comparisons among most species.

The lateral pronotal margin is arcuate, varying among members of different species from faintly to markedly so. In members of

N. lyelli Van Dyke (Fig. 94) and unique to them, is a shallow subapical sinuation in the margin. In all members of most species the margin is sinuate sub-basally, with considerable interspecific (and moderate intraspecific) variation evident in the depth and length of the sinuation (Figs. 84, 87). It is entirely lacking from or very shallow (Fig. 101) in members of a few species (e.g. N. virescens or N. obliqua LeConte). Width of the lateral explanation of the pronotum (delimited medially by the lateral groove) is also a useful character. Intraspecific variation is slight and interspecific variation considerable. The explanation may be of equal width throughout (Fig. 116), ranging from narrow to broad, or either narrowed or broadened anteriorly and/or posteriorly. Almost all combinations of the above are seen among members of one or more species (Figs. 84 - 122).

Shape of the basal (posterior) margin is related in part to shape of the basal (lateral) angles (see below). In members of some species, the margin is truncate (Fig. 84) or weakly bisinuate and concave medially (Fig. 111). In other species, members have the margin weakly concave (Fig. 94) or convex (Fig. 85), bisinuate and weakly convex medially (Fig. 87) or weakly (Fig. 105) to strongly (Fig. 100) sinuate laterally. Relative length of the margin is dependent on the degree to which the pronotum is constricted basally (see above).

The apical pronotal angles vary among Nearctic species in length (degree of projection anteriorly), width and shape of their apices. These three characters vary considerably interspecifically; but they have been most useful in distinguishing closely related species or

different subspecies. Intrapopulational variation is generally slight. In members of different species, range in length of the angles is from short (Fig. 103) to long (markedly projected) (Fig. 111); in width, from narrow (Fig. 94) to broad (Fig. 103); and in shape of the apices, from broadly rounded (Fig. 84) to bluntly pointed (Fig. 94).

Shape of the basal pronotal angles is also an extremely useful character. In members of most species, the angle is rectangular (Fig. 97), in those of a few species acute (Fig. 115) or obtuse (Fig. 101). In addition to degree of angle, the basal angles vary in degree of posterior projection, from not (Fig. 122) to markedly (Fig. 111) projected. The apices of the angles are themselves simple (Fig. 122) or denticulate laterally (as in N. paradisi Darlington, Fig. 86) or posteriorly (Fig. 115).

Anterior margination (Fig. 82) of the pronotum is present in members of all Nearctic species (absent only from a few members of N. zioni oasis n. ssp.), but not defined on the medial one-third of the apical margin. Width of the margination is relatively constant (Fig. 116), narrowed (Fig. 97) only in members of some species in the sahlbergii group. Definition of the margination is also relatively constant, but more or less marked in members of a few species. Lateral margination (the "lateral bead" of Lindroth, 1961) is complete, uninterrupted (Fig.) in most members of most species, basally obliterated (Fig. 103) in some members of some species and all those of others (e.g. N. virescens). Margination width varies within and among species from uniform throughout (Fig. 94) to apically (Fig. 95) and/or basally broadened. Variation in definition of the

lateral margination is similar to that for the apical margination. Posterior margination is absent from members of all species studied.

Inter- and intraspecific variation in depth (from shallow to deep), definition (from broad and vaguely defined [Fig. 84] to narrow and sharply delineated [Fig. 103]) and macrosculpture (from smooth to moderately punctate) of the anterior transverse impression is considerable. The posterior transverse impression is deep in all members of all species, narrow in members of most, broad in those of a few. Shape of the impression varies within some species and between others from straight (Fig. 100) to anteriorly deflected medially (Fig. 111). In macrosculpture, the posterior impression ranges from smooth to punctate among members of different species, with intraspecific variation slight. The median longitudinal impression also varies in depth (from very shallow [Fig. 106] to moderately deep [Fig. 94]) and macrosculpture. The impression is either smooth or faintly rugulose in members of all species. In most members of most species, the impression is defined only between the anterior and posterior transverse impressions (Fig. 99); but in some members of most species (and most members of N. ingens) it is extended toward or to the apical and basal margins (Fig. 117). The basal foveae are linear in members of all species and either continuous laterally with the basal portion of the lateral groove (Fig. 86) or separated from the latter by a faint (Fig. 92) or more markedly developed (Fig. 84) convexity. The foveae are deep in members of all species (except N. lyelli [Fig. 94]) but varied among species in width (from narrow [Fig. 94] to very broad [Fig. 101]). Nebria virescens is unique in

that most of its members have two longitudinal grooves etched in the foveae, separated by a weak convexity (Fig. 84). Members of all other species have a single longitudinal groove in the foveae and no similar convexity (Fig. 87). The foveae are weakly divergent posteriorly (Fig. 118) in members of most species, approximately parallel (Fig. 87) or more markedly divergent (Fig. 111) in those of a few species. They terminate anteriorly at the posterior transverse impression (Fig. 84) in most members of most species, but are extended slightly on the disc (Fig. 96) in all members of a few species and few members of others. Interspecific variation in foveal macrosculpture is from smooth to vaguely rugulose or punctate. Most characters mentioned above for the foveae and pronotal impressions have been useful in distinguishing among closely related species or subspecies, less useful in comparisons of more distantly related forms.

A maximum of two pairs of setae are on the pronotum among Nearctic Nebria, and members of all species have at least one pair. The basolateral seta (Fig. 82) is positioned on the lateral margination at the basal angle and is present in members of all species except N. kincaidi Schwarz (Fig. 112) and N. carri n. sp. (Fig. 111). Presence (Fig. 84) or absence (Fig. 106) of the mid-lateral seta is an extremely important character in studying Nebria. I have seen no single example of intraspecific variation in its occurrence among the many thousands of specimens studied. Relative position of the seta is apparently constant, but some interpopulational variation is evident in N. lacustris. Members of N. nivalis have a short, arcuate, longitudinal tubercle medial to the insertion of the mid-lateral seta (Fig. 89). Closely related Asian species have a similar tubercle, but it is seen in

members of no other Nearctic species. Presence of the tubercle appears to be related to a slight lateral displacement of the seta; and the tubercle may be an enlarged and medially-displaced derivative of the lateral margination at that point.

Venter

Macrosculpture is reduced or absent from the prothoracic venter in members of Nearctic species. The prosternum, proepisternum and proepimeron are smooth in most members of most species. A few members of most species and all members of a few others (e.g. N. gouleti n. sp.) have the prosternum faintly punctulate or punctate anteriorly and laterally (Figs. 123 - 124). Members of a few of these same species also have the proepisternum faintly punctulate or punctate anteriorly (Fig. 123), and members of still fewer species also have similar faint macrosculpture on the proepimeron. In contrast, members of several Palaearctic species have coarse punctation on the ventral prothoracic sclerites.

The prosternal intercoxal process is lanceolate (Fig. 126) or sublanceolate (Fig. 125A) in members of Nearctic species. Very little intraspecific variation in shape was observed; and interspecific differences in shape of the apex and relative width of the base were, therefore, quite obvious. Shape of the process in members of N. appalachia (Fig. 127) is unique. In members of all other species, the base of the process is much narrower than more apical regions. The process itself is smooth (without macrosculpture) and glabrous ventrally in all Nearctic species. Interspecific variation in margination of the process is apparent. In members of some species,

margination is restricted to the basal region (anterior to or at the level of the front coxae) (Figs. 130 - 131). Members of other species have the process with complete margination (Fig. 125) or with only the apex unmargined (Fig. 127), while those of a few species have the margination interrupted for a short distance basally (Fig. 132) independent of the extent of margination apically.

The front coxal cavities are basally open (not closed posteriorly by contact of the proepimeron with the prosternal intercoxal process) (Fig. 133), uniperforate ("unbridged" of Bell, 1967) internally, and confluent medially (dorsal to the intercoxal process (Fig. 134).

3.214 Pterothorax

Dorsum

The scutellum (i.e. mesoscutellum) is visible in all nebriines as a small triangular sclerite wedged between the basimedial angles of the elytra and base of the pronotum (Fig. 1). Other dorsal sclerites of the pterothorax are obscured by the base of the pronotum and/or the elytra and were not examined comparatively.

Elytra

The elytra are moderately convex in members of most species, slightly flat dorsally or more strongly convex in those of a few species. All nebriines lack elytral pubescence.

Elytral silhouette (outline shape of the elytra taken as a unit) (Figs. 135 - 143) contributes substantially to habitus; and differences observed grossly are often more apparent than real. Because in comparing elytral shape among intact specimens both elytra are normally viewed at once (halves of a whole), the visual effect of slight

differences in the shape of one elytron is doubled. Nonetheless, differences in silhouette are extremely useful in distinguishing taxa. Among members of Nearctic species, the following shapes are seen: (1) rectangular (Fig. 135), with lateral margins approximately parallel and width across the base about as broad as the greatest elytral width; (2) subrectangular (Fig. 136), with lateral margins slightly rounded and base broad; (3) subovoid (Fig. 137), with lateral margins moderately rounded and base slightly narrowed; (4) subovoid-narrowed (Fig. 138), similar to subovoid but with elytra narrowed sub-basally also and lateral margins approximately straight in the basal half; (5) ovoid (Fig. 139), with lateral margins markedly rounded and base narrowed; and (6) tear-shaped (Fig. 140), similar to ovoid but with elytra markedly narrowed basally and sub-basally. Components of elytral shape (including width of base, shape of lateral margins, shape of humeri, etc. [see below]) are markedly correlated with size of the metathoracic wing (see section 4.41 for discussion).

Study of the elytra singly (i.e. one elytron) provides numerous useful characters, a few recognizable as components of gross shape (silhouette) as discussed above. Detailed comparisons using these characters provide much more specific information than does silhouette alone. Terms used in reference to the elytron are illustrated in Fig. 146 . As noted above, width of the elytral base (distance from the scutellum to the humerus) is varied among members of different taxa, ranging from broad (Fig. 153) to very narrow, reaching an extreme in members of N. kincaidi kincaidi Schwarz (Fig. 149). The basal margination of the elytron is varied in form and shape. It is smooth

(Fig. 150) or wavy (Fig. 149), and, except in a few taxa, both forms are found among members of the same taxon. The margination may be straight or very weakly concave anteriorly (Fig. 153) or moderately (Fig. 150) or markedly (Fig. 149) so. The lateral terminus of the margination (i.e. at the humeral angle) is directly opposite the medial terminus (i.e. at or near the scutellum) (Fig. 153) or displaced anteriorly (Fig. 148) or posteriorly (Fig. 154). Distinction should be made here between the humerus itself (the laterobasal corner of the elytron) and the humeral angle (as I use the term, referring to the angle, if any, formed by the juncture of the lateral groove and basal margination of the elytron). Development of the humerus differs markedly among members of some different species and/or subspecies. It is rectangular (rounded apically only) (Fig. 153) or slightly (Fig. 152) to strongly (Fig. 154) rounded, or, at an extreme, flattened and essentially absent (Fig. 149). The apex of the humerus is smoothly rounded (Fig. 153), faintly (Fig. 158) or markedly (Fig. 157) carinate and anteriorly projected or, as in some members of N. virescens, slightly denticulate (Fig. 155). The humeral angle does or does not mirror the humerus itself. For example, the angle is markedly defined while the humerus is rounded (Fig. 149) in members of some species or rounded (therefore absent) with a rounded humerus (Fig. 154) in those of other taxa. A subhumeral sinuation in the lateral margin (Fig. 146) is present in members of most species but absent from (Fig. 150) or more markedly developed in members of a few. All members of all species have a subapical sinuation of the margin (Fig. 146), more markedly developed than the subhumeral sinuation. The subapical sinuation is associated with the apical

terminus of the internal elytral plica (see below). Interspecific differences in width of the lateral elytral explanation are slight but consistent, ranging among members of different species from narrow (Fig. 155) to relatively broad (Fig. 160). The explanation, delimited medially by the lateral groove, is clearly narrowed basally in members of most species. A subapical carina is present, in all nebriines examined, at the confluence of the fourth through seventh elytral intervals (Fig. 146). Among Nearctic Nebria, it varies in degree, from slightly to markedly developed, and length (moderate [Fig. 159] to long [Fig. 160]). Both development and length of the carina appear to correlate with depth of the subapical sinuation (i.e. increased development with increase in the subapical sinuation depth).

Shape of the elytral apices is another useful character. In most other nebriines and in members of some Nearctic species, the apices are narrowly rounded laterally, straight and closely approximated along the sutural (medial) margin (Fig. 163). In members of other species, the apices are: (1) broadly rounded apically, slightly arcuate and divergent medially (Fig. 167); (2) obliquely blunted apically and slightly divergent medially (Fig. 166); (3) broadened and obliquely blunted apically, slightly divergent medially (Fig. 164); (4) slightly pointed apically, arcuate and more widely divergent medially (Fig. 162); (5) broadly blunted apically and widely divergent medially (Fig. 168); or (6) slightly pointed apically and sinuate and divergent medially (Fig. 165). Intraspecific variation in this character is slight.

In members of all species, the internal plica of the elytron (Figs. 169 - 170) is longitudinal, simple, keel-like, just extended to

but not across the epipleural margin at the subapical sinuation of the lateral margin. The plica is demarcated externally (dorsally) by the lateral groove. The elytral locking mechanism in Nebria species is therefore, relatively simple. With the elytra in folded (closed) position, the dorsomedial edges of the abdominal sterna (see also below) appear to fit between the elytral epipleuron and the internal plica (Fig. 170), most securely so just anterior to the juncture of these two flanges (i.e. at the elytral margin).

In members of all Nebria species, each elytron bears eight complete striae, the "first" through "eighth" (beginning medially), and one abbreviated stria, the "scutellar striole", medial to the base of the first complete stria (Fig. 146). Interspecific variation in depth of impression and punctuation of the striae is evident. In members of most species, striae are moderately impressed, deeply impressed in members of several species and weakly so in those of only a few species. In N. virescens (Fig. 155) and N. suturalis (Fig. 159), all and some members, respectively, have the lateral striae much more weakly impressed than the medial three or four striae. Nearctic Nebria, compared with members of several Palaearctic species, have only weak punctuation of the striae. Among members of Nearctic species, striae range from faintly punctulate to evidently (but slightly) punctate. Density of punctation ranges from moderate to sparse (again compared with the Palaearctic Nebria).

Elytra, and especially the basal regions of same, are among those parts of beetles most commonly preserved as fossils. In my attempts to distinguish the elytra of Nebria specimens from those of other carabids of similar size in samples sent to me for identification, the most

useful characters found were (1) branching pattern of the first and second striae, and (2) relationship between the first stria and the scutellar striole. In all members of most nebriine species, and at least in some members of all species, first and second striae branch from a common stem at some distance from the basal margination (Fig. 171). In all nebriines, the scutellar striole is free, not joined distally with the first stria. All Pterostichus (Fig. 174) and Amara (Fig. 175) specimens examined agreed with nebriines in the branching pattern of first and second striae; but in members of each of these other genera, the scutellar striole either joins or crosses the first stria distally. Specimens of Diplous and Patrobus species agree with nebriines in both characters, except that they lack a basal margination (Fig. 177). In all Agonum specimens examined, the first and second striae arise separately from the basal margination (Fig. 176). In the Nebria individuals noted as exceptions above, first and second striae arise either separately (Fig. 173), as in Agonum specimens, or from a common point on the margination (Fig. 172). In all such exceptional Nebria individuals, fortunately, the elytral intervals are at least weakly catenate (see below), thus permitting recognition of the specimen as a Nebria. Individuals representing Nebria species are distinguished from those of Pelophila and Leistus (i.e. other nebriines), respectively, by the abbreviated scutellar striole (complete in Pelophila members) and the faint and sparse punctation of the striae (relatively coarse and dense in Nearctic Leistus members).

Characters of the elytral intervals are also useful in

distinguishing and relating taxa. Range in topography of the intervals among members of different Nearctic species is from flat to markedly convex. Intraspecific variation in topography is low in most species, but geographically correlated in some. All intervals are smooth (i.e. without macrosculpture) and approximately equal in width in members of all Nearctic taxa, continuous (uninterrupted) in members of several species. In members of many species, however, third, fifth and seventh intervals (singly or in various combinations, depending on the taxon) are interrupted by moderately (Fig. 156) to very markedly (Fig. 161) developed setiferous foveae. A number of fixed setae are present on these and certain other intervals. Conspicuous interspecific differences are in the presence and number of these setae and in modification of the intervals associated with their sockets. A single seta, the presence of which is most simply noted by reference to its socket (the "basal pore"), is found near the elytral base on the first interval between the first stria and the scutellar striole (Fig. 146). It is present in all members of most species and most members of others, but it is absent from all members of a few species. Lindroth's (1961:65) use of the presence of the basal pore as a key character was unfortunate because of the intraspecific variation in several species. Members of all species have one or more setae on the third interval, with a maximum of 10 in individuals of several species. Members of several species also have one or more setae on the fifth and/or seventh intervals (with a maximum of nine for each interval in some individuals of some species). Intraspecific variation in the numbers of setae on each of these intervals is very great; and presence of

setae on an interval rather than their number appears to be the more reliable charact in general. Continuity of the intervals is determined by development of setiferous pores (sockets). Intervals appear continuous (uninterrupted) if setae are absent (Fig. 157) or if setiferous pores are minute (Fig. 155) or slightly (Fig. 158) to moderately (Fig. 159) foveate (i.e. the foveae are shallow, with diameter less than or equal to the width of the interval). If the foveae are deep and broader than the interval and adjacent striae are slightly to moderately distorted loca ly, the interval is 'catenate' (Fig. 160). In members of species with markedly convex intervals (e.g. Nebria schwarzi Van Dyke), the catenations (if present) are quite spectacular, the deeply foveate setiferous pores punctuating short, tuberculate sections of interval, providing a visual affect similar to a 'chain of beads' (Fig. 161).

Setae on ninth elytral interval, form the umbilicate series. These are numerous (Fig. 156), ranging among members of different Nearctic species from eight to 19 in number. There is no apparent separation of the setae into groups (such as anterior or posterior groups noted in some carabids by Jeannel [1925]). Intraspecific variation in number of setae in the series is too great to permit useful interspecific comparisons. The first (most basal) seta of the series in members of N. virescens is unique in position (Fig. 155), relatively remote from the humeral angle. In members of other Nearctic species, the first seta is much closer to the base (Fig. 156).

Wings

Among members of Nearctic Nebria species, relative size and shape of the hind (metathoracic) wings (Figs. 181 - 195) vary markedly between and within species. Wings are either reduced in length and/or width or full-sized (Fig. 182)-- that is, long, with an acute, reflexed apex distal to the stigma (see Fig. 181), broadly membranous posteriorly and with a full venation pattern (see below). Several intermediate stages in a hypothetical transition from macroptery (presence of full-sized wings) to aptery (complete absence of wings) are identified among members of one or another Nearctic species with wings of reduced size. The stages (character states) are: (1) complete miniature (Fig. 183)-- the wing is identical in shape and venation to a full-sized wing but slightly smaller relative to body size of the individual; (2) narrowed/slightly shortened (Fig. 184)-- wing length is slightly reduced (complete reflexed apex is present), the membranous posterior region is reduced, decreasing overall width, but venation is essentially complete; (3) broad/truncate (Fig. 185)-- the wing is unmodified basally but abruptly truncate just distal to the stigma; (4) narrowed/truncate (Fig. 186)-- the wing is truncate as in (3) above, also narrowed as in (2) above, and with venation essentially unmodified; (5) 'brachypterous' (Fig. 187)-- the wing is considerably reduced in length and width (and slightly in venation of the posterior margin), but with the apex pointed and reflexed distal to the stigma; (6) 'micropterous' (Fig. 188)-- the wing is considerably reduced in length, width and venation but with a stigma evident (although displaced proximally in members of some taxa); (7) 'advanced

micropterous' (Fig. 189)-- the wing vestige appears vaguely wing-like, with some venation of the basal area evident; and (8) strap-like (Fig. 190)-- the wing vestige is very short, slender and lobate, with one or two veins still evident but highly distorted.

Interpopulational (i.e. geographical) variation in wing development is exhibited by several species. Intrapopulational variation, however is restricted to a very few taxa; and among members of these taxa, variation is continuous (from one character state to another, with intermediates also found) rather than discrete (di- or polymorphic). Such classic examples of wing dimorphism as those discussed by Lindroth (1945-49, 1963a, 1963b, 1969a and 1969c) and Darlington (1936 and 1943) are not, apparently, repeated in Nearctic Nebria species. See section 3.234 for comments on relationship between wing size and dispersal capability and section 4.41 for discussion of the structural modifications associated with wing reduction.

Folding pattern of the wing in Nebria was discussed by Forbes (1926) and is similar among members of all Nearctic species with full-sized wings. Reduction in wing size is accompanied by divergence from the basic folding pattern through simplification. 'Advanced micropterous' and 'strap-like' wing vestiges have no transverse folds.

The venation pattern basic to all Nearctic Nebria species with fully-winged members is illustrated in Fig. 181. Terms used are those of R. D. Ward (unpublished manuscript) and generally consistent with those of Hamilton(1972). As noted by Chiolino (1970), proper interpretation of venation patterns on other than full-sized wings is difficult or, when wings are markedly reduced, impossible. I have,

therefore, studied venation only of macropterous individuals. Among these, intraspecific variation in presence, continuity and position of various veins, cross-veins and cells is slight but surprisingly frequent, precluding reliable interspecific comparisons in many instances. Shape of the oblongum cell (0) and its relationship to the Cubitus Vein (Cu) varies slightly but consistently among members of different taxa. In members of all Nebria species sampled, the two median cubital (m-cu) cross-veins forming the cell join posteriorly at an acute angle. Interspecific and/or intersubspecific variation in this angle is observed (Figs. 197 - 205), due mainly to the degree to which the junction of the distal m-cu cross-vein with the Cu Vein is displaced proximally (toward the wing base). As a result, the 0 cell is subquadrate (clearly four-sided) (Fig. 197), or approximately triangular (Fig. 198), or intermediate in shape between these extremes (Fig. 182). Additional variation among taxa is seen in position of the junction of m-cu cross-veins. In members of some taxa, the junction is at the Cu Vein (Fig. 197); but in those of other taxa, the junction (and, therefore, the 0 cell itself) is slightly (Fig. 199) to quite (Fig. 200) removed from the Cu Vein and joined to it by a narrow stalk (the fused m-cu cross-veins). Surprising intraspecific variation is seen in the shape and occurrence of the wedge cell (W); but in every instance, most members of the taxon involved demonstrated the typical character state (Fig. 181). Variants seen included: (1) a W cell lacking the empusal-anal cross-vein proximally (Fig. 203), in some members of several taxa; (2) a doubled W cell (Fig. 201), in a few members of N. pallipes; and (3) a W cell open to the margin (Fig. 202),

in some members of a few taxa.

The sclerotized microtrichial field on the marginal cell between the P + Cu_2 and E_1 Veins in members of Trachypachus (Fig. 206), Amphizoa and of at least some dytiscids is lacking from Nebria members.

Venter

If present, punctation is restricted to the mesosternum (laterally only), mesepisternum, metasternum (laterally only) and metepisternum among members of Nearctic species. In members of many species all these sclerites are smooth, while among those of other taxa, range in macrosculpture is from weakly punctulate to moderately (but sparsely) punctate. In general, punctation of the mesepisternum is more strongly developed than that of other sclerites. In contrast to the above, members of several Palaearctic species exhibit relatively coarse punctation of the venter, including also the mesepimeron.

Interspecific variation in relative length of the metasternum (Figs. 207 - 210) is considerable, and intraspecific variation is low enough to make this a relatively useful character. Following Erwin (1970) and Erwin and Ball (1972), a measure of relative length was obtained by comparing longitudinal diameter of the right middle coxa with length of the metasternum (measured on a line centered on the right middle coxa center) (Fig. 207). Length of the metasternum was recorded as (1) clearly greater than (Fig. 208), or (2) approximately equal to (Fig. 209), or (3) clearly less than (Fig. 210) the diameter of the middle coxa. Metasterna in members of a few taxa are intermediate between these arbitrary character states and were so noted. Because relative metasternal length appears correlated with hind wing

length (refer to discussion in section 4.41; see also Erwin, 1970 and Erwin and Ball, 1972), taxa whose members display intermediate conditions in this character are expected; and their existence does not reduce the value of the character. Variation is also evident in extent of the margination of the anterior metasternal intercoxal process (i.e. between the middle coxa posteriorly) (Figs. 211 - 214). Margination is present basilaterally only (Fig. 211) or either faintly (Fig. 212) or distinctly (Fig. 213) present across the midline also (that is, complete).

3.215 Legs

Among members of Nearctic Nebria species, legs are quite similar in general form, especially if compared with those of other carabids. Interspecific variation is conspicuous, however, in relative overall length and proportion. The legs of members of a few taxa are relatively short and robust (Fig. 217) or very long and slender (Fig. 218), while members of most taxa have moderately long and slender legs (Fig. 219). Males of all taxa sampled have relatively longer legs than conspecific females.

Coxae

The front (Fig. 220) and middle (Fig. 221) coxae are globose, the former asetose. The middle coxa is bisetose in all members of most species, with one anteriomedial and one anteriolateral seta apically. Some members of N. metallica Fischer v. Waldheim, N. schwarzi schwarzi Van Dyke and N. spatulata Van Dyke have two anteromedial setae (Fig. 222); and in one of a few individuals of some other taxa two of

the medial and/or lateral setae were found. The hind coxa (Figs. 224 - 229) is flattened, transverse and laterally narrowed. The lateral portion, or "wing" (Lindroth, 1961), is divided by the transverse section of the coxal ridge (an extension of the lateral posteroventral margin of the expanded medial portion of the coxa). Lindroth noted that the posterior portion of the "wing" is flat (horizontal) in members of Pelophila species (Fig. 223) but vertical and obscured in ventral aspect by the flat and more ventrad anterior portion of the "wing" (Fig. 224) among Nebria members. However, some interspecific variation in the plane of the posterior portion is apparent among Nebria. In members of N. virescens (Fig. 225), the posterior portion is easily visible ventrally and its plane is clearly less than vertical (about 45 degrees from vertical). In members of all other Nebria sampled, the posterior portion is less visible (Fig. 226) or totally hidden (Fig. 224) and more nearly or completely vertical. Setae on the hind coxa are confined to the broad medial portion. Members of some species have a single basal seta (Fig. 225), but most members of most species have two or more (Fig. 224) (to a maximum of seven in some members of N.mannerheimii Fischer v. Waldheim). Inter- and intrapopulational variation in this character is considerable in some taxa. A single apical seta (Fig. 225) is found in all members of all species except N. schwarzi, in which almost all members have more than one seta (Figs. 226 - 227) (to a maximum of six).

Trochanters and femora

In members of all Nearctic species, the front (Fig. 230) and middle (Fig. 231) trochanters are roughly wedge-shaped, each with a

single apicoventral seta. The hind trochanter (Fig. 232) is lobate, weakly and roundly pointed apically and asetose. Femora are similar in members of all Nebria species sampled, the front femur (Fig. 233) slightly swollen dorsoventrally near its middle, the middle (Fig. 234) and hind (Fig. 235) femora approximately cylindrical, tubular.

Tibiae

In all nebriines studied, the anterior tibia (Fig. 236) has a simple, sulcate antennal cleaner ("Grade A" of Hlavac, 1971) occupying the distal 0.5 to 0.33 of its ventral surface. Insertion of both tibial spurs is apical; and although the apical tibial margin is moderately oblique, with the lateral (i.e. structurally posterior, or euposterior) margin slightly retracted proximad, the arrangement of spurs is essentially isochaetous (Jeannel, 1941; see also Bell, 1964 and 1967; Hlavac, 1971).

Interspecific variation is evident among members of Nearctic species in the topography and vestiture of the dorsal surface of the middle tibia (Figs. 237 - 240). The dorsal face is uniformly flat or slightly convex (Fig. 237) in all members of N. appalachia and N. pallipes and in some members of a few other taxa. In members of some other taxa, the face is moderately concave in its distal half (but not apically) (Fig. 238) ; but in those of most taxa, the face is broadly sulcate in its distal half, including the apex, as in N. virescens (Fig. 240), or not (Fig. 239). Slight intraspecific variation in linear extent of the concavity or sulcus is evident. The distal 0.33 to 0.5 of the dorsal face also bears numerous setae (Figs. 237 - 240) between the two dorsal longitudinal setal rows and situated in the

sulcus or concavity (if present). Together, the setae form a more or less dense brush, probably serving as a simple cleaning organ. The brush is well developed except in members of N. appalachia and N. pallipes.

The hind tibia is unmodified among Nearctic Nebria; but in members of the Palaearctic N. chalceola Bates and related taxa, the dorsal face of this tibia is also sulcate.

Tarsi

Character of the tarsi have been used extensively in Nebria classification (Bänninger, 1925; Jeannel, 1937), especially in recognition of subgenera (which are not considered in this presentation). In the Nearctic fauna, however, interspecific variation in tarsal characters is generally slight and/or restricted to peculiarities in members of a few taxa.

The basal three tarsomeres (i.e. first through third tarsomeres) of the front tarsus are relatively broad (laterally expanded) (Fig. 242) in males of all species. With only two exceptions, the tarsomeres of the middle and hind legs in males and of all legs in females are slender. In N. ingens (Fig. 245) and some populations of N. ovipennis (Figs. 246a,246b); all tarsomeres of the front legs in males are relatively broad; and tarsomeres of the male middle and hind legs and all legs in females are also (but slightly less) broadened (Fig. 245) compared with those of members of other species. An additional feature unique to members of N. ingens is the excavation (concavity) of the ventral surfaces of the tarsomeres (Fig. 245), especially prominent on those of the middle and hind legs. These surfaces are slightly

convex or flat in members of all other taxa.

Again, with members of N. ingens and some populations of N. ovipennis as exceptions, males of all Nearctic species have pads of adhesive setae (Figs. 241 - 243) on the ventral surfaces of the first through third tarsomeres on the front legs. In some members of N. ovipennis (Figs. 243a,243b), the pads on all three tarsomeres are slightly or moderately reduced in area (number of hairs). In members of N. ingens (Fig. 242), the pad is absent from the third tarsomere, greatly and moderately reduced on the second and first tarsomeres, respectively. The other tarsi in males and all tarsi in females are without ventral pads of setae in all species.

The sparse dorsal pubescence on tarsi in members of numerous Palaearctic species of Nebria is lacking from members of Nearctic taxa, except for a few members of N. diversa LeConte. Tarsomeres of the hind tarsus in members of N. superna Andrewes and a few other Palaearctic species are distinctly compressed basally; but these are quite cylindrical in members of all Nearctic species.

Interspecific variation in shape of the ventro-apical margin and length and position of associated setae on fourth tarsomere of the hind tarsus is quite conspicuous. In members of N. virescens (Fig. 249), the ventro-apical margin is truncate and the ventro-apical setae are approximately symmetrical in length and position. In members of all other Nearctic species, the margin is asymmetrical, either weakly (Fig. 250) or more strongly (Figs. 251 - 252) lobate ventro-laterally (i.e. anatomically anteriorly, or euanteriorly). Associated with development of this projected ventral lobe is increased asymmetry in

length, position and number of the ventro-apical setae (Figs. 249 - 252).

Tarsal claws are similar in members of all species-- simple, evenly arcuate and equal in length. Slight interspecific variation in length and thickness of the claws was observed but not analyzed.

3.216 Abdomen

Dorsum

The dorsum of the abdomen, including tergal and pleural regions, is completely obscured by the elytra and is, therefore, unavailable for study except after removal or displacement of the elytra and hind wings. A brief survey of dorsal structures among members of selected taxa revealed few differences. Detailed comparative study of dorsal abdominal structure was, therefore, deleted except for those structures associated with the genitalia and/or ovipositor (see below).

Venter

The abdominal sterna (Figs. 253 - 259) are, in general, without punctation or other macrosculpture. However, the first visible sternum (divided medially by the hind coxae into two small, lateral triangular sclerites), although smooth in all members of some species and some members of others, is faintly punctate or punctulate in all or some members of most Nearctic species. All sterna bear a pair of broad lateral pits (Fig. 253). In members of most taxa, the pits are most markedly developed on the first visible sternum, least so on the second. Some interspecific variation in depth and distinctiveness of the pits was observed.

The sterna are carinate dorsolaterally, the basal five (visible) sterna broadly deflected dorsomedially from the carina, the last visible sternum (that is, the sixth, or "anal" sternum) narrowly deflected basally and not at all apically (Fig. 254). The narrowed portion of the deflected area of the last sternum apposes the subapical sinuation of the elytron. Refer to the section on elytral structure above for brief comment on the elytral locking mechanism involving the sterna.

The second visible sternum is glabrous in members of most taxa; but in N. hudsonica and N. gouleti n. sp. (Fig. 255), all but a few members have a patch of setae medially between the hind coxae. In some members of N. ovipennis and related species, either a single pair of paramedial setae or a small number of scattered setae is present in the same region on this and (in fewer individuals) also on the third visible sternum. On the third, fourth and fifth visible sterna, a single pair of posterior paramedial ("ambulatory") setae (Fig. 257) is found in members of some species; but in those of most taxa, two or more (to a maximum of eight) pairs of these setae are present (Figs. 255, 258). One or more (to a maximum of 15) pairs of anterior paralateral setae are found in members of some species (Fig. 258); but these are absent from members of most taxa (Fig. 253). On the "anal" (sixth visible) sternum, two or more pairs of posterior paramedial setae (known on this sternum as the "anal setae") are present in both males and females of some species (Figs. 258 - 259). In most species, however, a single pair is present in males, two or more pair in females (Figs. 255 - 256). The usefulness of this character is somewhat

diminished, however, by the relatively frequent occurrence of individuals apparently atypical of their respective taxa in the character.

3.217 Male genitalia

Lindroth (1961a:61) noted that "the organization of the ♂ genitalia [in Nebria] is so simple, with no chitinized structures in the internal sac of [the] penis, that it is less useful than in most other genera". In spite of this overall structural simplicity and similarity, differences in shapes of one or more genitalic structures are recognized between members of almost any two taxa (i.e. species and/or subspecies). Intraspecific and intrapopulational variation in form and structure are slight but significant enough to require relatively large samples to insure valid comparisons among taxa. Differences among males of different species groups are relatively great; and, in most instances, male genitalic characters are at least as valuable in demonstrating relationship among species as in distinguishing them.

Male gentalia (Figs. 260 - 298) include the following parts (Fig. 60): the median lobe, comprised of a basal bulb, shaft, apex, and eversible internal sac which bears the gonopore; two parameres ("lateral lobes" of Sharp and Muir, 1912), each lateral to the median lobe and attached to the ventrolateral corner of the basal bulb of the latter; a 'dorsobasal sclerite'; and the modified sclerites of segment 9. Structural differences in each of these parts have been found among Nearctic Nebria. Orientation of the genitalia in the following discussion is in copulatory position (Fig. 261). In fact, however, this position represents a rotation of 180 degrees to the left for the median lobe and parameres relative to the primitive coleopteran

orientation. In repose, these structures lie on the (primitive) left side (rotated 90 degrees left) and rotate an additional 90 degrees left on eversion for copulation (see Jeannel, 1926).

Median lobe

Among all nebriines studied, the median lobe is complete (closed) dorsally. In members of all but one Nearctic species, the basal bulb is large, roughly rectangular in lateral aspect, with the basal orifice broadly open (occupying the entire base) (Fig. 264). Males of N. virescens, however, have the bulb slightly smaller, rounded dorsobasally, and with the basal orifice small and restricted to the ventral portion of the base (Fig. 262). In males of N. brevicollis (Fabricius) (Fig. 263) and several other Palaearctic species, the bulb is large and broadly open basally, but more triangular, wedge-shaped, in lateral aspect.

There are interspecific differences in several characters of the shaft of the median lobe. One such character is the angle to which the axis of the shaft is bent (Fig. 260). In males of all Nebria species sampled, the axis is bent at least 90 degrees (Fig. 264), in males of some species as much as 140 degrees. To simplify comparisons and further discussion, the shaft is divided into two portions (Fig. 260): (1) a basal portion, here called the 'mid-shaft', delimited by the basal bulb basally and the basal margin of the apical orifice apically; and (2) an apical portion, here called the 'preapical-shaft', delimited by the basal and apical borders of the apical orifice. Among males of different species, the 'mid-shaft' ranges in thickness (lateral aspect) from very slender (Fig. 263) to very broad (Fig. 278). Interspecific

variation in taper of the 'mid-shaft' is considerable. In males of different taxa it is cylindrical (i.e. of approximately equal width throughout) (Fig. 264) or moderately to markedly tapered either apically (Figs. 263 - 273) or basally (Figs. 281 - 285). Cross-sectional shape of the 'mid-shaft' also differs among species. In males of most species, it is weakly to moderately compressed (Fig. 268); but in members of a few others, it is either markedly compressed (Fig. 275) or circular (Fig. 264). In males of N. ovipennis (Fig. 280) and related species, the right lateral wall of the 'mid-shaft' is locally invaginated to form a small pouch (directed basad and open toward the apex) (see also Erwin and Ball, 1972). The pouch is unique to males of these few species but varies among them in depth and precise configuration.

The 'preapical-shaft' bears the apical orifice, through which the internal sac is everted during copulation. In part, shape characteristics of this part of the shaft are simply a continuation of those of the 'mid-shaft' (e.g. thickness and taper). Independent characters of the 'preapical-shaft' include its length and shape (in lateral, dorsal and apical aspects) and the resulting plane of the apical orifice. All these characters vary considerably interspecifically. In members of some taxa, the 'preapical-shaft' (lateral aspect) is long, with its dorsal margin (outer curvature), and therefore plane of the apical orifice, longitudinal (Fig. 263). In males of other taxa, it is shorter (Figs. 265 - 285), with its dorsal margin weakly (Fig. 265) to moderately (Fig. 275) oblique and apically convergent with the ventral margin (inner curvature). The plane of the apical orifice in

these adults faces a ventrodorsally rather than directly dorsad. The extreme example of the short and oblique condition is seen in males of Colorado populations of N. trifaria trifaria LeConte (Fig. 283). Both shortness and obliqueness are, in males of most taxa, associated with a basally tapered (i.e. apically expanded) 'mid-shaft'. Among males of different taxa, shape of the ventral margin ranges from smoothly arcuate (Fig. 264) to weakly but abruptly deflected ventrally (Fig. 267) or weakly (Fig. 265) to strongly recurved (Fig. 274). Comparisons of the shape of dorsal margin of the 'preapical-shaft' and plane of the apical orifice are complicated by the fact that interspecific differences in symmetry (i.e. shape in apical (euposterior) and dorsal aspects) are also evident. In males of a few taxa (e.g. N. gouleti n. sp., Fig. 286), the dorsal and ventral margins of the 'preapical-shaft' are bilaterally symmetrical (in apical aspect); but in males of most taxa, the shaft is moderately (Fig. 272) to markedly (Fig. 279) oblique (or twisted) and depressed. The plane of the apical orifice, independent of its orientation in lateral aspect, faces dorsad and right laterad in these beetles rather than directly dorsad. In males of some taxa, the 'preapical-shaft' is, in dorsal aspect, symmetrical and narrowly (Fig. 286) or more broadly (Fig. 275) tapered, or asymmetrically tapered toward the right (Fig. 287) or left (Fig. 285). Males of other taxa have the lateral margins approximately parallel (Fig. 267) or weakly divergent apically (Fig. 262).

The apex of the median lobe, here defined as that part distal to the apical margin of the apical orifice, exhibits great interspecific

and some interpopulational variation in shape. Differences in shape of the apex are, in many instances, alone sufficient for distinguishing members of different taxa. In dorsal aspect, range in shape among males of Nearctic species is from narrow and sharply pointed apically (Fig. 286) to broad, spade-like and rounded apically (Fig. 262), with numerous intermediate shapes also seen (e.g. Figs. 267, 275). Differences in symmetry are also evident in dorsal aspect among males of different taxa, ranging from symmetrical (Fig. 286) to deflected right (Fig. 268) or left (Fig. 284). In each instance, symmetry of the apex reflects symmetry trends initiated in the 'preapical-shaft' (see above). In apical (i.e. euposterior) aspect, the apex is depressed (flattened) and its apical margin horizontal in males of N. virescens (Fig. 2 ? In males of all other Nearctic taxa, the apex is compressed and its apical margin either vertical (Fig. 286) or moderately (Fig. 281) to strongly (Fig. 275) oblique (rotated) left. In lateral aspect, the apex ranges in length from very short (Fig. 283) to elongate (Fig. 282), with examples of both extremes among males of different subspecies of N. trifaria LeConte. Differences in shape and direction of the apex in lateral aspect are also striking. Range in shape is from narrow and sharply pointed (Fig. 286) to broadly rounded (Fig. 284) or hooked (Fig. 278). In males of most taxa, the apex is a straight or smoothly arcuate extension of the shaft (Fig. 286); but, in males of some taxa, it is deflected dorsally (Fig. 282) or ventrally (Fig. 267) from the arc of the shaft or faintly recurved at its base (Fig. 266).

As noted above, detailed comparative study of the form and

structure of the internal sac was deferred, pending development of an effective technique for full eversion and inflation of the sac. [Such a technique, developed by T. Gruenwald (Adelphi, Maryland), is now available (personal communication) and will be used in subsequent studies on Nebriini]. However, a brief survey of the internal sac among members of the Nearctic fauna indicates that marked interspecific differences exist in its shape (including length, symmetry and the number and arrangement of lobes). Figs. 288 and 289 present examples of two different sacs. In all males, the sac is membranous, without teeth, spines, hooks or plates seen in members of many other carabid genera. Microtrichial fields are evident, however; and while their position and number have not yet been studied, interspecific differences in these potential characters are probable.

Parameres

The parameres of males of all nebriine taxa sampled are asetose. Nebria virescens males have the parameres approximately symmetrical in length and shape (Figs. 290 - 291); but in males of all other Nearctic taxa, the parameres are asymmetrical (i.e. differ in both characters) (Fig. 294), with the right paramere longer than the left. Interspecific and interpopulational differences in shape and relative lengths of each paramere are evident, at least in some taxa. The left paramere is spatulate (short, broad, apically blunted) (Fig. 293) in males of most species, short and narrow (Fig. 291A) in males of a few, and broad, relatively elongate and acuminate (Fig. 295) in males of other taxa. The right paramere is very long, slender and arcuate (similar in arc to the median lobe) (Fig. 292) in males of all taxa

except N. virescens, in males of which it is short, spatulate and similar to the left paramere. Of some interest (but unknown homology and significance) is a vague to heavily sclerotized strap-like sclerite in the medial membrane of the right paramere in males of certain species (e.g. N. schwarzi) (Fig. 296). The sclerite, here termed the 'right medial parameric sclerite', articulates with neither the paramere nor the median lobe and appears to be simply a strengthened region of the medial membrane.

'Dorsobasal sclerite'

I use the term 'dorsobasal sclerite' to refer to structures (Figs. 262 - 265) located dorsobasally and associated with the basal bulb of the median lobe in members of Nearctic Nebria. There are considerable differences in the shape and position of this 'sclerite' among taxa and great variation in degree of its sclerotization within taxa. In males of N. virescens, it is well-sclerotized and positioned dorsobasally as a mid-sagittal crest or fin (Fig. 262). In males of all other Nearctic Nebria, the 'sclerite' (if homologous with the crest described above) forms a thin, flat collar around the dorsal and lateral surfaces of the basal bulb (Fig. 260). In some males of many taxa, it is very weakly sclerotized and difficult to see. The membrane bearing the 'sclerite' is attached to the margin of the basal orifice of the median lobe; and in some specimens in which the genitalia have been forcibly everted, the sclerite is seen in extended position, basal to the median lobe itself (Fig. 263).

The homology of this 'sclerite' is uncertain; but it may represent a remnant of the "basal piece" (pars basalis) seen in some Adephaga and in many other Coleoptera. The basal piece is usually described as

absent or membranous among Carabidae (Ball, 1960).

Sclerites of ninth abdominal segment

The sclerotized remains of the ninth abdominal segment (the "genital segment", or "urite X" of Jeannel, 1941) in nebriines comprise the so-called "ring sclerite" and associated structures. Enclosed within the ring are the other genitalic structures described above. Shape of the ring differs slightly among members of nebriine taxa examined, but comparisons using shape characters appear to be useful only at the generic and subgeneric levels. Among Nearctic Nebria, structure of the ring is as follows (Figs. 297 - 298). The posterodorsal portion of the ring corresponds to the ninth tergum (with the anal opening immediately ventral). The tergum is narrow and entire (not divided medially), with the apical margin weakly convex and minutely notched near the left margin (for the opening of the left pygidial defense gland). The remainder of the sclerotized ring loops anteroventrally into the abdominal cavity from the basolateral corners of the ninth tergum. The homology of this portion of the ring is uncertain; but Edwards (1951) identified this structure in Amphizoa specimens as the ventrally fused ninth pleura. Distinctly separate apodemes are present on the tergum in Amphizoa specimens (Fig. 299), suggesting that the loop is not formed from distally-fused tergal apodemes. Articulating ventrally with the right basolateral corner of the ninth tergum is a triangular, partially-sclerotized pouch (Fig. 298) which serves as a sheath for the apex of the median lobe in repose. Homology of this structure is also uncertain; but Edwards identified a similar but more medial and symmetrical structure in

Amphizoa specimens (Fig. 299) as the ninth sternum.

3.218 Female genitalia

To date, the only comparative study of female genitalia among nebriines has been that of Erwin and Ball (1972) on the sclerites of the bursa copulatrix in members of the trifaria group (in the sense of these authors) of Nebria. My own review of female genitalic structure among nebriines and other carabids has revealed differences among various tribes, genera, species and populations in one or more characters. In the present study, 61 female genitalic characters were recognized and used in comparing nebriine taxa, 23 of these represented by a single characters state among members of the Nearctic Nebria fauna. Many of these characters have been extremely useful in reconstructing phylogenetic relationships among taxa (see section 4.1 below), thoroughly justifying the time and effort required in dissection and preparation of specimens prior to their study.

The female genitalia (Figs. 300 - 353) include the following parts: ovipositor (in a broad sense), comprised of the modified eighth sternum, proctiger, two paraprocts, two valvifers, paired remnants of the tenth sternum and paired coxostyli; bursa copulatrix; spermatheca; and spermathecal duct. Terms used for parts of the ovipositor approximate those of Tanner (1927). In a recent comprehensive review of the terminalia of terrestrial Adephaga (including an extensive study of musculature), Bils (1976) has suggested radically different segmental relationships of these parts. I choose to follow Tanner here to facilitate possible intergroup comparisons through the existing

literature on other carabids but mention Bils' equivalent terms for each part as well.

Eighth sternum

The eighth abdominal sternum ("coxosternum VIII" of Bils)(Figs. 300 - 304) is split medially into two halves, or hemisterna. These hemisterna lack pubescence; but in all nebriine females sampled, a fringe of setae traverses the medial one-third of the apical margin of each (Fig. 301). Interspecific variation is seen in both density and length of the fringe setae (Figs. 300 - 304). Among Nearctic Nebria females, the basal apodeme of each hemisternum is moderately long and wide (Fig. 301) (at least basally), with its apex deeply emarginate (Fig. 302), forming two separate heads. In females of a few taxa, the two heads are of equal length (Fig. 302); but in those of most taxa, the lateral head is slightly (Fig. 303) to much (Fig. 304) shorter than the medial head, with an extreme example seen in females of N. virescens (Fig. 300). The apodeme is flat and uniformly thin in all nebriines, without a thickened rod-like longitudinal reinforcement characteristic of Hydradephaga and females of Trachypachus (Fig. 304A) and a few other carabid groups.

Proctiger

The proctiger ("fused terga IX and X", Bils; see his "Abb. 20") (Figs. 305 - 306) is heavily sclerotized (at least basally) and glabrous in females of all Nearctic Nebria. It is hemispheric, apically convex and completely sclerotized (Fig. 306) in females of all taxa except N. virescens, females of which have the apical portion membranous (Fig. 305).

I see no reason to conclude that terga IX and X (sensu Bils) are fused in nebriines as he suggests, because structures very similar (in location and musculature) to that labelled "T.IX" in his "Abb. 6" (p. 166) for Trachypachus holmbergi Mannerheim are present also in nebriines (i.e. as the paraprocts of Tanner, 1927). The proctiger would, therefore, be tergum X alone.

Paraprocts

The paired paraprocts (Figs. 305 - 308) (equivalent to the remnants of "tergum IX" in Trachypachus specimens ["T.IX" in "Abb. 6", p. 166] or to the dorsolateral part of the "lateral portion of tergum IX" in N. brevicollis ["LT.IX" in "Abb. 20", p. 172] of Bils) are heavily sclerotized and asetose in females of all taxa. They are narrow, triangular wedges positioned between the proctiger and the valvifers and narrowly (Fig. 307) to broadly (Fig. 308) continuous (fused) with the latter basally. Interspecific variation in thickness of the connection is evident and useful in relating taxa.

Valvifers

Interspecific differences are evident in several characters of the valvifers ("lateral portion of tergum IX" [possibly fused with the gonangulum] of Bils) among Nearctic Nebria (Figs. 307 - 311). Each valvifer is fused with the paraproct dorsobasally and articulates with the coxostylus mediobasally. Overall valvifer shape is similar in females of all taxa; but differences in the shapes and continuity of its sclerotized and membranous areas are apparent. In females of a majority of taxa, the sclerotized area is greatly reduced and confined to a narrow basal strip, expanded only laterally in association with the base of the apodeme (Fig. 309). In females of the remaining taxa,

an additional sclerotized area, separated from the basal strip by a membranous region, is located apicomedially (Fig. 308). It is weakly sclerotized and bears a few short, scattered setae in members of most of these taxa (Fig. 307). In females of N. virescens, the area is more heavily sclerotized, with the setae longer and more abundant (Fig. 308). All females of N. lyelli and some members of a few other taxa have the medial area weakly sclerotized and asetose (Fig. 310). The basal apodeme is broad and moderately long (Fig. 308) in most females of most species, but short (Fig. 311) in all females of N. gregaria Fischer v. Waldheim and N. arkansana oowah n. ssp. and some females of a few other taxa. It is positioned laterally in all nebriines.

Tenth sternum

The tenth sternum is represented in nebriines by a pair of small, narrow, pointed lobes (the "rami" or"genital appendages of segment VIII" of Bils) positioned medial to the coxostyli and ventral to the gonopore (Fig. 312). In females of most Nearctic Nebria, the lobes are fused to the basimedial angles of the coxostyli (Fig. 312); but in females of a few taxa, they are basally separate from the coxostyli (Fig. 313). I have examined the medial structure described by Edwards (1951) as the "tenth sternite" in Amphizoa specimens (Fig. 314) and find its position and articulation quite similar to that of the lobes described above in nebriines. I suggest that these parts are homologous, but cannot extend the suggested homology to particular structures in other groups or in the "generalized insect".

Coxostyli

In all nebriine females sampled, the gonocoxite ("cranial portion of the gonocoxite" of Bils) and the gonostylus ("caudal portion of the gonocoxite" of Bils) are fused to form the coxostylus ("gonocoxite" or "genital appendage of segment IX" of Bils) (Figs. 315 - 321). Fusion is, however, incomplete and restricted to the medial and ventromedial surfaces (Fig. 315). All members of N. darlingtoni n. sp. and N. mannerheimii have the medial face of each coxostylus deeply notched (from the dorsal margin) (Fig. 316) in the area of fusion, thus reducing the apparent extent of connection between the stylus and coxite significantly.

The stylar region of the coxostylus is unilobate, unsegmented, with no secondary or attached lobes or "teeth" (as are seen among cicindelines). In ventral aspect, it is broad basally, markedly arcuate and apically pointed and directed laterad (Fig. 315) in N. virescens females. It is narrower basally, less arcuate and apically pointed and more posterior in direction in females of all other Nearctic taxa (Fig. 316). In lateral aspect, the stylus is slightly to moderately excavate (concave) dorsolaterally and deflected ventrally (Fig. 316) in females of all species except N. virescens, in females of which it is straight (Fig. 315). Interspecific differences in length of the stylus are slight, with stylar length moderate (Fig. 316) in members of most species, longer (Fig. 317) or shorter (Fig. 315) in females of a few. A single, oval subapical pore is present on the ventromedial face (Fig. 315) and bears two long setae (tightly pressed together in most individuals and, therefore, apparent as a single seta).

Associated with the dorsomedial margin of the stylus in all Nearctic females is a row of setae. In females of N. virescens (Fig. 315), the row is composed of three or four medium-length, very stout setae and is positioned diagonally across the medial portion of the dorsal surface (directed basilaterally from the medial margin). In females of all other taxa, the setae are medium-length but slender, and, except in females of N. gebleri Dejean (Fig. 318), the row is positioned along the dorsomedial margin itself (Fig. 317). Both inter- and intraspecific variation in the number of these setae are evident.

The coxite region of the coxostylus is similar in general shape among females of all Nearctic species, with only slight interspecific differences in relative length evident. The dorsal surface of the coxite is open to accommodate muscles inserted internally. The lateral surface (Fig. 316) is membranous apically (basal to the stylus). In ventral aspect, the lateral membranous region is extended medially to a diagonal line (directed apicomedially from the lateral margin to the fused base of the stylus). A row of setae is associated with this line, positioned on the membrane (Fig. 319) on the margin of the sclerotized area (Fig. 316), or in some combination of both positions. In N. virescens Horn females (Fig. 315), the row is composed of five or six long, very stout setae positioned on the margin of the medial sclerotized area. In females of all other taxa, the setae are shorter, more slender, and varied in their position relative to the diagonal margin (Figs. 316 - 320).

The middle portion of the medial surface of the coxostylus bears numerous short, scattered setae in members of most species (Fig. 316), but is more sparsely (Fig. 321) or densely (Fig. 315) setose in

members of a few. Setae are entirely absent (Fig. 320) from females of some species (e.g. N. nivalis) or present, but very short and restricted to the apical half of the medial surface (Fig. 319), in those of a few other species. Dorsal, lateral and ventral surfaces of the coxostylus are asetose, except in N. virescens females, which have the setal field of the medial surface continued on the medial edge of the ventral surface (Fig. 315).

Bursa copulatrix

The general form of the bursa copulatrix in females of the trifaria group (sensu Ball and Erwin, 1972) of Nebria was illustrated by these authors with more detailed drawings of certain sclerites found on the bursa. This pioneer effort in the study of internal female genitalic structure in nebriines prompted me to include a more comprehensive survey of these structures in my own project as both an aid in interpreting their findings and a potential source of additional characters of use in studying members of the Nearctic fauna. The structures examined differed in numerous characters as discussed below.

I found few if any differences in shape or other characters among conspecifc specimens that could be attributed to manner of preservation of the specimens (e.g. as dried specimens, or specimens killed and/or preserved in 70% ethyl alcohol, Bouin's solution, or Weaver's Fixative). I conclude that preservation technique is not of prime importance for the study of bursa and associated structures (see comments of Erwin and Ball, 1972:78). However, interpretation of shape and orientation of these structures is extremely difficult if a mixture of specimens with genitalia in various states of extension or retraction is studied. I

obtained best results (i.e. simplest comparisons) by restricting my dissections of internal structures to specimens in which the genitalia were fully retracted. An additional problem was encountered as a result of heating the specimens during relaxation and/or treatment with potassium hydroxide (see methods, section 2.22 above). If specimens are heated too rapidly, the genitalia of some are explosively everted. In such instances, the bursa may become completely everted (turned inside out), presenting a confounding arrangement of parts and completely confusing any attempts at their proper orientation. Ali's (1967) description of the internal structures of the female genitalia in Notiophilus (? sp.) fits the arrangement of parts in such an 'exploded' specimen perfectly; and, in fact, I suggest that the peculiar arrangement of parts he described is an artifact of preparation [because all Notiophilus specimens I studied were very similar in structure to nebriines and not as described by Ali]. Specimens taken directly from fluid preservation (especially alcohols) must be slowly heated.

For convenience (and, in part, structurally) the bursa copulatrix (Figs. 322 - 344) is divided into a posterior 'vestibular chamber' and an anterior (or dorsal) 'spermathecal chamber' (refer to Figs. 322 - 323 for an illustration of terms used in relation to bursal and associated structures). The 'vestibulat chamber' is open posteriorly through the gonopore, receives the common oviduct ventrally and is continuous with the 'spermathecal chamber' anterodorsally but partitioned from the latter at a dorsal flexure of the bursa (see below). The 'spermathecal chamber' is dorsal and, in females of most

taxa, anterior to the 'vestibular chamber' and bears the opening of the spermathecal duct (see below). Interspecific differences are evident in the main longitudinal axis of the bursa (i.e. a line drawn from the gonopore to the apex of the 'spermathecal chamber' along the midline) in lateral aspect. In N. virescens females, the axis is weakly deflected dorsally (Fig. 324). In females of other taxa, the axis is more strongly deflected dorsally (Figs. 325-326), recurved posterodorsally (Fig. 327), or loosely (Fig. 335) or tightly (Fig. 329) sigmoidal. Interspecific differences in shape of the 'spermathecal chamber' tend to obscure axis direction in some instances.

The confluence of the common oviduct with the 'vestibular chamber' is ventral and near the gonopore (Fig. 323) in all Nearctic females. The chamber is, therefore, very short ventrally but longer dorsally and laterally. In dorsal aspect, it is very broad, symmetrical and bell-shaped. The anterolateral angles of the chamber are weakly (Fig. 327) to markedly (Fig. 330) flared or recurved posteriorly (Fig. 336) among females of different taxa.

Shape of the 'spermathecal chamber' is quite complex and difficult to describe, due especially to variation in its orientation accompanying differences in direction of the longitudinal bursal axis. In dorsal aspect, it is distinctly narrower than the 'vestibular chamber' (Fig. 334) in females of all species except N. virescens (Fig. 324) and N. paradisi (Fig. 340), in females of which it is very slightly narrower than or equal in width to (respectively) the 'vestibular chamber'. Again in dorsal aspect (ventral aspect if the bursal axis is recurved posteriorly; apical aspect if the axis is deflected directly dorsad), the chamber is symmetrical (Fig. 328) in females of most taxa,

but apically deflected right (Fig. 327) or left (Fig. 326) in females of a few; and it is extremely varied in shape -- broadly lobate (Figs. 324a,324b), spatulate (Fig. 335), quadrate (Figs. 326 - 327), longitudinally (Fig. 341) or transversely (Fig. 329) ovoid, or some variant of one of these forms. In lateral aspect, the chamber is varied in length, from short (Fig. 327) to long (Fig. 324), but moderate in length (Fig. 334) in females of most taxa. Shape in lateral aspect is also varied among females of different taxa -- thin, longitudinally lobate (Fig. 324), thin, fusiform (Fig. 335), thick, globose (Fig. 328) or thick and apically narrowed and straight (Fig. 338) or anteriorly (Fig. 330) or posteriorly (Fig. 325) recurved. Slight intraspecific variation in different aspects of shape of the chamber is evident in most species, but considerably less than interspecific variation in the same characters.

There appear to be no dorsal or ventral chambers of the bursa separate from its two-chambered main axis among females of Nearctic taxa. The 'spermathecal chamber' itself, however, has one or more accessory lobes in members of certain taxa. Nebria desolata Kavanaugh females (Fig. 342) have a pair of thick, elongate accessory lobes on the dorsal surface of the chamber. Females of N. kincaidi and related taxa (but not N. carri n. sp.) have a thin, boat-like lobe (Fig. 335) (varied in length among members of these taxa) on the posterior surface of the chamber, which partially sheaths the base of the spermathecal duct and its insertion. Nebria paradisi Darlington is unique among Nearctic taxa in that its females have a small accessory lobe on the anteroventral surface of the chamber (Fig. 340). As noted below, the

basal portion of the spermathecal duct is (apparently) thickened abruptly (Figs. 327, 333) in females of a few taxa. In such instances, the swollen duct mimics an accessory lobe on the chamber (which it may actually be).

The shapes of certain parts of the bursa are rigidly maintained by the presence of sclerites (or at least more heavily sclerotized areas) or a reinforcement rod in females of almost all Nebria taxa. Sclerites are restricted to three bursal regions among members of Nearctic taxa. In all N. paradisi Darlington females examined, a pair of broad, flat, weakly sclerotized paramedial plates were located in the dorsal wall of the 'vestibular chamber' (Fig. 340). Neither these nor any other sclerite are located in this chamber in females of other taxa. A second location for bursal sclerites is in the posterior or dorsal wall (depending on bursal axis orientation) of the 'spermathecal chamber'. If present, a sclerite is, in females of most taxa, closely associated with the insertion of the spermathecal duct (Fig. 338) (remotely associated [Fig. 342] in members of a few taxa). Females of many taxa (including all those in which members have the duct inserted ventral) have no sclerite in this wall of the chamber (Fig. 325). In females of almost all Nearctic taxa, a distinct, opaque reinforcement rod is present (Fig. 323) in the ventral wall of the 'spermathecal chamber', extended posteriorly into the 'vestibular chamber' to the confluence of the latter with the common oviduct, then reversed anteriorly in the dorsal wall of the oviduct (see below). In females of N. obliqua and related species, the rod is weakly developed and restricted to the 'vestibular chamber' of the bursa (Fig. 343). It is further extended

anterodorsally (Fig. 325) in the ventral wall of the 'spermathecal chamber' in females of some taxa (especially those in which members have the spermathecal duct inserted ventrally) and/or apically broadened and plate-like (Figs. 326, 344). It is non-sclerotized (possibly composed of resilin) in all nebriines examined. The third location for bursal sclerites, however, is in association with the apex of this rod (Figs. 326, 344) (i.e. in the ventral, or anterior wall of the 'spermathecal chamber'). If present, the sclerite is also associated with the insertion of the spermathecal duct (Fig. 344), except as present in females of N. pallipes, N. gebleri rathvoni LeConte, or N. gebleri strawberriensis n. ssp., which have the duct insertion on the posterior wall of the chamber.

Interspecific and interpopulational differences in the shape, size and position of various bursal sclerites are often quite striking. Descriptions of these sclerites are presented below, with descriptions of the taxa (section 3.43). Both similarities within and differences between species groups are also evident in characters of the sclerites, and they are, therefore, quite useful in testing hypotheses on relationships suggested by analyses based on other characters. Interpopulational variation in size and shape of the sclerites was seen in several taxa; but as noted by Erwin and Ball (1972) in their study, this variation is slight compared with interpopulational differences.

Spermatheca and associated structures

Due principally to the pioneer work of L. Schuler (see for example Schuler, 1960, 1962 or 1965), the spermathecae and associated structures in carabids are now frequently examined in systematic

studies. Differences I observed in these structures among females of Nearctic Nebria are less striking than some reported by Schuler among females of other groups, but quite useful nonetheless.

The spermatheca is very weakly sclerotized in all Nearctic females. In females of most species, it is short, narrow, arcuate and lanceolate (Fig. 345); but in those of a few other species it is less arcuate (Fig. 346) or elongate, convoluted and apically (Fig. 347) or subapically (Fig. 348) swollen.

As noted by Ali (1967), a spermathecal gland, present in Notiophilus females (Fig. 349), is lacking from Nebria females.

The spermathecal duct is also very weakly sclerotized in all nebriines examined. Interspecific differences are evident in length, shape and diameter of the duct. Among females of different taxa, range in duct length is from short (Fig. 336) to long (Fig. 351). In shape, the duct is loosely (Fig. 346) or tightly (Fig. 351) and unevenly convoluted or evenly sinusoidal (Fig. 350). Differences in diameter of the duct are conspicuous, ranging from very narrow (Fig. 345) in females of most taxa to moderately (Fig. 346) or very (Fig. 352) thick in those of a few. As discussed above, females of some taxa have either the basal portion of the duct abruptly thickened (Figs. 347, 352) or the duct itself inserted at the apex of an accessory lobe of the 'spermathecal chamber'. Interpretations of relationship between the bursa and the duct made for individual taxa are discussed in descriptions of the taxa (section 3.43).

Interspecific variation in the point of insertion of the spermathecal duct on the bursa has been noted above. Insertion is on

the midline (Fig. 324) in members of most taxa, but displaced slightly to the right in N. frigida Sahlberg females (Fig. 327) and to the left in females of a few related taxa (Fig. 326), in association with similar asymmetry in the apex of the 'spermathecal chamber'. The duct inserts on the posterior (or dorsal) surface of the chamber (Figs. 340, 331) in females of most species, on the anterior (or ventral) surface in those of a few species. Interspecific differences in the precise point of insertion on either face are also evident and noted in the descriptions of taxa.

Common oviduct

I did not study form and structure of the common oviduct in Nearctic Nebria; but I should note that, in all females examined in which a remnant of the oviduct was present, the ventral reinforcement rod described above in the bursa extended anteriorly in the common oviduct as well (Fig. 354). In at least some females, the rod extends for a short distance in the dorsal wall, then loops transversely and/or ventrally (Fig. 353) and imparts a rigid and specific shape to the oviduct at that point.

3.22 Chorology

Study of geographical distributions is of prime importance in systematics for providing an accessible and unique set of characters of use in studying taxa. Knowledge of present distributions of taxa can help to elucidate their past distributions and evolutionary histories as well as phylogenetic relationships among them (Hennig, 1966). In addition, analysis of present distributions of taxa in single groups provides derivative data of use in recognition and study of general (synoptic) biogeographical patterns. Because geographical data are essentially independent of data acquired through morphology and other studies, distributional patterns can be used in tests for consistency among relationships inferred from the analyses of these other data (Mayr, 1969) (see section 4.3 below for discussion of compatibility of the proposed phylogeny with zoogeographic reconstructions).

Distributional data are of particular relevance to application of the species and subspecies concepts outlined above (section 2.29). Knowledge of geographical relations (i.e. sympatry, parapatry or allopatry) of different populations of the same or different species-group taxa is often crucial in determining their probable status.

My original intent was to present a separate, detailed discussion of Nearctic Nebria distribution equivalent to the preceding treatment of form and structure. However, because data on the distributions of individual taxa are presented with the taxon descriptions and comparisons of distributions and analyses of distributional patterns are treated with other data in section 4.22 on contemporary zoogeography, there is no need to repeat details here. This section is,

therefore, restricted to a brief discussion of the characters used and the kinds of data acquired. My purpose is to stress the need to consider distributional characters in the same perspective as structural or any other characters. Characters used apply either to single localities where members of a taxon have been found or to the known geographical range of a taxon; and these classes of characters are discussed separately below.

3.221 Characters of single localities

Knowledge of distributions of taxa is dependent on accumulation of observations on their occurrence in particular places, localities; and these are characterized in a number of ways. Each is identified in this study according to political units (i.e. country; state, province or territory; and county or district) and place name. Because the boundaries of political units are subject to change and their permanence is often questionable, and because place names may change with time or become inappropriate as human activity alters the surface features of a region, it has been argued that latitudinal and longitudinal geographical coordinates are preferable locality designations. However, the relocation of these localities, by subsequent workers interested in collecting or observing individuals of a particular taxon, from coordinate data alone requires detailed maps not readily available or equipment not in everyday use. In contrast, place names are normally recognized through the use of readily available maps or from a variety of local information sources. The large amount of locality data presented here precludes presentation of

both place names and coordinates for each. A list of localities is provided (see Appendix B) for each of the Nearctic taxa, and dot maps (Figs. 380 - 411) illustrate the distributions of these known localities.

As noted above, most Nebria members occupy montane, riparian habitats. In this study, it was therefore useful to characterize each locality (if appropriate) in terms of its relationship to a mountain range or system and/or drainage system. These data for each taxon are summarized under the geographical distribution section of its description (section 3.43) and in Tables 2 (see also Table 1) and 4 (see also Table 3), respectively.

Presence or absence of members of other Nebria taxa was recorded (when possible) for each locality of a taxon. These data on microsympatry (or indirect evidence for microallopatry or microparapatry) are of use, as noted above, in application of species and subspecies concepts as well as in considerations of possible interactions (e.g. competitive exclusion) among taxa. Data are summarized in Table 5.

3.222 Known ranges of taxa

Characters used in study of the ranges of Nearctic Nebria taxa include their relationship to political, physiographic and faunal regions and their size, continuity and geographical relations with the ranges of other taxa. An attempt was made to relate the geographical distributions of all taxa (Figs. 380 - 411) to major faunal regions, physiographic features and major political units and record these data.

Table 1. Mountain systems and ranges of North America[1, 2]

1. Pacific Coast Range system.
   - A. Alaskan Coast Ranges
     - a. Aleutian Range
     - b. Alaskan Range
     - c. Chugach Mountains
     - d. Wrangell and St. Elias Mountains
   - B. North Coastal Mountains
   - C. Coastal Mountains of Puget Sound area
     - a. Vancouver Island Mountains
     - b. Olympic Mountains
   - D. Middle Coast Ranges
     - a. Coast Range of Oregon
     - b. Siskiyou Mountains
     - c. Klamath Mountains system
     - d. Coast Range of northern California
   - E. South Coast Ranges
     - a. Santa Cruz Diablo, and Santa Lucia Ranges
     - b. San Gabriel and San Bernardino Ranges
2. Cascade-Sierra Nevada Mountain system
   - A. Cascade Range
     - a. Cascade Range north of Columbia River
     - b. Cascade Range south of Columbia River
   - B. Sierra Nevada
     - a. Sierra Nevada north of Mammoth Lakes area
     - b. Sierra Nevada south of Mammoth Lakes area

Table 1. (continued)

3. Plateau and Basin and Range Provinces

   A. Yukon Plateau

   B. Northern interior ranges

      a. Cassiar, Skeena and Omineca Mountains

   C. Fraser Plateau

      a. Cariboo and Columbia Mountains

   D. Columbia Plateau

      a. Clearwater Mountains

      b. Salmon River Mountain system

      c. Seven Devils Mountains

      d. Wallowa Mountains

      e. Blue Mountains

   E. Ranges of Basin and Range Province[3]

      a. Warner Mountains

      b. Washoe Mountains

      c. Independence Mountains

      d. Jarbridge Mountains

      e. Ruby Mountains

      f. Toiyabe Mountains

      g. Stansbury Mountains

      h. Pavant Mountains, Tushar Range, and Midget Crest

      i. Parowan and Cedar Mountains

      j. Pine Valley Mountains

   F. Colorado Plateau

      a. Markagunt Plateau

Table 1. (continued)

b. Sevier Plateau

c. Paunsaugunt Plateau

d. Aquarius Plateau

e. Henry Mountains

f. La Sal Mountains

g. Abajo Mbuntains

h. Chuska Mountains

4. Rocky Mountain System

A. Alaska-Yukon Rocky Mountains

a. Brooks Range

b. Richardson, Ogilvie, Mackenzie, Selwyn, and Pelly Mountains

B. Northern Rocky Mountains

a. Rocky Mountains north of Peace River

b. Front Ranges of Alberta and Montana (includes Cypress Hills, Big Snowy Mountains, etc.)

c. Selkirk Mountains

d. Bitterroot Mountains

e. Absaroka Plateau

f. Bighorn Mountains

C. Central Rocky Mountains

a. Black Hills

b. Teton Range

c. Gros Ventre Range

d. Wind River Range

Table 1. (continued)

e. Wyoming, Salt River, Snake River, and Bear River Ranges

f. Wasatch Range

g. Uinta Mountains

D. Southern Rocky Mountains

a. Laramie Mountains

b. Medicine Bow Mountains

c. Park Range

d. Front Range of Colorado

e. Sawatch Range and Elk Mountains

f. Gore, Mosquito, and Tenmile Ranges

g. White River Mountains

h. Grand Mesa

i. Uncompahgre Plateau

j. Sangre de Cristo Range and Wet Mountains

k. Sacramento Mountains

l. San Juan Mountains

m. Jemez Mountains

5. Ozark System

a. Ozark Plateau

b. Boston Mountains

c. Ouchita Mountains

6. Appalachian Mountain System

A. Northern Ranges

a. Notre Dame Mountains

b. Longfellow Mountains

Table 1. (continued)

c. White Mountains

d. Green Mountains

e. Adirondack Mountains

B. Blue Ridge Mountains

a. Blue Ridge north of French Broad River

b. Blue Ridge south of French Broad River

C. Appalachia Ridges and Plateau

a. Catskill Mountains

b. Allegheny Plateau

c. Cumberland Plateau

---

[1] The classification of mountain systems and ranges used here is my own, based in part on those of Fenneman (1931 and 1938) and Map Information Office, U. S. Federal Board of Surveys and Maps (1929) (see also Clark and Stearn, 1968). All units are grouped for convenience in discussion of Nebria distribution and, therefore, are not necessarily placed with other units having similar geologic history. Refer to Fig. 428 for illustration of the above classification. The alpha-numeric code presented here is used in Table 2 on the distributions of Nearctic Nebria taxa.

[2] Only mountain systems and/or ranges known to be inhabited by Nebria populations have been included. One exception, however, is the Ozark system, from which Nebria are not yet known. I list the Ozark system here to emphasize that point.

[3] Sampling for Nebria populations in the Basin and Range Province is

yet very incomplete; and such populations undoubtedly inhabit ranges not listed here.

Table 2. Distribution of Nearctic Nebria taxa in relation to mountain systems and ranges.[1]

Name of Taxon	Mountain system (1) A Alaskan Coast: a b c d	(1) B North Coast: a b	(1) C Puget Coast: a b	(1) D Middle Coast: a b c d	(1) E South Coast: a b	(2) A Cascade: a b	(2) B Sierra Nevada: a b	(3) A Yukon Pl.: a	(3) B No. Interior: a	(3) C Fraser Pl.: a b c d e	(3) D Columbia Pl.: a b c d e	(3) E Basin & Range: a b c d e f g h i j
virescens			X X			X X X X				X	X X	
paradisi						x x						
gouleti			X							X X	X X	
hudsonica		X						X X X				
l. lacustris												
l. bellorum												

Table 2. (continued)

Name of taxon	Mountain system (3) F Colorado Pl.								(4) A Al.-Yu. Rockies		B No. Rockies				C Cent. Rockies							D So. Rockies											
	a	b	c	d	e	f	g	h	a	b	a	b	c	d	e	f	a	b	c	d	e	f	g	a	b	c	d	e	f	g	h	i	j	k	l	m
virescens																																				
paradisi																																				
gouleti																																				
hudsonica											X	X	X	X	X		X	X	X	X	X	X		X		X	X	X	X							
l. lacustris																																				
l. gaspesiana																																				

Table 2. (continued)

	Mountain system												
	(5)			(6)									
				A				B		C			
	Ozark Plateau			North. Ranges				Blue Ridge		Ridges and Plateau			
Name of Taxon	a	b	c	a	b	c	d	e	a	b	a	b	c
virescens													
paradisi													
gouleti													
hudsonica													
l. lacustris				X	X	X	X				X	X	X
l. bellorum									X				

Table 2. (continued)

Name of taxon	(1) A a	(1) A b	(1) A c	(1) A d	(1) B a	(1) C b	(1) C a	(1) C b	(1) C c	(1) D d	(1) E a	(2) A b	(2) B a	(2) B b	(3) A a	(3) B a	(3) C a	(3) C b	(3) C c	(3) D d	(3) D e	(3) E a	(3) E b	(3) E c	(3) E d	(3) E e	(3) E f	(3) E g	(3) E h	(3) E i	(3) E j
n. nivalis	X	X	X	X											X	X	X														
n. gaspesiana												X																			
c. crassicornis						X										X	X				X	X									
c. intermedia					X																										
gyllenhali castanipes												X				X	X	X	X	X	X	X									
g. lassenensis													X	X																	
g. lindrothi																															
frigida	X	X	X	X												X	X														
lyelli												X																			
a. acuta					X	X	X					X	X	X																	
a. quileute						X																									

Table 2. (continued)

Name of taxon	(3) F a	b	c	d	e	f	g	h	(3) A a	b	(4) B a	b	c	d	e	f	C a	b	c	d	e	f	g	D a	b	c	d	e	f	g	h	i	j	k	l	m
n. nivalis									X	X																										
n. gaspesiana																																				
c. crassicornis																																				
c. intermedia	X										X	X	X	X	X		X	X	X	X	X	X														
gyllenhali castanipes											X	X	X	X	X	X	X	X	X	X			X													
g. lassenensis																																				
g. lindrothi						X																			X	X	X	X	X	X	X	X	X	X	X	X
frigida									X	X	X																									
lyelli																																				
a. acuta																																				
a. quileute																																				

Table 2. (continued)

Name of taxon	(5) a	b	c	(6) A a	b	c	d	e	B a	b	C a	b	c
n. nivalis													
n. gaspesiana				X	X								
c. crassicornis													
c. intermedia													
gyllenhali castanipes					X	X		X					
g. lassenensis													
g. lindrothi													
frigida													
lyelli													
a. acuta													
a. quileute													

Table 2. (continued)

Name of taxon	(1) A a	(1) A b	(1) A c	(1) A d	(1) B a	(1) B b	(1) C a	(1) C b	(1) C c	(1) C d	(1) D a	(1) D b	(2) A a	(2) A b	(2) B a	(2) B b	(3) A a	(3) A a	(3) A a	(3) B b	(3) C c	(3) D d	(3) D e	(3) E a	(3) E b	(3) E c	(3) E d	(3) E e	(3) E f	(3) E g	(3) E h	(3) E i	(3) E j
s. sahlbergii	X		X	X	X	X	X	X					X	X			X	X	X				X										
s. modoc																								X									
s. triad									X																								
gregaria	X																																
charlottae					X																												
a. arkansana																																	
a. edwardsi																	X		X	X	X	X	X										
a. oowah																																	
a. uinta																																	
f. fragilis																																	
f. teewinot																																	

Table 2. (continued)

| | (3) | | |

Table 2. (continued)

Name of taxon	(5)			(6)								
				A				B		C		
	a	b	c	a	b	c	d	e	a	b	a	b	c
s. sahlbergii												
s. modoc												
s. triad												
gregaria												
charlottae												
a. arkansana												
a. edwardsi												
a. oowah												
a. uinta												
f. fragilis												
f. teewinot												

Table 2. (continued)

	(1)										(2)																											
	A				B		C			D					E					A			B		A		B	C			D					E				
Name of taxon	a	b	c	d	a	b	a	b	c	d	a	b	a	b	a	b	a	a	a	b	c	d	e	a	b	c	d	e	f	g	h	i	j				
z. zioni																															X	X						
z. oasis																																	X					
suturalis																																						
obliqua		X	X	X									X		X		X	X	X	X	X		X	X	X		X	X	X	X		X	X					
appalachia																																						
pallipes																																						
darlingtoni														X																								
mannerheimii		X	X	X	X	X	X						X	X				X	X					X														
desolata																																						
navajo																																						
eschscholtzii							X	X	X	X	X	X	X	X	X	X	X			X				X				X			X								

Table 2. (continued)

| | (3) | (4) | | |

Table 2. (continued)

Name of taxon	(5) a	b	c	(6) A a	b	c	d	e	B a	b	C a	b	c
z. zioni													
z. oasis													
suturalis				X	X	X							
obliqua													
appalachia									X	X			
palmipes				X	X	X	X	X	X	X	X	X	X
darlingtoni													
mannerheimii													
desolata													
navajo													
eschscholtzii													

Table 2. (continued)

	(1)										(2)				(3)																
	A				B		C			D				E	A			B	A		B	C			D						E	
Name of taxon	a	b	c	d	a	b	a	b	c	d	a	b	a	b	a	b			a	a	a	b	c	d	e	a	b	c	d	e	f	g	h	i	j
diversa																																			
g. gebleri					X														X	X	X	X	X	X	X										
g. cascadensis					X	X									X	X																			
g. rathvoni																X	X																		
g. siskiyouensis								X	X																										
g. strawberriensis																									X										
carri																						X	X												
k. kincaidi					X	X	X								X																				
k. balli															X	X																			
s. spatulata																	X																		
s. sierrae																X	X																		

Table 2. (continued)

	(3)	(4)																																			
	F								A		B				C							D																
Name of taxon	a	b	c	d	e	f	g	h	a	b	a	b	c	d	e	f	a	b	c	d	e	f	g	a	b	c	d	e	f	g	h	i	j	k	l	m
diversa																																					
g. gebleri												X	X	X	X																						
g. cascadensis																																					
g. rathvoni																																					
g. siskiyouensis																																					
g. strawberriensis																																					
carri																																					
k. kincaidi																																					
k. balli																																					
s. spatulata																																					
s. sierrae																																					

Table 2. (continued)

Name of taxon	(5) a	b	c	(6) A a	b	c	d	e	B a	b	C a	b	c
diversa													
g. gebleri													
g. cascadensis													
g. rathvoni													
g. siskiyouensis													
g. strawberriensis													
carri													
k. kincaidi													
k. balli													
s. spatulata													
s. sierrae													

Table 2. (continued)

Name of taxon	(1) A a	(1) A b	(1) A c	(1) A d	(1) B a	(1) B b	(1) C a	(1) C b	(1) C c	(1) D d	(2) E a	(2) A b	(2) B a	(2) A b	(3) A a	(3) A a	(3) A b	(3) B c	(3) C d	(3) D e	(3) E a	(3) E b	(3) E c	(3) E d	(3) E e	(3) E f	(3) E g	(3) E h	(3) E i	(3) E j
ovipennis												X	X								X									
m.meanyi						X						X	X																	
m. lamarckensis														X																
m. sylvatica							X	X																						
metallica	X	X			X	X	X	X				X																		
i. ingens														X																
i. riversi																														
v. vandykei								X				X																		
v. wyeast														X																
piperi							X	X				X	X																	
s. schwarzi																														

Table 2. (continued)

	(3)	(4)																																			
	F								A		B				C							D																
Name of taxon	a	b	c	d	e	f	g	h	a	b	a	b	c	d	e	f	a	b	c	d	e	f	g	a	b	c	d	e	f	g	h	i	j	k	l	m
ovipennis																																					
m. meanyi																																					
m. lamarckensis																																					
m. sylvatica																																					
metallica											X	X	X	X																							
i. ingens																																					
i. riversi																																					
v. vandykei																																					
v. wyeast																																					
piperi											X																										
s. schwarzi												X																									

Table 2. (continued)

Name of taxon	(5) a	b	c	(6) A a	b	c	d	e	B a	b	C a	b	c
ovipennis													
m. meanyi													
m. lamarckensis													
m. sylvatica													
metallica													
i. ingens													
i. riversi													
v. vandykei													
v. wyeast													
piperi													
s. schwarzi													

Table 2. (continued)

Name of taxon	(1) A a	(1) A b	(1) A c	(1) A d	(1) B a	(1) B b	(1) C a	(1) C b	(1) C c	(1) C d	(1) D a	(1) D b	(2) A a	(2) A b	(2) B a	(2) B b	(3) A a	(3) B a	(3) C a	(3) C b	(3) C c	(3) D a	(3) D b	(3) D c	(3) D d	(3) D e	(3) E a	(3) E b	(3) E c	(3) E d	(3) E e	(3) E f	(3) E g	(3) E h	(3) E i	(3) E j
s. beverlianna																																				
purpurata																																				
t. trifaria																											X	X	X							
t. catenata																																				
t. utahensis																																				
coloradensis																																				
piute																																		X		

Table 2. (continued)

	(3)																																		
	F							A		B					C								D												
Name of taxon	a	b	c	d	e	f	g	h	a	b	a	b	c	d	e	f	a	b	c	d	e	f	g	a	b	c	d	e	f	g	h	i	j	k	l	m
s. beverlianna																		X																		
purpurata																											X	X	X			X		X	X	
t. trifaria	X	X	X	X									X				X	X	X	X	X	X	X	X	X	X	X									
t. catenata						X	X																								X		X	X		
t. utahensis					X																														
coloradensis																											X	X	X	X						
piute																																				

Table 2. (continued)

Name of taxon	(5) a	b	c	(6) A a	b	c	d	e	B a	b	C a	b	c
s. beverlianna													
purpurata													
t. trifaria													
t. catenata													
t. utahensis													
coloradensis													
piute													

1 Refer to Table 1 for explanation of code for mountain systems and ranges. An "X" in any column denotes occurrence of a taxon in the mountain range or system represented.

Table 3. Principal drainage systems of North America[1]

1. California Central Valley drainage
   - A. Sacramento River system
   - B. San Joaquin River system
2. Mid-Pacific coastal drainage
   - A. Klamath River system
   - B. Rogue River system
   - C. Umpqua River system
3. Columbia River drainage
   - A. Willamette River system
   - B. Deschutes River system
   - C. John Day River system
   - D. Snake River system
   - E. Columbia River system
   - F. Okanagan River system
   - G. Yakima River system
4. Fraser River drainage
   - A. Fraser River system
   - B. Thompson River system
5. North-Pacific coastal drainage
   - A. Puget Sound local drainage
   - B. Skeena River system
   - C. Stikine River system
   - D. Copper River system
   - E. Susitna River system

Table 3. (continued)

6. Yukon River drainage
   - A. lower Yukon River
   - B. Koyukuk River system
   - C. Tanana River system
   - D. Porcupine River system
   - E. upper Yukon River system
7. Mackenzie River drainage
   - A. lower Mackenzie River
   - B. Liard River system
   - C. Hay River system
   - D. Peace River system
   - E. Athabasca River system
8. Nelson River-Lake Winnipeg drainage
   - A. North Saskatchewan River system
   - B. South Saskatchewan River system
   - C. Assiniboine River-Red River systems
9. Great Basin internal drainage
10. Colorado River drainage
    - A. San Juan River system
    - B. upper Colorado River system
    - C. Green River system
    - D. lower Colorado River system
    - E. Virgin River system

Table 3. (continued)

11. Rio Grande River drainage
    - A. Rio Grande River system
    - B. Pecos River system
12. Mississippi River drainage, I. Arkansas Unit
    - A. Arkansas River system
13. Mississippi River drainage, II. Missouri Unit
    - A. South Platte River system
    - B. North Platte River system
    - C. Yellowstone River system
    - D. upper Missouri River system
    - E. Cheyenne River system
14. Mississippi River drainage, III. Mississippi Unit
    - A. upper Mississippi River system
15. Mississippi River drainage, IV. Ohio Unit
    - A. Ohio River system
16. Atlantic coastal drainage
17. St. Lawrence River-Great Lakes drainage
18. East-Arctic drainage
19. Mid-Arctic drainage
    - A. Churchill River system
    - B. Anderson River system

---

[1] Refer to Fig. 429 for illustration of the above drainage classification. The alpha-numeric code presented here is used in Table 4 on the distributions of Nearctic *Nebria* taxa.

Table 4. Distribution of Nearctic Nebria taxa in relation to drainage systems.[1]

Name of taxon	Drainage system: 1 California		2 Mid-Pacific			3 Columbia				4 Fraser			5 No.-Pacific					6 Yukon				7 Mackenzie					8 Nelson			9 Great Basin
	A	B	A	B	C	A	B	C	D	E	F	G	A	B	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C
virescens	X	X		X	X	X			X		X	X	X		X																	
paradisi							X					X			X																	
gouleti									X	X																						
hudsonica									X	X		X	X	X		X	X						X		X		X	X	X	X		X
l. lacustris																															X	
l. bellorum																																
n. nivalis																		X	X	X	X	X	X	X	X		X					
n. gaspesiana																																

Table 4. (continued)

Name of taxon	Drainage system																			
	10 Colorado					11 Rio Grande		12 Arkansas U.	13 Missouri U.					14 upper Miss.	15 Ohio Unit	16 Atlantic	17 St. Lawrence	18 East-Arctic	19 Mid-Arctic	
	A	B	C	D	E	A	B	A	A	B	C	D	E	A	A				A	B
virescens																				
paradisi																				
gouleti																				
hudsonica	X	X						X	X	X	X	X								
l. lacustris														X	X	X	X			
l. bellorum																X	X			
n. nivalis																		X	X	X
n. gaspesiana																	X	X		

Table 4. (continued)

Name of taxon	1	2	3								4			5				6				7					8		9
	A	B	A	B	C	A	B	C	D	E	F	G	A	B	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C
c. crassicornis												X	X		X																
c. intermedia									X	X			X	X												X	X	X	X	X	X	
gyllenhali castanipes									X	X	X	X	X	X		X	X		X			X	X	X	X	X	X	X	X	X		
g. lassenensis	X						X																									
g. lindrothi																																
frigida																		X	X		X	X	X		X							
lyelli		X																														
a. acuta	X			X	X							X	X		X	X	X	X	X													
a. quileute														X																		
s. sahlbergii				X	X		X	X	X	X	X	X	X	X	X	X	X	X			X		X			X	X	X					
s. modoc	X																															
s. triad	X																															
gregaria																																

Table 4. (continued)

Name of taxon	10					11		12	13					14		15	16	17	18	19	
	A	B	C	D	E	A	B	A	A	B	C	D	E	A		A				A	B
c. crassicornis																					
c. intermedia			X								X	X									
gyllenhali castanipes			X							X	X	X	X				X	X	X		
g. lassenensis																					
g. lindrothi	X	X				X	X	X	X	X											
frigida																				X	
lyelli																					
a. acuta																					
a. quileute																					
s. sahlbergii																					
s. modoc																					
s. triad																					
gregaria																					

Table 4. (continued)

Name of taxon	1	2	3							4		5				6					7				8		9	
	A	B	A	B	C	A	B	C	D	E	F	G	A	B	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C
charlottae																												
a. arkansana																												
a. edwardsi								X	X	X											X			X	X	X		X
a. oowah																												
a. uinta																												X
f. fragilis																												X
f. teewinot									X																			
z. zioni																												X
z. oasis																												
suturalis									X															X				
obliqua						X	X	X	X	X	X	X	X	X		X	X	X		X		X	X	X	X	X	X	X
appalachia																												

Table 4. (continued)

Name of taxon	10					11		12	13					14	15	16	17	18	19	
	A	B	C	D	E	A	B	A	A	B	C	D	E	A	A				A	B
charlottae																				
a. arkansana	X	X				X	X	X	X	X										
a. edwardsi											X	X								
a. oowah			X																	
a. uinta				X																
f. fragilis																				
f. teewinot				X																
z. zioni					X															
z. oasis					X															
suturalis			X							X							X	X	X	
obliqua	X	X	X		X	X	X	X		X	X	X	X	X						
appalachia															X	X				

Table 4. (continued)

Name of taxon	1		2			3				4				5				6					7				9		
	A	B	A	B	C	A	B	C	D	E	F	G	A	B	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C
pallipes																																
darlingtoni			X																												
mannerheimii						X		X	X	X	X	X	X	X	X	X	X															
desolata																																
navajo																																X
eschscholtzii	X	X	X	X	X	X	X	X	X	X		X			X																	
diversa																																
g. gebleri								X	X	X	X		X	X		X	X										X		X	X	X	X
g. cascadensis						X	X						X	X	X	X	X															
g. rathvoni			X	X																												
g. siskiyouensis						X	X																									
g. strawberriensis								X																								
carri									X																							

Table 4 (continued)

Name of taxon	10					11		12	13					14	15		16	17	18	19	
	A	B	C	D	E	A	B	A	A	B	C	D	E	A	A					A	B
pallipes														X	X		X	X			
darlingtoni																					
mannerheimii																					
desolata				X	X																
navajo				X																	
escscholtzii																					
diversa																					
g. gebleri											X	X									
g. cascadensis																					
g. rathvoni																					
g. siskiyouensis																					
g. strawberriensis																					
carri																					

Table 4. (continued)

	1	2	3							4		5				6					7				8	9	
Name of taxon	A	B	A	B	C	A	B	C	D	E	F	G	A	B	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C
k. kincaidi															X	X	X															
k. balli						X	X					X			X																	
s. spatulata		X																														
s. sierrae		X																														
ovipennis	X	X																													X	
m. meanyi	X					X	X					X			X	X	X															
m. lamarckensis																															X	
m. sylvatica															X																	
metallica										X		X			X	X	X								X	X						
i. ingens		X																													X	
i. riversi		X																													X	
v. vandykei												X			X																	
v. wyeast						X	X																									

Table 4. (continued)

Name of taxon	10					11		12	13				14	15	16	17	18	19	
	A	B	C	D	E	A	B	A	A	B	C	D	E	A	A			A	B
k. kincaidi																			
k. balli																			
s. spatulata																			
s. sierrae																			
ovipennis																			
m. meanyi																			
m. lamarckensis																			
m. sylvatica																			
metallica																			
i. ingens																			
i. riversi																			
v. vandykei																			
v. wyeast																			

Table 4. (continued)

	1	2			3						4				5				6					7				8		9
Name of taxon	A	B	A	B	C	A	B	C	D	E	F	G	A	B	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C
piperi						X						X	X	X	X	X	X								X							
s. schwarzi										X																			X	X	X	
s. beverlianna									X																							
purpurata																																
t. trifaria									X																						X	
t. catenata																																
t. utahensis																																
coloradensis																																
piute																															X	

Table 4. (continued)

Name of taxon	10 A	10 B	10 C	10 D	10 E	11 A	11 B	12 A	13 A	13 B	13 C	13 D	13 E	14 A	15 A	16	17	18	19 A	19 B
piperi																				
s. schwarzi																				
s. beverlianna																				
purpurata	X	X				X		X	X											
t. trifaria		X	X		X			X	X	X	X									
t. catenata	X					X		X												
t. utahensis				X																
coloradensis		X						X	X											
piute																				

[1] Refer to Table 3 for explanation of code for drainage systems. An "X" in any column denotes occurrence of a taxon in the mountain range or system represented.

For example, the geographical distribution of N. gouleti n. sp. (Fig. 383) is Nearctic, apparently confined to the Columbia River Basin and its mountainous rim in central Idaho, northeastern and northcentral Oregon and southeastern and southcentral Washington. These general range characteristics for each taxon are summarized with its description (section 3.43).

Size (maximum linear extent) of the range of each species-group taxon was estimated by measuring the straight-line distance between the two most distant localities on the dot map. As discussed below in section 4.22, interspecific differences in range size are extreme, ranging from an estimated 22,550 km for the Holarctic N. gyllenhali (Schönherr) (Fig. 388) to no range (arbitrarily recorded as 1 km) for several taxa known only from a single locality (e.g. N. navajo n. sp., Fig. 400). Refer to Table 6 for a summary of these data. The distributions of taxa were also characterized as to their probable relative continuity or discontinuity (i.e. presence of significantly disjunct populations). For example, the range of N. pallipes (Fig. 396) is relatively continuous, with few significant gaps between localities except those due possibly to gaps in collecting. The known range of N. suturalis (Fig. 398), however, is grossly discontinuous, with a minimum gap of about 2200 km between eastern and western populations; and this hiatus is almost certainly due to inadequate collecting. In those taxa with relatively discontinuous ranges, the polarity of disjunctions was also recorded. For example, as noted above, a major east/west disjunction is evident in the range of N. suturalis; but several significant north/south disjunctions are also apparent. These

Table 5. Geographical relations of Nearctic Nebria taxa: sympatry, parapatry, and allopatry.

Name of taxon	Taxa 01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23
01 virescens		M	M	M					m	M	M	M			M	M	M	m	M				M
02 paradisi	M		M	M					m		M					m		M					
03 gouleti	M	M		m					M	M	m					M		m					M
04 hudsonica	M	M	m				M			m	m		m	m		M		m					m
05 l. lacustris											M												
06 l. bellorum																							
07 n. nivalis											m		m			M		M					
08 n. gaspesiana											m												
09 c. crassicornis	m	m									M					m	M	m					
10 c. intermedia	M		M	m							m		M			M		m					M
11 gyllenhali castanipes	M	M	m	m	M		m	m	M	m			M			M		m					
12 g. lassenensis	M														M	M		M					
13 g. lindrothi				m																			m
14 frigida				m			m				M					M		m			M		

Table 5. (continued)

Name of taxon	Taxa																					
	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
01 virescens									M			M	M			m	M	M	M	M			
02 paradisi									M				M			M			M				
03 gouleti									m				m			m		m	M				M
04 hudsonica	m		m		m			M	m				m			m		m					
05 l. lacustris								M			m												
06 l. bellorum										m	m												
07 n. nivalis								M	m				M					m					
08 n. gaspesiana								m															
09 c. crassicornis									M				M			m			m				
10 c. intermedia			m	m	m	m		M	m				M			M		m					M
11 gyllenhaali castanipes	m				m			m	m		M		M			M		m	M				m
12 g. lassenensis												M	M			M			M	m			
13 g. lindrothi								m	m														
14 frigida	M								M				M					M					

Table 5. (continued)

Name of taxon	Taxa 47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68
01 virescens	M	M	M	M	m	M	M		M	M	M	M		M								
02 paradisi		M				m			M			m	m	M								
03 gouleti		M				M								M								
04 hudsonica		M				M			m					m	m	m	m	m			m	
05 l. lacustris																						
06 l. bellorum																						
07 n. nivalis									m													
08 n. gaspesiana																						
09 c. crassicornis	m	m				m			M			m		m								
10 c. int media	M					M			M					M	M	M		m				
11 gyllenhali castanipes						M			m					M	m	m						
12 g. lassenensis				M	m	M					M		M	M								
13 g. lindrothi																	m	m	m		m	
14 frigida									M													

Table 5. (continued)

Name of taxon	Taxa 01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23
15 lyelli	M											M											
16 a. acuta	M	m	M	M			M		m	M	M	M						m					
17 a. quileute									M									m					
18 s. sahlbergii	m	M	m	m			M		m	m	m	M		m		m	m				m	M	
19 s. modoc	M																						
20 s. triad																							
21 gregaria														M				m					
22 charlottae																		M					
23 a. arkansana				m									m										
24 a. edwardsi	M		M	m					M	M	m			M				p					
25 a. oowah													m										
26 a. uinta				m						m													
27 f. fragilis										m													
28 f. teewinot				m						m	m												

Table 5. (continued)

Name of taxon	Taxa 24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
15 lyelli																M				M			
16 a. acuta									M			M	m			m		m		m			
17 a. quileute													m			M							
18 s. sahlbergii	p							M	m				m			m	M	m	m				
19 s. modoc									M														
20 s. triad																m					m		
21 gregaria																							
22 charlottae													M				M						
23 a. arkansana								m	m														
24 a. edwardsi					p			M	m				M			M		m					
25 a. oowah																							
26 a. uinta				p					M														
27 f. fragilis			p						M														
28 f. teewinot	p							m	m														

Table 5. (continued)

Name of taxon	Taxa																					
	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68
15 lyelli				m	m						m											
16 a. acuta	m	m			m	m			m			m	m	m								
17 a. quilcure	m				M			m	m			m		M								
18 s. sahlbergii	m	m				m		m	m			M	M	m	m							
19 s. modoc																						
20 s. triad																						
21 gregaria									m													
22 charlottae																						
23 a. arkansana																	m	m	m		m	
24 a. edwardsi									m					M	m				m			
25 a. oowah																			m			
26 a. uinta																		m				
27 f. fragilis																		m				
28 f. teewinot																m					m	

Table 5. (continued)

Name of taxon	Taxa 01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23
29 z. zioni										m													
30 z. oasis																							
31 suturalis				M	M		M	M		m	m		m					M					m
32 obliqua	M	M	m	m			m		M	m	m		m	M				m	M				m
33 appalachia					M	n																	
34 pallipes					m	m					M												
35 darlingtoni	M																						
36 mannerheimii	M	M	m	m			M		M	M	M	M		M		m	m	m				M	
37 desolata																							
38 navajo																							
39 eschscholtzii	m	M	m	m					M	M	M	M			M	m	M	m		m			
40 diversa	M																	M				M	
41 g. gebleri	M		m	m			m			m	m			M		m		m					
42 g. cascadensis	M	M	M						m		M	M						m					

Table 5. (continued)

Name of taxon	Taxa																						
	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
29 z. zioni									m					M									
30 z. oasis																							
31 suturalis	M				m				M		M							M					
32 obliqua	m		M	M	m	m		M					m	M		m		m	M	M		M	M
33 appalachia											m												
34 pallipes								M		m													
35 darlingtoni																m				m			
36 mannerheimii	M								m							m	M	M	m				
37 desolata									M														
38 navajo																							
39 eschscholtzii	M								m			m	m				m	M	m	m	m	M	
40 diversa													M			m							
41 g. gebleri	m							M	m				M			M						m	
42 g. cascadensis									M				m			m							

Table 5. (continued)

Name of taxon	Taxa 47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68
29 z. zioni																		m			m	
30 z. oasis									M						M	M	m	m				
31 suturalis															m	m	m	m	m		M	M
32 obliqua	M				M	M			m													
33 appalachia																						
34 pallipes																						
35 darlingtoni					M																	
36 mannerheimii	M	M				m			M	m			m	M	m				M			
37 desolata																						
38 navajo																						
39 eschscholtzii	M	M	M	M	M	M			M	m	M	M	M	M	m							
40 diversa																						
41 g. gebleri	M					M			m						M	m						
42 g. cascadensis		M				m			M	m			m	M	m							

Table 5. (continued)

Name of taxon	Taxa 01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23
43 g. rathvoni	M											m			M.	m							
44 g. siskiyouensis																				m			
45 g. strawberriensis																							
46 carri			M							M	m												
47 k. kincaidi	M								m	M						m	m	m					
48 k. balli	M	M	M	M					m							m		m					
49 s. spatulata	M																						
50 s. sierrae	M											M			m								
51 ovipennis	m											m			m	m							
52 m. meanyi	M	m	M	M					m	M	M	M				m		m					
53 m. lamarckensis	M																						
54 m. sylvatica																	m	m					
55 metallica	M	M		m			m		M	M	m			M		m	m	m					
56 i. ingens	M																						

Table 5. (continued)

Name of taxa	Taxa 24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
43 g. rathvoni									M			m				m							
44 g. siskiyouensis																m							
45 g. strawberriensis									M							M							
46 carri	m								M									m					
47 k. kincaidi									M				M			M		M					
48 k. balli													M			M			M				
49 s. spatulata																M				M			
50 s. sierrae																M				M			
51 ovipennis									M			M				M				m			
52 m. meanyi									M				m			M		M	m				
53 m. lamarckensis																							
54 m. sylvatica													M			M			M				
55 metallica	m							M	m				m			m		m	m				
56 i. ingens																			M	M			

Table 5. (continued)

Name of taxon	Taxa 47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68
43 g. rathvoni			M	M	m					M	M											
44 g. siskiyouensis																						
45 g. strawberriensis																						
46 carri																						
47 k. kincaidi						m	m		M			M		M								
48 k. balli						m			M			M	M	m								
49 s. spatulata					m					m												
50 s. sierrae					m		m			m	m											
51 ovipennis			m	m			m			m	m											
52 m. meanyi		m							m			m	m	m								
53 m. lamarckensis	m			m	m					m												
54 m. sylvatica									M			M		M								
55 metallica	m	m	M			m						M	M	m	m							
56 i. ingens			m	m	m		m															

Table 5. (continued)

Name of taxon	Taxa 01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23
57 i. riversi	M											M			m								
58 v. vandykei	M	m							m							m	m	M					
59 v. wyeast	M	m										M				m		M					
60 piperi	M	M	M	m					m	M	M	M				m	M	m					
61 s. schwarzi				m						M	m							m					
62 s. beverlianna				m						M	m												
63 purpurata				m									m										m
64 t. trifaria				m						m			m										m
65 t. catenata													m										m
66 t. utahensis																							
67 coloradensis				m									m										m
68 piute																							

Table 5. (continued)

Name of taxon	Taxa																					
	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
57 i. riversi																M				M			
58 v. vandykei													m			M			m				
59 v. wyeast																M			M				
60 piperi	M								m				m			m		M	m				
61 s. schwarzi	m							M	m				m			m			m				
62 s. beverlianna					M			M	m														
63 purpurata								m	m														
64 t. trifaria	m		m	m	m	m		m	m					M									
65 t. catenata		m							M														
66 t. utahensis																							
67 coloradensis									M														
68 piute						m			M														

Table 5. (continued)

Name of taxon	Taxa 47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68
57 i. riversi				m	m																	
58 v. vandykei	M	M				m		M	M					m								
59 v. wyeast		M				m			M					M								
60 piperi	M	m				m		M	m			m	M									
61 s. schwarzi									m									m				
62 s. beverlianna																		m	m		m	
63 purpurata																m	m				p	
64 t. trifaria																	m					
65 t. catenata																						
66 t. utahensis																	m	p				
67 coloradensis																						
68 piute																						

Abbreviations used M = macrosympatric; m = microsympatric; p = parapatric; blank = allopatric

Table 6. Maximum linear extent of geographical range of Nearctic *Nebria* taxa.

Name of taxon	Maximum linear extent of range[1,2] Subspecies	Species
virescens		940
paradisi		320
gouleti		685
hudsonica		3350
l. lacustris	2160	2160
l. bellorum	60	
n. nivalis	15891[3]	17100[3]
n. gaspesiana	1585	
c. crassicornis	350	2830
c. intermedia	2830	
gyllenhali castanipes	6900	22550[3]
g. lassenensis	720	
g. lindrothi	685	
frigida		4870[3]
lyelli		1[4]
a. acuta	3330	3330
a. quileute	60	
s. sahlbergii	4090	4160
s. modoc	60	
s. triad	30	
gregaria		1540
charlottae		
a. arkansana	650	339
a. edwardsi	2500	
a. oowah	1[4]	

Table 6. (continued)

Name of taxon	Subspecies	Species
a. uinta	220	555
f. fragilis	170	
f. teewinot	150	185
z. zioni	157	
z. oasis	1^4	
suturalis		4030
obliqua		4440
appalachia		150
pallipes		2240
darlingtoni		20
mannerheimii		2870
desolata		110
navajo		1^4
eschscholtzii		1800
diversa		1740
g. gebleri	2400	3100
g. cascadensis	800	
g. rathvoni	650	
g. siskiyouensis	80	
g. strawberriensis		240
carri		
k. kincaidi	1260	1570
k. balli	170	
s. spatulata	50	280
s. sierrae	200	
ovipennis		480
m. meanyi	2390	3000

Table 6. (continued)

Name of taxon	Subspecies	Species
m. lamarckensis	20	
m. sylvatica	185	
metallica		5160
i. ingens	90	200
i. riversi	30	
v. vandykei	315	550
v. wyeast	130	
piperi		2060
s. schwarzi	370	1330
s. beverlianna	1[4]	
purpurata		530
t. trifaria	960	1390
t. catenata	60	
t. utahensis	1[4]	
coloradensis		200
piute		20

1 Linear distance between the two most distant localities in the geographical range of a taxon.

2 All distances given in kilometers.

3 Linear range includes populations in Palaearctic Region.

4 Taxon known only from a single locality; linear range arbitrarily assigned a value of 1 km.

Table 7. Size and orientation of significant disjunctions[1] in the geographical ranges of Nearctic Nebria.

Name of taxon	(1) Distance (km)	(2) Orientation	(3) Nature of Intervening area[2]
virescens	300	N/S	l
paradisi	100	N/S	r
hudsonica	220	N/S	l
	960	E/W	p
l. lacustris	580	E/W	p
n. nivalis	300	N/S	w
	500	E/W	w
n. gaspesiana	300	N/S	l
	700	E/W	w
c. crassicornis	150	E/W	l
c. intermedia	130	N/S	l
gyllenhali castanipes	870	E/W	p
	880	E/W	p
frigida	360	E/W	w
a. acuta	290	N/S	l
	300	N/S	l

Table 7. (continued)

Name of taxon	(1)	(2)	(3)
s. sahlbergii	170	E/W	w
gregaria	170	E/W	w
a. arkansana	140	N/S	1
a. edwardsi	190	N/S	1
suturalis	1300	E/W	1
	1800	E/W	1
obliqua	200	E/W	1
appalachia	80	N/S	1
desolata	65	E/W	1
eschscholtzii	230	N/S	1
diversa	560	N/S	w
carri	210	E/W	1
k. kincaidi	150	E/W	w
k. balli	100	N/S	r
m. meanyi	290	N/S	1
m. sylvatica	120	N/S	w
metallica	430	E/W	w
v. vandykei	190	E/W	1
v. wyeast	90	N/S	1
piperi	330	N/S	r
purpurata	140	N/S	1
t. trifaria	260	E/W	1

Table 7. (continued)

Name of taxon	(1)	(2)	(3)
	280	E/W	1
t. catenata	460	N/S	1
coloradensis	90	N/S	1
	100	E/W	1

1 I suggest that disjunctions noted here represent actual discontinuities in distributions rather than inadequate regional sampling.

2 Code used in characterizing intervening areas is as follows:

l = lowland area, any type; p = open prairie; r = river, forming a divide; w = water, sea between island and mainland.

data are considered in the zoogeographic discussion below and in Table 7.

Data on geographical relations (i.e. sympatry, etc.) between the range of one taxon and those of others were also used in considerations of the probable status of various populations of the taxon. For example, the geographical ranges of N. gouleti n. sp. (Fig. 383) and N. hudsonica (Fig. 384) overlap narrowly in certain areas of Washington and Idaho. Slight differences in external structural characters among members of allopatric populations of each are maintained among members of sympatric populations, supporting the hypothesis that these two taxa are distinct species. These data are summarized in Table 5.

With few exceptions, I am confident that the known geographical distributions of Nearctic Nebria closely approximate their true ranges. Certain areas in North America remain inadequately sampled or completely unsampled for Nebria and other carabids. These areas are discussed in section 5.1 under suggestions for future study. I should also note that the distributions of Nebria taxa are known at present only from observations of adults. Because migratory activity is neither known nor likely (except for slight seasonal microhabitat shifts) in Nebria members, and because adults and immatures seem to occupy the same or adjacent microhabitats, range estimates based on adults would not be altered or improved by inclusion of observations on other life stages.

3.23 Natural history

The data and discussions presented in this section represent a first attempt at a comparative natural history of Nearctic Nebria. Topics covered in this section are diverse and include those normally considered under the heading "biology" or "bionomics." Data from the literature and from my own field and laboratory observations have been integrated to present a detailed review of present knowledge on Nebria species. Unequal coverage of various topics is due to great gaps in comparative data on the natural history of Nearctic taxa. At present, data on some topics (e.g. flight, population size and density, etc.) are so random and sparse that no comparative study of these is yet possible. In such instances, data are presented descriptively (rather than comparatively) in the hope that these few details will encourage others to gather additional pertinent data.

One of the stated aims of this project has been to acquire a broad data base, using a variety of character systems, with which to reconstruct cladistic relationships among the Nearctic taxa. These relationships, in turn, serve as the bases for the classification provided (section 3.32). Of the natural history data presented, only those on habitat distribution and life history represent a sufficient number of Nearctic taxa to be of use at present in the study of relationship and, therefore, contribute to the classification. These same data supplement geographical distribution data in both contemporary and historical zoogeographic analyses (section 4.2 below) and contribute to a more detailed picture of the spatial and, to some extent, temporal distributions of these beetles at present and in the

past.

I hope that detailed data on the preferred macro- and microhabitats of members of each taxon (provided under the descriptions of the taxa, section 3.43, but surveyed here) will be of use to paleontologists in reconstructing past regional environments and biotas, and to anyone interested in collecting and/or observing individuals of a particular taxon.

3.231 Habitat distribution

For convenience, I have divided the discussion of habitat distributions among Nebria into two parts: macrohabitat range (gross altitudinal and/or life zone ranges) and microhabitat preference (the range of local conditions preferred by individuals within the macrohabitat range). Although this distinction is at times arbitrary, it facilitates comparisons among different taxa and has permitted organization of data into a form easily handled in zoogeographic analyses.

3.2311 Macrohabitat

Nearctic Nebria are a predominantly montane group. Of the 68 taxa recognized here, 50 (75%) are restricted to montane regions and habitats; six (eight percent) are restricted to mountains in southern parts of their ranges but are more widely distributed in northern parts; seven (10%) occupy low-altitude montane habitats and also range broadly in lowlands; two (three percent) occupy far-northern lowland and low-altitude montane habitats; and two (three percent are restricted to non-montane habitats. The habitat distribution of

N. charlottae Lindroth is unknown.

In montane regions, all Nebria taxa occupy more or less restricted altitudinal ranges; and where the geographical ranges of several species overlap, striking altitudinal zonation patterns are evident (see section 4.22 below for discussion). For example, Fig. 443 illustrates the respective altitudinal ranges of several taxa and the resultant zonation pattern in the Front Range, Colorado. However, the habitat distributions of taxa with latitudinally- or longitudinally-extended ranges cannot be characterized by reference to altitudinal range data alone because their respective altitudinal ranges change with geographical location. As discussed below (section 4.22), altitudinal range of a given taxon is, in most instances, lowered either with increased latitude or with transition from regions of continental to more maritime climate (e.g. a coastward shift in longitude). Figures 355 - 358 graphically illustrate altitudinal shifts with latitude shifts within the ranges of certain taxa. This phenomenon was first noted in scientific literature early in the 1800's (e.g. von Humbolt and Bonpland, 1805). Further investigation (e.g. by Allen, 1871, and Merriam, 1892, 1894a, 1894b, 1898) of this relationship between altitude and latitude or, to some degree, longitude in the distributions of certain organisms and biotas led to formulation of various life zone concepts. Although recognized today as over-simplifications of complex interactions between organisms and their time- and space-extended environments, life zone concepts can be useful tools in facilitating brief characterizations of macrohabitat distributions of taxa. I have found them extremely useful in describing Nebria distributions because life zone concepts

can be applied equivalently throughout geographical ranges of taxa while altitudinal characterizations apply only locally (Kavanaugh, in press [A]). Local differences in topography or exposure also affect altitudinal ranges of taxa, further confounding their characterization by altitude.

Life zones concepts used here are those of Merriam (1892, 1894a, 1898). Those zones occupied by members of one or more Nebria taxon include the Upper Sonoran ("Upper Austral"), Transition, Canadian, Hudsonian, and Arctic/Alpine zones. Other regional life zone classifications have been proposed (e.g. that of Ramaley, 1907 [see also Marr, 1967], for the Front Range, Colorado). These apply more precisely within the area of their intended coverage but are not more generally applicable. Merriam life zones are most easily recognized by the conspicuous and/or abundant plant species present (especially the trees); and although species composition of the different zones changes with geography, ambience and climate of respective zones are relatively constant. For example, the Hudsonian zone can be characterized by the presence of Engelmann Spruce (Picea engelmannii Engelm.) and Subalpine Fir (Abies lasiocarpa Nutt.) in the Front Range, Colorado, but by Mountain Hemlock (Tsuga mertensiana Sarg.) and Whitebark Pine (Pinus albicaulis Engelm.) in the Sierra Nevada, California. In both areas, however, the subalpine-parkland nature of the zone is maintained.

Life zone distributions of Nearctic Nebria taxa are summarized in Table 8. Variation in the range of life zones occupied by members of different taxa is extreme. For example, N. paradisi members are restricted to the Arctic/Alpine zone and those of N. gouleti to the

Upper Sonoran and Transition zones, while members of N. gyllenhali lindrothi n. ssp. occupy a range from the Arctic/Alpine to the Transition zone. The relationship between life zone and geographical ranges is discussed in section 4.22 and illustrated in Fig. 436.

Life zone ranges appear to be continuous in all taxa. No taxa exhibit 'disjunct distributions' with respect to life zone range, as was suggested by Armin (1963) for N. suturalis ("N. longula LeConte") in the Front Range. Also, no shifts in life zone range with geography are apparent among Nearctic taxa except in N. purpurata LeConte (Figs. 358, 409). Members of this species are restricted to the Arctic/Alpine and Hudsonian zones in northern Colorado, to the Hudsonian and Canadian zones in southern Colorado, and to the Transition zone in northern New Mexico (Kavanaugh and Martinko, 1972) --a complete reversal of the usual relationship of increased range altitude with a decrease in latitude (see section 4.23 for discussion).

I assume that present macroclimatic ranges of taxa are determined by intrinsic tolerance limits of their members for one or more environmental factors (e.g. temperature, humidity, etc.), but that present geographical ranges result from the interplay of both time- and space-extended effects of these intrinsic constraints and various historical events (e.g. the existence of past barriers to distributions, glaciations, etc.). Factors affecting geographical distribution are therefore potentially more diverse and difficult to isolate. Attempts to relate the macrohabitat distributions (ranges) of Nebria taxa to their respective tolerance limits for certain environmental factors, however, are limited mainly by the paucity of detailed environmental data available. With such data and existing

Table 8. Life zone distributions of Nearctic Nebria taxa.

Name of taxon	Life zone[1] A/A	H	C	T	US	?[4]
virescens	(X)[2]	(X)	X	X		
paradisi	X					
gouleti				X	X	
hudsonica			X	X		
l. lacustris			(X)	X	X	
l. bellorum			X			
n. nivalis	X	X				
n. gaspesiana	X	X				
c. crassicornis	X	X	(X)			
c. intermedia	X	X	(X)			
gyllenhali castanipes	(X)	X	X	(X)		
g. lassenensis		X				
g. lindrothi	X	X	X	X		
frigida	X	X				
lyelli	X					
a. acuta	X	X	X			
a. quileute		X	X			
s. sahlbergii		X	X	(X)		
s. modoc			X	(X)		
s. triad			X	(X)		
gregaria		X[3]				
charlottae						X

Table 8. (continued)

Name of taxon	Life zone A/A	H	C	T	US	?
a. arkansana	X	X	X			
a. edwardsi		X	X			
a. oowah			X			
a. uinta			X	(X)		
f. fragilis			X	(X)		
f. teewinot		(X)	X			
z. zioni			X	(X)		
z. oasis			X	(X)		
suturalis	X					
obliqua		(X)	X	X	X	
appalachia			X	(X)		
pallipes			(X)	X	X	
darlingtoni			(X)	X		
mannerheimii			X	(X)		
desolata					X	
navajo					X	
eschscholtzii				X	X	
diversa			X[2]			
g. gebleri		(X)	X	(X)		
g. cascadensis		(X)	X	(X)		
g. rathvoni		(X)	X	(X)		
g. siskiyouensis			X	(X)		

Table 8. (continued)

Name of taxon	Life zone A/A	H	C	T	US	?
g. strawberriensis			X			
carri		X				
k. kincaidi		X	X			
k. balli		X	(X)			
s. spatulata	X	X				
s. sierrae	X	X				
ovipennis	(X)	X	X			
m. meanyi	(X)	X	(X)			
m. lamarckensis	(X)	X	(X)			
m. sylvatica			X			
metallica			X			
i. ingens	X					
i. riversi	X					
v. vandykei	X	(X)				
v. wyeast	X	(X)				
piperi		X	X			
s. schwarzi		(X)	X			
s. beverlianna			X			
purpurata	X	X	X	X		
t. trifaria	(X)	X	X	X		
t. catenata	(X)	X	X	X		
t. utahensis				X		

Table 8. (continued)

Name of taxon	Life zone[1] A/A	H	C	T	US	?
coloradensis	(X)	X	(X)			
piute		X	X			

[1]Life zones abbreviated as follows: A/A = Arctic/Alpine Zone; H = Hudsonian Zone; C = Canadian Zone; T = Transition Zone; and US = Upper Sonoran Zone; modified from Merriam, 1894 and 1898.

[2]Parentheses around an entry denote occurrence of few individuals in a particular zone, or only partial occupation of the zone (i.e. upper or lower extreme only) by taxon members.

[3]For taxa restricted to seacoast habitats, designations of life zones occupied are relatively arbitrary, but represent reasonable approximations of macrohabitat equivalence.

[4]Life zone distribution unknown.

knowledge of macrohabitat distribution, the tolerance limits of these taxa could be estimated. Figs. 355 - 358 illustrate a crude graphic attempt to estimate temperature tolerance limits of several taxa by plotting the altitudinal and latitudinal co-ordinates of their respective distributions and relating these to certain isotherms for mean annual air temperature (generalized temperature data from Mani, 1962 and 1968). This particular temperature character was chosen only because rough data were available. Nonetheless, restriction within a limited (but unspecified) temperature range is indicated, for example, by the distribution of N. obliqua (Fig. 357), perhaps with some shift in tolerance with shift in latitude. Detailed and meaningful analyses must await better climatic data.

One interesting effect of human environmental alteration on the macrohabitat (and geographical) distributions of certain Nearctic Nebria taxa deserves comment here. I have frequently collected members of certain species along streams under bridges at elevations well below the life zone range normally occupied by these species. In fact, individuals were not seen at these elevations except under bridges. Apparently, these cool, shaded, man-made habitat 'islands' may be routinely populated and/or repopulated by downstream drift from life zones above; and there is reason to suspect that small, resident populations can become established in these areas. The short-term result of this 'trollism' is an artificial extension of macrohabitat and, in some instances, the geographical ranges of the taxon. Possible long-term effects are discussed in section 3.234.

3.2312 Microhabitat

Within macrohabitat ranges occupied by members of different Nebria taxa, individuals are found only in a limited subset of available microhabitats. I have attempted to characterize the microhabitats preferred according to type (e.g. stream bank, glacial margin, closed forest, etc.), size, substrate, cover size and type, vegetation, exposure and moisture. Many of my findings agree with those of Lindroth (1961) for the taxa he considered. Other published notes relating to microhabitat preferences in Nearctic Nebria species include the following: Spence (1974), for N. lacustris lacustris Casey and N. pallipes; and Blake (1945), for N. trifaria trifaria. Andersen (1968), Greenslade (1968), Kryzhanovski and Molodova (1973), Lindroth (1965) and Shilenkov (1974) published notes on microhabitats for Palaearctic members of N. gyllenhali. Shilenkov included data on N. nivalis nivalis in far-eastern Asia. Microhabitat preferences for N. brevicollis, the type species of Nebria, have been well-documented (see Greenslade, 1963a, 1963b and 1968; Richards, 1946; Schiller, 1973; Schiller and Weber, 1975; and Thiele, 1968 and 1969a).

Microhabitat preferences of adults and immatures are, in most instances, apparently identical. In the following discussions and in taxon descriptions (section 3.43), statements about microhabitat can therefore be assumed to refer to all life stages unless otherwise noted. Data are summarized in Tables 9, 10, and 11.

Microhabitat type

Habitat types occupied by at least some members of Nearctic taxa include the following: (1) banks of streams, lakes and ponds;

(2) margins of glaciers and snowfields; (3) sea strands; (4) forests; (5) meadows; (6) arctic and alpine tundras; and (7) fellfields and talus slopes. Table 9 summarizes known microhabitat spectra preferred by members of Nearctic Nebria taxa. Only N. charlottae remains uncharacterized in its habitat preferences.

Riparian habitats.--Members of 63 taxa (93% of the fauna) are riparian (i.e. prefer stream banks or the shores of lakes or ponds) at least in part. Members are strictly riparian in 31 taxa (46%), riparian except at upper altitudinal range limits in 13 taxa (19%), riparian only at lower altitudinal range limits in 13 taxa (19%), facultatively riparian in six taxa (nine percent), and non-riparian in four taxa (six percent). Members of seven taxa, including N. lacustris lacustris and N. pallipes, are commonly collected on the banks of lakes and ponds as well as streams, while members of the remaining riparian taxa are restricted to, or common only on, stream banks. In general, there is an inverse relationship between altitude and the degree to which members of a taxon are restricted to riparian habitats (see further discussion below in this section).

Organisms which occupy stream banks (e.g. members of most Nebria taxa) must face seasonal and/or catastrophic changes in water levels which result in inundation of the banks. Beetles may be drowned or swept downstream from suitable habitats. Andersen (1968) discussed inundation of riparian habitats and responses of organisms (including members of N. gyllenhali) to these events. Spence (1974) noted downstream drift of adults and larvae of N. lacustris lacustris and N. pallipes as a result of increased runoff after rains. It can be

Table 9. Microhabitat distribution of Nearctic Nebria taxa.

Name of taxon	Microhabitat type[1]							
	O	S	L	M	F	Tu	Ta	N	?[3]
virescens				X	X		X	X	
paradisi						X		X	
gouleti		X							
hudsonica		X							
l. lacustris		X	(X)[2]						
l. bellorum		X							
n. nivalis		X				(X)		X	
n. gaspesiana		X					X	X	
c. crassicornis		(X)	(X)	X	(X)	X		X	
c. intermedia		(X)	(X)	X	(X)	X		X	
gyllenhali castanipes		X	X	X	X	X			
g. lassenensis				X	(X)				
g. lindrothi		X	X	X	X	X	(X)	(X)	
frigida		X				X		(X)	
lyelli		X					X	X	
a. acuta		X						X	
a. quileute		X							
s. sahlbergii		X						(X)	
s. modoc		X							
s. triad		X							
gregaria	X								
charlottae									X

Table 9. (continued)

Name of taxon	Microhabitat type								
	O	S	L	M	F	Tu	Ta	N	?
a. arkansana		X					(X)	(X)	
a. edwardsi		X							
a. oowah		X							
a. uinta		X							
f. fragilis		X							
f. teewinot		X							
z. zioni		X							
z. oasis		X							
suturalis						(X)	X	X	
obliqua		X							
appalachia		X							
pallipes		X	X						
darlingtoni		X							
mannerheimii		X							
desolata		X							
navajo									X
eschscholtzii		X							
diversa	X								
g. gebleri		X							
g. cascadensis		X							
g. rathvoni		X							
g. siskiyouensis		X							

Table 9. (continued)

Name of taxon	Microhabitat type								
	O	S	L	M	F	Tu	Ta	N	?
g. strawberriensis		X							
carri		X			(X)				
k. kincaidi		X			(X)				
k. balli		X			(X)				
s. spatulata		X					X	X	
s. sierrae		X		(X)			X	X	
ovipennis		X		(X)			X	(X)	
m. meanyi		X						X	
m. lamarckensis		X							
m. sylvatica		X							
metallica	X	X		(X)					
i. ingens		X					X	X	
i. riversi		X					X	X	
v. vandykei		(X)						X	
v. wyeast		(X)						X	
piperi		X							
s. schwarzi		X							
s. beverlianna		X							
purpurata		X					X	X	
t. trifaria		X	X	X	X	X		(X)	
t. catenata		X	X	X	X				
t. utahensis									?

Table 9. (continued)

Name of taxon	Microhabitat type O	S	L	M	F	Tu	Ta	N	?
coloradensis		X		(X)	(X)				
piute		X		X	X				

[1]Microhabitat types abbreviated as follows: O = open seacoast, in supralittoral zones; S = streambanks; L = banks of lakes or ponds; M = meadows; F = forest; Tu = tundra; Ta = talus slopes; N = perinival areas, margins of glaciers or snowfields.

[2]Parentheses around an entry denote what I consider an uncharacteristic occurrence for members of a particular taxon.

[3]Microhabitat distribution unknown.

Table 10. Data on characteristics of microhabitats preferred[1] by members of Nearctic Nebria taxa, I. Association with water bodies (including streams, lakes, oceans, snowfields, or glaciers).

Name of taxon	(1) Size of water body						(2) Distance to water body			
	(A) stream	(B) lake or pond	(C) ocean or sea	(D) snowfield	(E) glacier	(F) unassociated	(A) stream or lake	(B) snow or ice	(C) ocean or sea	(D) unassociated
virescens	1-3[2]			1-3		X	2-6	4-6		X
paradisi				1-3	X			1-5		
gouleti	3-8						1-5			
hudsonica	2-8						1-5			
l. lacustris	2-8	1-5					2-4			
l. bellorum	2-5						2-5			

Table 10. (continued)

Name of taxon	(1) (A)	(B)	(C)	(D)	(E)	(F)	(2) (A)	(B)	(C)	(D)
n. nivalis	3-4			1-2			1-4			
n. gaspesiana	2-6			1-2		(X)[3]	1-3	1-5		(X)
c. crassicornis	(6)			1-3		X	(1-6)			X
c. intermedia	(3-5)	(2-4)				X	(2-6)	1-6		X
gyllenhali castanipes	2-7	2-4				X	1-6	1-6		X
g. lassenensis	2	2				X	2-6			X
g. lindrothi	1-6	1-2		2		X	1-6	1-6		X
frigida	3-7			1		X	2-6	5-6		X
lyelli	1-3			1-3			1-6	1-6		X
a. acuta	1-6			1-3			0-6	1-6		
a. quileute	4-5						1-4			
s. sahlbergii	3-8		X				1-4		2	
s. modoc	3						1-4			

Table 10. (continued)

Name of taxon	(1) (A)	(B)	(C)	(D)	(E)	(F)	(2) (A)	(B)	(C)	(D)
s. triad	3-5						1-4			
gregaria			X						(2)	
charlottae			unknown					unknown		
a. arkansana	2-4	2					1-5			
a. edwardsi	1-7			1-2			1-4	1-4		
a. oowah	4						1-4			
a. uinta	3-6						1-4			
f. fragilis	3-5						1-4			
f. teewinot	2-6						1-4			
z. zioni	1-6						0-4			
z. oasis	3						0-4			
suturalis	2-3			1-2	X	X	1-6	1-6		X

Table 10. (continued)

Name of taxon	(1) (A)	(B)	(C)	(D)	(E)	(F)	(2) (A)	(B)	(C)	(D)
obliqua	3-8						1-6			
appalachia	3-5						1-5			
pallipes	3-8	1-5					1-6			
darlingtoni	6						1-5			
mannerheimii	5-8						1-6			
desolata	3-5						1-5			
navajo			unknown					unknown		
eschscholtzii	2-8						1-6			
diversa			X						1-2	
g. gebleri	1-7						1-5			
g. cascadensis	2-7						1-6			
g. rathvoni	2-6						1-4			
g. siskiyouensis	5						1-5			

Table 10. (continued)

	(1)						(2)			
	(A)	(B)	(C)	(D)	(E)	(F)	(A)	(B)	(C)	(D)
g. strawberriensis	3-4						1-5			
carri	2-3					(X)	1-6			(X)
k. kincaidi	1-5					(X)	1-4			(X)
k. balli	1-6					(X)	1-6			(X)
s. spatulata	1-3			1-3		X	0-6	1-6		X
s. sierrae	1-3	1		1-3		X	3-6	1-6		X
ovipennis	1-4			(1-3)		X	1-6	1-6		X
m. meanyi	3-6			1-3	X		1-4	1-5		
m. lamarckensis	3-4						0-4			
m. sylvatica	4-5						1-4			
metallica	3-7		X			X	1-6		2-3	X
i. ingens	3-4			1-3			0-4	1-6		
i. riversi	1			1-3			1-5	1-6		

Table 10. (continued)

	(1)						(2)			
	(A)	(B)	(C)	(D)	(E)	(F)	(A)	(B)	(C)	(D)
v. vandykei	4-5			1-3	X		1-3	0-5		
v. wyeast	3-5			1-3	X		1-3	0-6		
piperi	4-7						1-4			
s. schwarzi	6-8						1-5			
s. beverlianna	7						0-5			
purpurata	3-5			1-2		(X)	1-4	4		(X)
t. trifaria	1-7	1-2		(1-3)		X	1-6	1-6		X
t. catenata	1-3	1-2				X	1-6			X
t. utahensis				unknown				unknown		
coloradensis	3-4					(X)	1-5			(X)
piute	1-4			(1)		X	1-6	3-6		X

[1]Data presented here represent my field observations supplemented by selected data from the literature (Edwards, 1975; Lindroth, 1955a, 1961, and 1963a; and Spence, 1974). Most observations were made during daylight hours. "Preferred" microhabitat therefore refers specifically to places where beetles hide during the day (see text for further comment). Ranges in data reflect ranges of observations only; and these are presented as crude estimates of actual preference ranges of taxa.

[2]Code used for data presented here is as follows:

(1) Size of water body. (A) stream: 1=small seep or snowmelt trickle, width (w.) less than 5cm; 2=very small creek (rivulet), w. 5cm to 1 m; 3=small creek, w. 2m to 3m; 4=medium creek, w. 4m to 5m; 5=large creek, w. 6m to 10m; 6=small river, w.15m to 25m; 7=medium river, w. 30m to 60m; and 8=large river, w. greater than 60m. (B) lake or pond: 1=small pond, average diameter (a.d.) less than 30m; 2=small lake, a.d. 30m to 150m; 3=medium lake, a.d. 160m to 1.5km; 4=large lake, a.d. 1.6km to 8 km; 5=very large lake, a.d. greater than 8km. (C) ocean or sea: size unclassified; (D) snowfield: 1=small snowfield, a.d.less than 10m; 2=medium snowfield, a.d. 10m to 60m; 3=large snowfield, a.d. greater than 60m. (E) glacier: size unclassified. An "X" denotes association only, under any of the above headings.

(2) Distance from water body. (A) stream or lake and (B) snow or ice: 0=in or at edge of water or on snow; 1=1cm to 5cm distant; 2=6cm to 15cm distant; 3=16cm to 25cm distant; 4=0.3m to 0.6m distant; 5=0.7m to 4m distant; and 6=more than 4m distant. (C) ocean or sea: 1=at high

tideline; 2=above highest tideline.

[3]Parentheses around an entry denote what I consider an uncharacteristic occurrence for members of a taxon.

Table 11. Data on characteristics of microhabitats preferred[1] by members of Nearctic Nebria taxa, II. Substrate[2], cover type[3], and exposure[4, 5].

Name of taxon	(1) Substrate								(2) Cover type				(3) Exposure
	(A) Alluvium	(B) Moraine	(C) Pyroclastics	(D) Talus	(E) Bedrock	(F) Soil	(G) Leaf litter	(H) Other	(A) Stones	(B) Logs	(C) Leaf litter	(D) Other	
virescens					X	X	X			1	X	m	0-3
paradisi			1-2		X	X			1-5				0
gouleti	2-5								2-3				0-2
hudsonica	3-7								1-3				0-3
l. lacustris	2-5								1-2				1-3
l. bellorum	2-5								1-3				2-3
n. nivalis	2-6								2-4				0

Table 11. -(continued)

Name of taxon	(1) (A)	(B)	(C)	(D)	(E)	(F)	(G)	(H)	(2) (A)	(B)	(C)	(D)	(3)
n. gaspesiana	3-6			X					3-4				0-2
c. crassicornis	2-6	X	1			X			2-4	1,2			0-1
c. intermedia	2-6					X			2-4	1,2		m	0-3
gyllenhali castanipes	2-5			X		X	X		2-3	1,2	X		0-3
g. lassenensis						X			2-3				0-3
g. lindrothi	2-5			X		X	X		2-3	1,2	X		0-3
frigida	2					X			1-3	1,2	X		0-2
lyelli		X		X	X				3-5				0
a. acuta	3-6	X	1			X			1-5				0-3
a. quileute	3-6								1-3				3
s. sahlbergii	2-6								1-3	2		d	0-3
s. modoc	3-6								1-3				3

Table 11. (continued)

Name of taxon	(1) (A)	(B)	(C)	(D)	(E)	(F)	(G)	(H)	(2) (A)	(B)	(C)	(D)	(3)
s. triad	3-6								1-3				1-3
gregaria	3-5		1		x				2-5			d	0
charlottae					unknown					unknown			?
a. arkansana	3-6				X	X			1-3				0-3
a. edwardsi	3-6				X	X			1-3				0-3
a. oowah	3-6								1-3				1-2
a. uinta	3-6					X			1-3				1-3
f. fragilis	3-6								1-3				1-3
f. teewinot	2-6								1-4				0-3
z. zioni	1-6								1-3				0-3
z. oasis	3-6				X				1-3				3
suturalis	2-6	X		X	X				1-5				0

Table 11. (continued)

Name of taxon	(1) (A)	(B)	(C)	(D)	(E)	(F)	(G)	(H)	(2) (A)	(B)	(C)	(D)	(3)
obliqua	1-4								1-3	2			0-3
appalachia	3-6								1-3				3
pallipes	2-6					X			1-3	1,2			1-3
darlingtoni	2-6								1-3				1-3
mannerheimii	1-7								1-4				0-3
desolata	3				X				1-5				3
navajo					unknown					unknown			?
escholtzii	1-7								1-4				0-3
diversa	3									3			0
g. gebleri	2-6					X			1-4				1-3
g. cascadensis	2-6					X			1-4	1,2			1-3
g. rathvoni	3-6								2-4				0-3

Table 11. (continued)

Name of taxon	(1) (A)	(B)	(C)	(D)	(E)	(F)	(G)	(H)	(2) (A)	(B)	(C)	(D)	(3)
g. siskiyouensis	3-7								2-4				1-3
g. strawberriensis	3-6					X			2-4				3
carri	3-7					X			1-3				2-3
k. kincaidi	3-7					X		b	1-4	1,2		m	3
k. balli	3-6					X		b	2-3	1,2		m	3
s. spatulata	3-6	X		X	X	X			2-5				0
s. sierrae	3-6	X		X	X	X			2-5				0
ovipennis	3-6	X		X	X	X			2-5				0-3
m. meanyi	2-6	X	1						1-5				0-3
m. lamarckensis				X	X				2-5				0
m. sylvatica	3-6								1-4				3
metallica	2-3		1			X			1-3	1,2			0-3

Table 11. (continued)

Name of taxon	(1) (A)	(B)	(C)	(D)	(E)	(F)	(G)	(H)	(2) (A)	(B)	(C)	(D)	(3)
i. ingens				X	X				3-5				0
i. riversi	4-6			X	X				2-5				0
v. vandykei		X	1-2						4-5				0
v. wyeast		X	1						4-5				0
piperi	3-6	X							3-4				0-3
s. schwarzi	2-6								1-3				0
s. beverlianna	3-								2-4				0
purpurata	3-6				X	X			2-4				0-3
t. trifaria	3-6					X			2-4	2			0-3
t. catenata	3-6					X			2-4	2			0-3
t. utahensis				unknown						unknown			?
coloradensis	3-6					X			2-4				0-3

Table 11. (continued)

	(1)								(2)				(3)
	(A)	(B)	(C)	(D)	(E)	(F)	(G)	(H)	(A)	(B)	(C)	(D)	
piute	3-6					X			2-4	2			0-3

[1]Data presented here represent my field observations supplemented by selected data from the literature (Edwards, 1975; Lindroth, 1955a, 1961, and 1963a; and Spence, 1974). Most observations were made during daylight hours. "Preferred" microhabitat therefore refers specifically to places where beetles hide during the day (see text for further comment). Ranges in data reflect ranges of observations only; and these are presented as crude estimates of actual preference ranges of taxa.

[2]Substrate: material upon which beetles stand or move.

[3]Cover type: material under which beetles hide.

[4]Exposure: degree of exposure of hiding place to direct sunlight.

[5]Code used for data presented here is as follows:

(1) Substrate. (A) Alluvium: 1=clay; 2=silt; 3=fine sand; 4=medium sand; 5=coarse sand; 6=fine to

Table 11. (continued)

medium gravel; 7=coarse gravel. (B) Moraine: unsorted till, material range from silt to boulders; unclassified. (C) Pyroclastics: 1=volcanic ash; 2=pumice lapilli. (D) Talus: unclassified. (E) Bedrock: weathered surface material (in situ); unclassified. (F) Soil: organic; unclassified. (G) Leaf litter: unclassified. (H) Other: b=under loose bark.

(2) Cover type. (A) Stones: 1=average diameter (a.d.) less than 5cm; 2=a.d. 5cm to 15cm; 3=a.d. 16cm to 25cm; 4=a.d. 30cm to 60cm; 5=a.d. greater than 60cm. (B) Logs: 1=fallen twigs, branches, bark chips; 2=trunks of fallen trees; 3=beach driftwood. (C) Leaf litter: unclassified. (D) Other: d=unclassified debris (e.g. discarded, sheet metal, beer cans, lumber, etc.); m=moss or other moist vegetative carpets.

An "X" denotes association only, under any of the above headings.

(3) Exposure: 0=open ground, completely unshaded; 1=open ground, partially shaded during few daylight hours; 2=area shaded during midday; 3=area fully shaded, except perhaps during early morning or late afternoon.

assumed, however, that selective pressures are strong for development of behavior patterns in riparian organisms which optimize avoidance of flooding danger. I have observed such behavior in members of several taxa, including N. eschscholtzii Ménétriés, and N. obliqua (in California and Alberta, respectively). Prior to the onset of the rainy season (winter in California, spring in Alberta), individuals (adults and larvae) disappear from the typical streamside habitat and, presumably, retreat to higher ground. This retreat is well in advance of any actual rise in water level and must be triggered by essentially unrelated environmental events (e.g. change in temperature or photoperiod). T. L. Erwin (personal communication) has observed identical behavior in riparian members of Brachinus species (Brachinida). As discussed below (section 3.233), riparian Nebria are apparently also able to make use of streams for certain activities, such as escape from potential predators and locomotion. Their adaptation to riparian life, therefore, steps beyond pure survival in this habitat toward more complex use of it.

Perinival habitats.--Members of 20 Nearctic Nebria taxa (29% of the fauna) are at least marginally associated with glaciers or snowfields. All members of N. paradisi and most members of N. vandykei, N. ingens, N. spatulata, and N. lyelli are perinival (i.e. prefer areas at the margins of glaciers or snowfields). At the lower altitudinal range limits for the last four taxa, members are riparian in most areas. Members of several other taxa (e.g. N. meanyi meanyi Van Dyke, N. acuta acuta Lindroth, and N. purpurata) are perinival only at the upper latitudinal range limits of their respective taxa.

Lindroth (1965) and Friden (1971) have shown that microclimate even near margins of large glaciers or icefields is much milder (as inferred from the species composition of perinival faunas) than previously assumed. However, members of Nebria taxa which specialize in use of such habitats must possess special behavioral and metabolic adaptations. Mani (1962 and 1968) discussed peculiarities of this environment and the kinds of adaptations to it seen in a variety of perinival insects. Some interesting behavior patterns observed in perinival Nearctic Nebria are discussed below.

Sea strands.--Members of two taxa, N. diversa and N. gregaria, are found only in the supralittoral zone of sea strands. I found members of N. sahlbergii sahlbergii Fischer von Waldheim and N. metallica in this habitat at Cold Bay, Alaska; but members of these taxa are riparian in most other areas sampled.

Forest and meadow habitats.--No Nearctic taxa have members which are restricted to true forest or meadow habitats (i.e. unassociated with some defined water body) although the macrohabitat ranges of most taxa are within forested zones. Members of several taxa are, however, common in moist forest and/or meadow areas. Among these taxa are N. virescens, N. gyllenhali, N. crassicornis Van Dyke, and N. trifaria and its closest relatives. In general, members of these species are riparian at lower altitudinal range limits for their respective taxa. Members of N. spatulata are found in moist, subalpine meadows at the lower altitudinal range limit for the species but completely avoid forested areas. Other taxa whose members are found in meadows (e.g. N. crassicornis, N. gyllenhali, or N. trifaria are also well

represented in moist forest areas at the same or lower altitudes.

As noted above, members of several taxa leave stream banks at certain times (e.g. to avoid possible inundation). Frequently, these beetles enter forest microhabitats and become temporary residents. Members of N. kincaidi, for example, are extremely abundant in forests during and just after spring snowmelt. By mid-summer, most individuals have moved to streambanks, where breeding and other life cycle events occur. At least some of these temporary migrations from streambanks by members of certain taxa may reflect a seasonal expansion of suitable microclimatic conditions (e.g. in temperature or moisture) which permits, rather than requires, movement (see also below).

Arctic and alpine tundras.--Members of few Nearctic taxa are found in true tundra habitats unassociated with streams, lakes, glaciers or snowfields. Members of N. crassicornis are most common in alpine tundra habitats, and those of N. gyllenhali lindrothi are as common in these areas as in other habitats. Members of N. trifaria trifaria, N. frigida, N. gyllenhali castanipes (Kirby) and N. suturalis are found on tundra only in certain geographical areas. For example, members of N. gyllenhali castanipes are restricted to tundra as on Mount Washington, New Hampshire, but to lower riparian or forest habitats in the Northern Rocky Mountains.

Talus slopes and fellfields.--Members of N. suturalis are common only in these habitats, while those of several other species, including N. purpurata, N. nivalis gaspesiana, N. lyelli, and N. spatulata are found in talus or fell areas but not restricted to them. On the surface, these habitats appear extremely barren and inappropriate for members of

a basically riparian group. However, the depths of these formations often contain flowing water, snow or ice which persists (in what are essentially cold-desert areas) throughout the year and contributes to a stable, favorable environment for Nebria.

Stream size

A relationship was found, in some instances, between size of a stream (measured as stream width) and taxon representation in its riparian Nebria fauna. For example, members of N. piperi Van Dyke, N. schwarzi and N. mannerheimii are found only on the banks of small to large rivers (width from 10m to over 60m) in most areas. Members of N. gebleri cascadensis n. ssp. are common only on the banks of small to large creeks (width from one meter to 10m) at similar altitudes. Few members of N. gebleri cascadensis are found along larger streams (i.e. with members of N. piperi and N. mannerheimii); but these are probably individuals washed out from smaller tributaries. Similar downstream drift may obscure stream size preferences in members of other taxa; and because stream size is generally correlated with altitude (i.e. larger streams at lower elevations), opportunities for valid comparisons of stream size preferences among taxa restricted to mid- and high-altitudes are few.

No clear preferences were recognized among Nearctic taxa with riparian or perinival members in relation to the size of standing water bodies (e.g. lakes, ponds, snowfields, etc.). For example, members of N. pallipes have been collected repeatedly on the shores of small ponds as well as large lakes. Members of N. paradisi and N. vandykei are found at the margins of both very small snow patches and vast

snowfields. Individuals of each appear to be relatively more abundant at the edges of small, isolated snow patches in mid- to late-summer. However, this is probably a concentration effect due simply to shrinkage of the more extensive early-season snowpack, with individuals converging as they follow receding snow margins.

Substrate, cover, exposure and moisture

Diurnal hiding places.--Members of Nebria species are most often collected during daylight hours while hiding under cover (e.g. stones or logs). Their apparent preferences for certain diurnal hiding places (characterized by substrate, cover, vegetation, exposure and moisture) are of interest not only to collectors, but also to those interested in how these cool- or cold-adapted nocturnal beetles survive the heat of day. The choice of certain hiding places is really a choice among a spectrum of diurnal microclimatic regimes. Mani (1962 and 1968) discussed (and illustrated) temperature gradients under and around surface cover (e.g. stones) relative to its size, thickness and degree of contact with the substrate. For example, spaces under or between large, thick, deeply-embedded stones provide constant, cool, moist conditions throughout the day, while the same spaces under small, thin, shallowly-embedded stones may be subject to high diurnal temperature and humidity fluctuations. Mani also briefly discussed the characteristics of different substrates in relation to temperature and moisture. Clay and silt, for example, hold more moisture than sand or gravel. However, highest evaporative cooling rates in warm, dry areas (and, therefore, the coolest microhabitats in these areas) are found in sandy substrate.

Observations indicate that Nebria are very efficient "behavioral homeotherms" (that is, they maintain body temperature within a metabolically acceptable range by following temperature gradients and confining themselves to thermally suitable areas (see also below)). I assume, therefore, that homeothermy is a driving force behind observed or presumed preferences for cover, substrate, exposure and moisture. However, selection of a hiding place with certain characteristics may also reflect other requirements (e.g. proximity to foraging areas). Further study is required before apparent preferences can be understood in relation to homeothermy or other demands in Nebria. My field data on N. desolata may, however, provide one example of the manner in which homeothermy is maintained through selection of particular substrate, cover, etc. Members of this species are found during the day only in moist, sandy substrate under sandstone blocks at the undercut bases of cliffs. They avoid all other types of cover (e.g. granite stones) in the area. Temperature data recorded on June 22, 1971 at 15:00 in one locality (see further notes in section 3.43) were as follows: air (at waist height), 33°C; stream, in sun (at 3cm depth), 30°C; stream, in shade of overhanging cliff, 25°C; moist sand in shade, 14°C. This amazing thermal gradient occurred over a linear distance of about two meters and resulted from evaporative cooling in the shaded cliff base. Because sandstone blocks, but not granitic stones, can absorb and release moisture readily and thereby participate in the evaporative cooling process, only the sandstone provided sufficiently cool hiding places for the beetles (see comments of Lindroth, 1949:817). Temperature in the microhabitat occupied by the beetles (i.e. 14°C) was similar to values

recorded in hiding places of members of numerous other taxa in other geographical areas; but other microhabitats in the area described above were too hot.

One implication of the example above is that what are observed as preferences for certain substrate, cover or exposure characteristics might be better interpreted as simple responses to temperature, moisture, or other environmental gradients. However, in the absence of additional detailed environmental data to compare with microdistributional data on taxa, observed 'preferences' are treated as such in the following discussion.

Substrate preferences are evident among members of several Nearctic Nebria taxa, although members of most taxa show no such preferences. Members of N. diversa are found only on coarse sand (under driftwood and other debris on open, sandy ocean beaches). Members of N. metallica and N. frigida are, in most areas, found only on silt substrates, those of N. piperi and N. desolata only on sand. Members of N. vandykei and N. paradisi clearly prefer volcanic ash substrates when these are available; but those of the former taxon prefer morainal substrate (i.e. mixed silt ["glacial flour"], gravel and stones of varying size) at lower altitudes. Members of N. suturalis, N. ingens, N. lyelli and N. spatulata appear to prefer bare rock substrates and are found most commonly in talus slopes hiding between stones.

Members of N. virescens, N. gyllenhali and N. crassicornis are commonly found in forests on organic soil; but neither these nor members of other Nearctic taxa are restricted to this substrate. Members of a majority of taxa are found on a variety of substrates,

dependent on the array available. An altitudinal transect along the course of any stream will generally demonstrate transition, with decreasing altitude, from bare rock, through gravel and sand, to silt and clay as the most common substrate--a fact consistent with details of the erosion cycle. Examples of apparent substrate preference noted above do not include those in which altitudinal range of the taxon significantly restricts the substrate range available. It is often tempting, however, to label instances of differential substrate availability as substrate preferences. For example, members of N. lacustris lacustris are found commonly only in sand/gravel substrates at high elevations in the Adirondack Mountains, New York, but on clay/silt substrates at lower elevations in that state. Members, therefore, occupy a wide range of substrates over the range of the taxon, but appear restricted to certain substrates in certain areas. These apparent local substrate preferences merely reflect differences in the availability of various substrate types at different altitudes.

I have repeatedly observed an interesting behavioral response to disturbance by members of three taxa (N. acuta acuta, N. meanyi meanyi and N. vandykei) commonly found in morainal substrate (at high altitudes). Recent (post-Glacial), barren moraines, especially those being undercut or eroded by streams, are extremely unstable formations of mixed composition (including silt, boulders and particles of intermediate size). Removal of a single stone (or an errant footstep) can initiate substantial slides of this unconsolidated material. Most Nebria seek deeper cover when their hiding places (e.g. in talus slopes or on rocky stream banks) are disturbed. When moraines described above are disturbed, however, members of these three taxa immediately begin

to leave their hiding places, often in large numbers, and run on the surface, even in broad daylight. I term this exodus the 'avalanche response' and suggest that it may be highly adaptive for survival in this substrate. The size composition of morainal deposits is such that interstitial spaces normally occupied by the beetles could easily be compressed or filled by small-sized particles during or as a result of landslide, thereby trapping or smashing the beetles. With other cover/substrate combinations (e.g. stones in gravel), interstitial spaces may change position but are not eliminated with disturbance. The 'avalanche response' is therefore viewed as a mechanism to avoid burial in this unique microhabitat.

Preferences for particular type and size of cover are apparently rare among Nearctic Nebria (see Machard, 1970, for brief notes on cover preferences in members of some Palaearctic alpine species). In general, cover of all sizes and types (e.g. stones, logs or other available debris) are used by members of mid-altitude taxa. At lowest altitudes, beetles seek shaded areas (see below) or only larger stones or water-soaked logs. At highest altitudes, larger stones are clearly favored.

Examples of apparent preferences for cover type or size include the following. Members of N. frigida are common, in most areas, only in thin leaf litter or under twigs, bark chips or small logs but not stones. In forests, members of N. gyllenhali are common only under logs and apparently avoid stones in the same but not in other habitats (e.g. members are commonly found under stones along streams). As noted above, members of N. desolata are found only under sandstone blocks and chips and avoid other cover. Members of N. piperi appear to prefer

very large stones adjacent to broad, flat, moist sandy beaches for cover; and those of N. vandykei are most often found under very large and deeply-embedded stones at the margins of snowfields.

Members of most Nearctic taxa are found on barren ground, whether on rocky stream banks, margins of snowfields or in talus slopes. Some members of N. ovipennis, N. gyllenhali and N. crassicornis are found under stones in alpine and subalpine meadows of sparse to dense, low vegetation (e.g. Carex spp., alpine Salix spp.). Members of N. virescens, N. gyllenhali and N. crassicornis are common in forests with sparse to moderately dense understory vegetation; and those of N. frigida are found commonly only under streamside vegetation (Salix, Alnus and Populus spp.), except above or north of treeline.

Preferences for different degrees of exposure are conspicuous only in a few instances. Members of N. gebleri cascadensis, N. kincaidi, N. carri and some other taxa are common only on streambanks which are barren (free of vegetation) but fully-shaded by the adjacent forest canopy. Members of N. desolata are found only in the shade of undercut sandstone cliffs. Nebria inhabiting arctic and alpine areas are subject to extreme exposure. Members of some of these taxa (e.g. N. vandykei) have been found in exposed, but not in shaded, areas below treeline, suggesting an actual preference for the former. Members of most taxa exhibit no clear exposure preference, but rather seek shaded hiding places in warmer areas (e.g. at lower altitudes and latitudes) and more exposed places at upper altitudinal or latitudinal limits for their respective taxa.

Moisture appears to be an extremely important factor in both the macro- and microhabitat distributions of Nebria. Members of most taxa

are closely associated with water bodies (streams, lakes, glaciers, etc.) or at least moist areas (in meadows or forests). Field observations have convinced me, however, that the temperature-modifying effects of these water sources are much more important for Nebria than moisture or humidity considerations per se. It is possible that moisture may be a critical factor for the egg stage of the life cycle in most or all species; but adults, larvae and pupae exhibit marked independence from water bodies in areas where thermal requirements are otherwise satisfied. For example, members of N. gyllenhali lindrothi are restricted to the margins of streams only at low altitudes (ca. 2500m) in the Rocky Mountains of Colorado and New Mexico. At highest altitudes (ca. 3900m) in the same region, members are found on open, dry tundra. Similarly, members of N. meanyi meanyi are confined to stream margins at low altitudes (ca. 800m) on Mount Rainier, Washington, but range widely in relation to streams and snowfields at or above timberline there (ca. 1700m). Members of N. diversa and N. gregaria are found along exceptionally cool stretches of sea coast and have no direct association with the ocean or other water bodies.

Members of all strictly riparian taxa show much more subtle, but equally impressive responses to temperature as modulated by streams. Over a taxon's altitudinal range in a particular area, members are found to occupy hiding places of differing distance from the stream margin, depending on altitude. This distance/altitude relationship is always direct (i.e. increased distance from the water margin with increased altitude). For example, members of N. hudsonica are found only within 10cm of stream edges in exposed areas at 2000m in the Front

Range, Colorado, but at distances up to two meters from the water at 3000m on the same streams. Where members of several different species are found together on a streambank, the distances of their respective hiding places from the water almost always reflect (conversely) the altitudinal ranges of their respective taxa--that is, members of taxa with higher altitudinal ranges are found closer to the water at a given altitude than members of taxa with lower altitudinal ranges. Fig. 359 illustrates this relationship using field data on members of N. hudsonica, N. obliqua and N. gyllenhali lindrothi in the Front Range. Spence's (1974) findings for members of N. pallipes and N. lacustris lacustris in Vermont also reflect this relationship. My interpretation of these and similar findings with other taxa is that temperature rather than moisture is the critical factor limiting microhabitat distribution.

Substrates for nocturnal activity.--Data on substrate preferences during nocturnal activity periods are few. My own field observations (and those of Edwards, 1975, and Spence, 1974) suggest that these beetles are active at night in roughly the same microhabitats in which they take cover during the day, except for perinival forms. Daytime collecting, therefore, gives an approximation of substrate preferences during activity. Perinival beetles are active on the snow surface at night but leave it to hide elsewhere during the day. Table 12 summarizes available data on nocturnal substrate preferences.

In some areas, members of several different taxa are commonly found hiding together under the same stone(s) during the day. The assumption that members of each also prefer similar substrates at night

may be correct in many instances. For example, members of N. paradisi, N. vandykei, N. meanyi meanyi, N. acuta and N. crassicornis are found together under stones in one or another locality, and all are found on snowfields at night. However, preferences for similar diurnal hiding places do not necessarily mean that nocturnal preferences are also identical. At an altitude of 600m on Nisqually River, Mount Rainier, Washington, for example, members of N. acuta acuta, N. mannerheimii, N. piperi, and N. sahlbergii sahlbergii were together hiding under stones within one meter of the stream margin during daylight hours. At night, however, members of these taxa differed in their respective preferences for substrate and substrate moisture. Members of N. piperi were only on open, moist, sandy flats between rocky areas; those of N. acuta acuta were only on stones; those of N. mannerheimii were active on dry sand and silt at distances up to 10m from the stream margin; and those of N. sahlbergii sahlbergii were on various substrates within two meters of the water margin.

Additional data on nocturnal substrate preferences are critically needed. Meager data presented above are sufficient to suggest that members of different taxa may utilize slightly different microhabitats at night, a fact not apparent from daytime collecting and observations. Night collecting can provide more pertinent data as well as more interesting encounters with these beetles (i.e. during their periods of activity) than daytime collecting.

Summary: microhabitat preferences, distribution and temperature

Geographical and habitat distribution patterns of taxa result from a complex interplay of environmental and historical factors with the

Table 12. Summary of data on nocturnal activity in members of Nearctic Nebria taxa.

Name of taxon	(1) Date[1]	(2) Time[2]	(3) Lunar phase[3]	(4) Substrate[4] (A) clay	(B) silt	(C) sand	(D) gravel	(E) boulders	(F) snow, ice
l. lacustris[5]	7/15-8/9	19:00-01:00	?				X		
c. crassicornis	8/11	21:30-23:30	NM						X
c. intermedia[6]	6/31-8/8	02:00	LQ-FQ						X
gyllenhali castanipes[6]	8/17-8/28	03:30	NM				X		X
a. acuta	8/1-8/30	dusk-23:30	FM-NM						X
s. sahlbergii	8/6-8/9	22:00-23:15	NM		X^m	X^m	X^m	X	
obliqua	6/11-7/23	23:30-01:00	FM				X^m		
pallipes[5]	7/15-8/9	19:00-01:00	?				X		
mannerheimii	8/6-8/9	22:00-23:15	NM		X^d	X^d			
desolata	6/21	22:00-23:00	NM			X^m			

Table 12. (continued)

Name of taxon	(1)	(2)	(3)	(4) (A)	(B)	(C)	(D)	(E)	(F)
eschscholtzii	5/10-11/7	23:00	FM			X[m]		X	
g. gebleri[6]	8/28	03:30	NM						X
g. cascadensis	8/9	22:00-23:15	NM			X[m]			
m. meanyi	8/3-8/29	20:15-23:30	FM-LQ						X
metallica	8/9	22:00-23:15	NM		X[m]	X[m]			
v. vandykei	8/5-8/10	dusk-23:30	LQ-NM						X
v. wyeast	8/3-8/30	20:15-23:30	FM-LQ						X
piperi	8/1-8/6	20:15-23:30	LQ-NM			X[m]			
purpurata	6/11	23:30-01:00	FM			X[m]	X[m]		

[1]Data on date of observation include earliest and latest month/day records.

[2]Data on time of observation include earliest and latest nighttime records.

Table 12. (continued)

[3]Code for lunar phase data is as follows: NM=new moon; FQ=first quarter; FM=full moon; and LQ=last quarter.

[4]Superscript letters for substrate data denote the following: [m]=substrate moist; [d]=substrate dry.

[5]Data from Spence (1974)

[6]Data from Edwards (1975, and personal communication)

intrinsic capacities (tolerance) of their members over time. Explanations based on few environmental factors for such long-term and complex interactions are seldom accurate or sufficient. However, my review of macro- and microhabitat distributions among Nearctic Nebria, as discussed above, leads me to conclude that thermal requirements of members of these taxa are preeminent in limiting habitat distributions. I interpret shifts in apparent microhabitat preferences with altitude, latitude and season as responses to temperature. Preferences for certain microhabitat types and substrate, cover, exposure and moisture characteristics of the environment are actually choices among respective effects on temperature--that is, in each instance, temperature effects appear to be critical. One probable exception is seen in nocturnal substrate preferences, presumably because temperatures at night are generally well within tolerance limits of members of most taxa. By extension, it is reasonable to suggest that these same thermal tolerances are (and have been) important in limiting the geographical ranges of taxa (see Kavanaugh (in press A) and section 4.2 below for further discussion).

The ways in which temperature may be operative in limiting habitat and/or geographical distribution are potentially numerous and, at present, impossible to designate for any Nebria taxon. Relationship between microhabitat distribution and temperature may be relatively simple--dependent, for example, on thermal characteristics of available daytime hiding places. Macrohabitat and geographical distributions are probably related to temperature in complex ways, different for and perhaps unique to members of each taxon. For example, Kavanaugh (in press A) noted that northern and eastern limits to the geographical

range of N. eschscholtzii corresponded to certain isotherms for mean monthly minimum in air temperature for January. Because members of this species overwinter most commonly as larvae (presumably a more fragile stage than the adult), cold winter temperatures may well limit distribution. However, any number of other circadian, seasonal or longer-term temperature effects may actually be critical in this example and are undoubtedly so in other instances. Temperature relationships may also be different for each life cycle stage, at least in some taxa. The extent to which critical temperature effects can be recognized for any given Nebria taxon is dependent on the quality and completeness of temperature and other environmental data. Lindroth (1963a) demonstrated what can be done with sound climatic data. Unfortunately, such data are generally unavailable at present.

3.232 Life history

Lindroth (1961), in his treatment of the majority of Nearctic Nebria taxa, presented data on life histories. Through my field and laboratory studies on these taxa and a review of recent literature, a body of new data can now be integrated with his. The results of my review of this expanded data pool are summarized here. Details on life history for the various taxa are presented with descriptions of taxa (section 3.43).

For convenience, I have divided discussion on life history into two parts: (1) diel (daily) activity cycles, and (2) life cycles and seasonal activity.

3.2321 Diel activity cycles

As noted above, members of apparently all Nebria taxa are nocturnal--that is, they are actively moving about (at least "on foot"), feeding, etc. on the surface (out from under cover) only at night. That this activity is strictly nocturnal has been substantiated by field experiments only for members of N. brevicollis (Williams, 1959; see also Schiller and Weber, 1975, Thiele, 1969a, and Thiele and Weber, 1968) in western Europe. Instances of diurnal or crepuscular activity in one or a few individuals of certain taxa have been noted. Allen (1967) collected two individuals of N. ingens riversi Van Dyke seen running on snowfields at midday on the slopes of Mt. Lyell (at 3510m), Sierra Nevada (California). I found one N. suturalis individual active on the rocky summit of Grays Peak (4350m) (Colorado) during a heavy, dense mist at about 14:00 hours. I have repeatedly observed a few members each of N. acuta acuta, N. piperi and N. vandykei leaving cover just before sunset at various localities. In spite of these few exceptions, an assumption of strict nocturnal activity is probably valid for members of all Nearctic taxa. Nothing is known, however, about the activity of members of populations living in far northern areas where daylight is continuous during summer months. [See section 3.233 for discussion of flight activity, which, when present, may be strictly diurnal!]

Observations on the nocturnal activity of Nearctic Nebria are few. Edwards (1975) has found members of several different taxa active on snowfields at night (Glacier National Park, Montana). Data now available are presented in Table 12 (see also the discussion above on

nocturnal substrate preferences). Times listed represent collecting periods or times of capture of specimens; and, therefore, these data are insufficient for defining actual temporal ranges of activity. Williams (1959) used time-sorting pitfall traps to study activity period in N. brevicollis. He showed that activity of adults was restricted to the period between sunset and sunrise; but his sampling intervals were too long to permit more detailed analysis of activity during the night (e.g. comparing activity at different hours). At present, details on the temporal range of nocturnal activity are not known for members of any Nearctic Nebria taxon. We also know nothing about the possible effects of such factors as temperature, humidity, precipitation and the lunar cycle on nocturnal activity in these taxa, although we can assume that one or more of these factors must have some effect.

All existing data on Nearctic taxa suggest that larval activity is also strictly nocturnal. Spence and Bell (unpublished manuscript) have confirmed this for larvae of N. pallipes and N. lacustris lacustris. However, Williams (1959) found that, in N. brevicollis, first and second instar larvae apparently spread their activity period more uniformly over 24 hours, while third instar larvae are similar to adults (i.e. nocturnal). The extent to which this difference between larval instars occurs in Nearctic taxa is unknown.

As discussed above, Nebria individuals spend daylight hours hiding under cover. In general, the beetles are inactive (motionless) during this time unless disturbed. However, I have found individuals feeding or pairs of individuals copulating in these hiding places. I assume that diurnal feeding results when a potential prey blunders into the

beetle in its hiding place, and that diurnal copulation is either a continuation of an encounter of the previous night or the result of an encounter in the hiding place. I see no need to suggest active, diurnal searching by these beetles for either food or mates.

3.2322 Life cycle and seasonal activity

Life cycle

The life cycle of all Nebria studied includes egg, larval, pupal and adult stages, with the larval stage comprising three instars, as in most carabids. Timing of the cycle with the seasons varies considerably among taxa; but, in general one year is required for its completion. However, as discussed below, considerable plasticity is evident in both duration and timing of life cycle events in at least some taxa.

Adults.--Individuals are most commonly seen and collected in the adult stage. Regardless of cycle timing, at least some adults of all taxa can be found during any month of the year, provided that snowcover does not preclude collecting. Even in the extreme example of N. virescens, adults of which are not found abundantly in any season and are especially rare during summer months, individuals have been collected in all months of the year. Average longevity of adults is unknown for all taxa; but because at least a few adults are present at any given time, some overlap of consecutive generations must be routine. The extent to which adults are reproductively active for additional years is also unknown. However, Joyce Bell (personal communication) recaptured one N. pallipes female in September, 1970, which she had

marked and released one year before. This female laid one egg before dying, and, on autopsy, was found to contain "15 mature eggs and clusters of immature ones." It is probable, therefore, that at least some adults of this and other species live and are reproductively active for more than a single year.

Eggs.--I have not yet found eggs of Nebria in the field. Under laboratory conditions, eggs were, in most instances, deposited in the substrate, singly or in loose clusters. Among those taxa kept in culture, females of N. hudsonica were unique in depositing their eggs in very tight clusters of two to four eggs each. Depth of oviposition is apparently dependent on substrate. In most instances, cultures were maintained on moist peat moss, and eggs were deposited as deep as one centimeter below the surface in this medium. Occasionally, eggs were deposited on the surface. Without exception, these eggs proved to be inviable. One particular group of N. lacustris lacustris females collected on 13 June 1973 at Port-au-Saumon, Quebec, and kept alive in culture deposited eggs on the substrate surface on 23 June. None of these eggs developed further. These same females deposited more eggs beginning on 20 August 1973, a date within the oviposition period for members of this taxon in the field (Spence, 1974). All eggs were deposited in the substrate and numerous larvae eventually emerged. Females may rid themselves of inviable or unfertilized eggs by dumping them on the surface, thereby saving the extra energy needed to carry or bury them.

Eggs of all species studied have a very sticky surface film. Even moist substrate sticks tightly to eggs, suggesting that the substance involved is insoluble in water. Such a binding substance would be of

particular importance for riparian beetles (e.g. most Nebria), because without some holdfast capability, eggs, which float, would be washed from the substrate quite easily.

No data on fecundity or duration of the egg stage are available for members of Nearctic taxa. Penney (1966) reported that females of N. brevicollis, kept in an outdoor insectary (at Rossdhu, Scotland) laid an average of 31 eggs each over an average oviposition period of 27 days. Most eggs required 17 days to hatch. Luff (1976) found roughly equivalent fecundity in N. brevicollis females at Close House (Heddon on the Wall, Northumberland, England) but a much longer oviposition period (lasting from October, 1965 to April, 1966). In my own studies, rate of development was clearly affected by temperature. All cultures were kept at a constant 18°C, a temperature well below daytime temperatures in the field. Development in the laboratory was much slower than in the field for members of most taxa.

Preliminary comparative study of chorionic structure, using a scanning electron microscope (S.E.M.), indicates that eggs of different taxa may exhibit very great surface differences. I plan to explore use of this and other egg characters in a future study.

Larvae.--Nebria larvae have been infrequently collected or studied, probably because they are relatively inconspicuous and because their occurrence is, in general, quite seasonal compared to that of adults. However, during the peak larval period for a particular taxon, larvae are very abundant and easy to collect and observe.

The main obstacle to comparative natural history studies on larvae is (and has been) inability to distinguish larvae of different taxa.

Larvae of N. pallipes and N. lacustris lacustris are the only ones yet described (Spence, Bell and Bell, 1976) among Nearctic taxa. Andersen (1970) redescribed the larvae of N. nivalis nivalis (Holarctic range) and N. gyllenhali gyllenhali (Palaearctic subspecies) from localities in Norway. I plan to develop a key to larvae of Nearctic taxa as part of a future study on the immature stages of Nebria.

Larvae are extremely voracious predators, especially as first instars (see also Penney, 1966:511). Those of all taxa studied in culture were found to be highly cannibalistic, even when other acceptable food was available. They appear to react positively to movement, attacking any small, moving prey (including other conspecific larvae) which pass nearby. In many of these encounters between larvae, however, both participants attack simultaneously and then withdraw from the fray.

I doubt that cannibalism is restricted to laboratory conditions, and, in fact, have occasionally found larvae feeding on other Nebria larvae in the field. It is therefore possible that, in those instances when other prey are scarce, conspecific prey may be an important food source. However, selection for behavior which reduces the incidence of cannibalism should be strong. One possible behavioral adaptation would be adoption of sedentary habits, thereby decreasing or eliminating encounters between larvae. I have repeatedly observed, both in cultures and in the field, that larvae of some taxa (e.g. N. gyllenhali castanipes and N. diversa) construct cells under cover, even as second instar larvae. Some cells, especially those of some third instar larvae, are undoubtedly for pupation and/or overwintering; and larvae in these cells are, in most instances, inactive after the cell is

completed. However, these functions cannot account for all instances of cell construction. Cells in which N. diversa second and third instar larvae were found on 28 October 1972 (Chesterman Beach, Vancouver Island) are illustrated in Fig. 360 . Each cell included a broad, shallow upper chamber and a narrow, deep lower chamber. Larvae in the cells were quite active, frequently found with forebody in the upper chamber and abdomen in the lower. When disturbed, they retreated backward into the lower chamber, much like cicindeline larvae. I suggest that prey are seized as they take cover in the upper chamber, and that forays on the surface are seldom made by or are necessary for these larvae. Encounters with other N. diversa larvae would, therefore, be few. Larvae of many taxa are, however, active on the surface (i.e. they are frequently collected in pitfall traps), as was shown by Luff (1976), Penney (1966) and Williams (1959) for N. brevicollis larvae and by Spence (1974) for N. pallipes and N. lacustris lacustris larvae. Mechanisms for reduction of cannibalism among members of these taxa are unknown. Greenslade's (1964a) pitfall data for N. brevicollis suggest that larval activity is considerably less than adult activity, although, logically, larvae must be more abundant at some time than adults. This finding could be interpreted as evidence for some level of sedentary habits even among species with relatively active larvae.

Rates of larval development in Nebria are, within limits, temperature-dependent (Luff, 1976), and, therefore, vary from year to year and between different localities. Developmental rates have not been studied in Nearctic taxa. Penney (1966) reported that N. brevicollis larvae spent 11 to 14 days in the first instar, 11 to 14

days in the second instar, and a highly varied period in the third (overwintering) instar at ambient temperatures in an outdoor insectary (Rossdhu). Luff (1976) reported that mean development times for the same instars in N. brevicollis members kept at 10°C in an incubator were approximately 23, 27 and 83 days, respectively. As noted above for eggs, laboratory conditions appear to retard larval development, probably because higher field temperatures promote more rapid development there.

Pupae.--In more than eight years of collecting, I have found only six Nebria pupae in the field, including two not yet identified and one each of the following taxa: N. crassicornis crassicornis Van Dyke (15 August 1972, Mount Rainier, Washington), N. fragilis teewinot n. ssp. (13 July 1972, Green Rivers Lakes, Wyoming), N. gyllenhali castanipes (11 June 1973, Mount Albert, Quebec) and N. obliqua (3 April 1973, Edmonton, Alberta). That pupae are so rarely seen suggests that some peculiar microhabitat shift precedes pupation. However, all pupae found were under cover in areas where adults and larvae of the same taxa are commonly collected. Several pre-pupal third instar larvae, representing various taxa, have also been collected in areas commonly occupied by individuals at adult and larval stages. All pupae and pre-pupal larvae were found in relatively large cells (diameter, 1.5 to 2.0cm); and although digging capabilities of Nebria larvae are probably not great, some capacity for excavation is apparent. Pupation may, therefore, generally occur deeper in the substrate than my few discoveries suggest (see also Penney, 1966:507).

Several days prior to the pupal molt (e.g. three days in members

of N. brevicollis, Penney, 1966), third instar larvae enter a quiescent pre-pupal stage. Following molt, pupae assume a supine position, supported above the substrate by long, erect setae on the dorsum, just as in other carabids studied (e.g. see Erwin, 1967). At least in members of N. brevicollis, duration of the pupal stage is also temperature-dependent (Luff, 1976). In laboratory experiments, pupal period ranged from seven days (at 22°C) to more than 40 days (at 5°C). Penney (1966) reported that eight days were spent in the pupal stage under field conditions at Rossdhu in 1963 and 1964 (Penney, 1966).

Adults of some taxa apparently remain in their pupal cells for a considerable time following eclosion (imaginal molt). Darlington (Lindroth, 1961:74) noted that, in members of N. suturalis on Mount Washington (New Hampshire), eclosion occurs in autumn, but adults remain in pupal cells until spring. I found fully-sclerotized and pigmented adults of N. piute Erwin and Ball in pupal cells on Circleville Mountain (Utah) in June, 1973. Teneral N. piute adults have been collected in September, unassociated with pupal cells (T. L. Erwin, personal communication), suggesting that members overwinter as adults but do not necessarily remain in pupal cells until spring. As teneral adults, Nebria are soft, easily injured and, as observed in both the field and laboratory, subject to predation by fully-sclerotized conspecific adults or other predators. Because mature adults rarely attack one another, a tendency to remain in pupal cells at least through the teneral phase could increase survival and reduce cannibalism among adults.

Life cycle timing

Variation in seasonal timing of the life cycle among carabids as been studied by Greenslade (1965), Larsson (1939), Lindroth (1949) nd Thiele (1971). These authors discussed timing of life cycles in relation to geography and synoptic climate, and to geographical and habitat distributions of taxa. They classified beetles according to temporal characteristics of their respective life cycles. Larsson noted that carabids could be described as either "spring breeders" or "autumn breeders," terms also used by Thiele. Lindroth, followed by Greenslade, classified carabids according to stage in which they overwinter--that is, either as "larval overwintering" or "adult overwintering" beetles. These two classification schemes are essentially equivalent. However, as discussed below (section 4.22), stage of overwintering may be important in limiting distributions of taxa and is, therefore, the more significant character.

As outlined by Greenslade (1965), timing of life cycles for taxa in which members overwinter as adults is as follows: breeding, oviposition and larval hatching in spring or early summer; pupation in late summer or early autumn; eclosion in autumn (Fig. 361). On this regime, adults of some taxa may enter a cold (winter) diapause. For taxa in which members overwinter as larvae, timing is as follows: pupation in spring; eclosion in spring or early summer; oviposition and larval hatching in late summer or autumn; larval development in autumn and winter. Adults of some taxa (e.g. N. brevicollis) on this regime enter a summer diapause while those of other taxa are active throughout the summer. Overwintering larvae of some taxa (e.g.

N. diversa) remain active until the pre-pupal phase, but those of other taxa may enter a cold diapause (see below).

Life cycle timing in N. brevicollis has been studied in great detail, through both field studies (Gilbert, 1958; Greenslade, 1964a and 1965; Penney, 1966; Richards, 1946; Schiller and Weber, 1975; and Williams, 1959) and laboratory experiments (Luff, 1976; Penney, 1969; and Thiele, 1969b). As noted above, most members of this species overwinter as larvae, and most adults enter a summer diapause (aestivation). Spence (1974) and Spence and Bell (unpublished manuscript) have shown that most members of both N. pallipes and N. lacustris lacustris in Vermont also overwinter as larvae, but that adults there do not enter a summer diapause. Except for Spence's study and brief statements on life history provided by Lindroth (1961), no synthesis of information on life cycle timing in Nearctic taxa has appeared. Table 13 provides a survey of temporal data on life history of Nearctic Nebria. Sources of data used in the table include field collections and observations, laboratory observations from rearing studies, museum specimens and literature records. Museum specimens were principally useful in estimating temporal distributions of adults, especially teneral adults. Statements on life cycle timing in discussions below represent interpretations of data surveyed in the table and presented in more detail with the descriptions of taxa (section 3.43).

Members of 34 (50%) of the 68 Nearctic taxa recognized apparently overwinter almost exclusively as adults. In 11 other taxa (16%), a majority of members overwinter as adults, but some members overwinter as larvae. Members of 10 taxa (15% of the fauna) overwinter almost

Table 13. Summary of data[1] on life cycle timing in Nearctic Nebria taxa.

Name of taxon	(1) Adults		(2) Eggs[2,3]	(3) Larvae			(4) Pupae	(5) Overwintering stage[4]
	(A) hardened	(B) teneral		(A) first instar	(B) second instar	(C) third instar		
virescens	2-12	4-6	11-12	12-1	1	2	?	L[a]
paradisi	6-9	6-8	8	9	10	8	8	A[b]
gouleti	4-10	4-7	8	9-10	9-10	10	?	L
hudsonica	4-10	[5-8][5]	7-8	?	?	9	?	[A/L]
l. lacustris	4-11	[4-8]	6[1]-8	9-10	9-10	9-12	?	[L/A]
l. bellorum	5-10	5-6	8	9	9	10	?	L
n. nivalis	6-9	7-9	7	7	8	8	?	[L/A]
n. gaspesiana	6-7	7	6	6	7	?	?	A

Table 13. (continued)

Name of taxon	(1) (A)	(1) (B)	(2)	(3) (A)	(3) (B)	(3) (C)	(4)	(5)
c. crassicornis	5-9	7-9	8	8	9	8	8	A[b]
c. intermedia	5-10	5-9	6-7	7-8	7-9	5-10	?	L[a]
gyllenhali castanipes	4-10	[4-8]	6-8	6-10	8	6	6	[L/A]
g. lassenensis	8-10	7-8	?	?	?	?	?	A
g. lindrothi	6-9	6-8	?	?	?	11	?	A
frigida	6-9	6-8	7	7	8	8	?	A
lyelli	7-9	9	?	?	?	?	?	A
a. acuta	5-9	6-8	8	8	10	10	?	A[b]
a. quileute	5-8	7	?	?	?	?	?	A
s. sahlbergii	4-10	[5-10]	8-10	9-11	10-11	10-2	?	L
s. modoc	5-6	6	?	?	?	?	?	L
s. triad	6-8	6-7	?	?	?	?	?	L

Table 13. (continued)

Name of taxon	(1) (A)	(1) (B)	(2)	(3) (A)	(3) (B)	(3) (C)	(4)	(5)
gregaria	5-9	5-8	7	9-10	10	10	?	L
charlottae	?	?	?	?	?	?	?	?
a. arkansana	6-9	6-9	9	?	10	11	7	A[b]
a. edwardsi	5-9	[7-9]	7-8	?	?	?	?	[A/L]
a. oowah	8	8	8	10	11	?	?	A
a. uinta	8	8	?	?	?	?	?	A
f. fragilis	6-8	6-8	8	10	11	12	?	A
f. teewinot	7-8	7-8	?	?	?	?	?	A
z. zioni	5-8	6-7	7	9	10	11	?	A
z. oasis	6	?	9	10	11	1	?	A
suturalis	6-9	7-8	[6-9]	7-9	7-9	10	?	A[b]
obliqua	4-10	[4-9]	7-8	8-9	8-11	9-11	5	[L/A]

Table 13. (continued)

Name of taxon	(1) (A)	(1) (B)	(2)	(3) (A)	(3) (B)	(3) (C)	(4)	(5)
appalachia	5-9	[5-8]	8	9	9-10	?	?	[L/A]
pallipes	3-11	[4-10]	8-10	8-10	8-10	10	?	L
darlingtoni	6-9	?	?	?	?	?	?	?
mannerheimii	3-10	4-8	8-9	10	10	10	?	L
desolata	4-7	6	8	9	10	10	?	A^b
navajo	6	6	?	?	?	?	?	?
eschscholtzii	1-12	2-8	8-9	10	10	11	?	L
diversa	2-12	4-7	11-12	12	10	10	?	L
g. gebleri	5-9	5-9	7	7-8	9	10	?	A^b
g. cascadensis	5-10	5-9	7	7-8	9	10	?	A^b
g. rathvoni	4-9	7-9	7-8	9	9-10	10-11	?	A
g. siskiyouensis	6-8	?	7	7-8	8	?	?	A

Table 13. (continued)

Name of taxon	(1) (A)	(1) (B)	(2)	(3) (A)	(3) (B)	(3) (C)	(4)	(5)
g. strawberriensis	5	?	?	?	?	?	?	A
carri	7-8	8	?	?	?	?	?	A
k. kincaidi	6-8	7-8	8	9	10	11	?	A
k. balli	5-9	6-9	?	?	?	?	?	A
s. spatulata	7-9	9	8	9	9	11	?	A
s. sierrae	7-9	7-9	?	?	?	?	?	A
ovipennis	5-9	7-9	8	9	10	11	?	A
m. meanyi	6-10	6-9	7	9	10	11	?	A
m. lamarckensis	7-8	8	7	9	9	10	?	A
m. sylvatica	5-8	7-8	?	?	?	?	?	A
metallica	5-9	5-9	7-8	9	9	10	?	A/L
i. ingens	7-9	7-9	7-8	9	10	?	?	A

Table 13. (continued)

Name of taxon	(1) (A)	(1) (B)	(2)	(3) (A)	(3) (B)	(3) (C)	(4)	(5)
i. riversi	7-8	?	?	?	?	?	?	A
v. vandykei	7-8	8	8	8	9	10	?	A
v. wyeast	6-8	7-8	?	?	?	?	?	A
piperi	5-9	6-9	7	9	10	11	?	A[b]
s. schwarzi	6-9	7-8	7	7	8	8	?	A
s. beverlianna	7-8	8	8	8	9-10	10	?	A[b]
purpurata	6-9	6-9	6-8	8	9	9	?	A
t. trifaria	5-9	7-9	7	9	9	10	?	A
t. catenata	6-9	7-9	?	?	?	?	?	A
t. utahensis	7	7	?	?	?	?	?	A
coloradensis	6-8	7-8	?	?	?	?	?	A
piute	6-9	7-9	7	9	9	9-6	6	A[b]

Table 13. (continued)

---

[1]Temporal data presented here are derived from field and laboratory observation, specimen labels, and the literature. Numbers refer to consecutive months of the year (e.g. 1=January).

[2]Data in italics are from laboratory rearing studies alone.

[3]No eggs were collected in the field; but many were obtained as soon as adults were captured. These are considered here as obtained from the field. Superscript "i" denotes eggs which were apparently inviable when deposited.

[4]Assignment of a taxon to one or more classes of overwintering stages is based on review of all available evidence, however meager. Code used for data on overwintering stage is as follows: A =all or almost all individuals overwinter as adults; A^b =most individuals overwinter as adults, but some do so as larvae; L =all or almost all individuals overwinter as larvae; L^a =most individuals overwinter as larvae, but some do so as adults. A/L and L/A =overwintering of individuals in either adult or larval stage, but a few more do so in the first-mentioned stage than in the other.

[5]Brackets denote apparent geographical variation in timing.

exclusively as larvae; and those of another two taxa (three percent) overwinter mainly but not exclusively as larvae. Combining classes, I find that most members of 66% of Nearctic taxa overwinter as adults and those of 18% of the fauna do so mainly as larvae. Variation in overwintering stage among members of N. appalachia, N. obliqua, and other taxa is too complex to permit assignment of these taxa to one of the above classes at present (see below and species descriptions for further discussion on life cycle timing in these taxa). Overwintering stage is yet unknown for members of N. charlottae, N. darlingtoni, and N. navarrae.

An impression obtained from review of the literature on timing of life cycles (see Greenslade, 1965; Larsson, 1939; Lindroth, 1949; and Thiele, 1971) is that individuals of a given taxon are sufficiently synchronous in their development to permit assignment of that taxon to one of the above classes. However, some level of asynchrony appears to be universal in Nebria, in some instances so common that classification of the taxon as a whole is almost impossible (e.g. N obliqua). Luff (1976) reported that some small percentage of N. brevicollis individuals overwinter as adults; and Greenslade (1965) cited evidence for slight geographical variation in adult activity periods in the same species. Evidence for at least slight asynchrony among conspecific individuals is available for all well-sampled Nearctic taxa. Fortunately, general timing patterns are still apparent for most taxa.

I found life cycle timing of some Nearctic taxa surprisingly difficult to characterize, mainly because of interpopulational variation in this character. Variation appears to be correlated, in

one or another taxon, with altitude, latitude, synoptic climate, or with some combination of these factors. For example, at least some members of N. obliqua populations at southern latitudes (e.g. in Colorado; ca. 39°N latitude) overwinter as adults; but members of the same taxon in populations at more northern latitudes (e.g. Edmonton, Alberta; ca. 54°N latitude) overwinter almost exclusively as larvae. Also, most members of N. obliqua populations at high altitudes in Colorado overwinter as adults, while populations at lower altitudes in the same area have many members overwintering as larvae. An example of possible correlation between cycle timing and synoptic climate is provided by N. hudsonica. Members of Rocky Mountain populations (i.e. in an area of "continental" climate) overwinter exclusively as adults; but some members of populations on the Columbia Plateau, an area of more "maritime" climate, overwinter as larvae. Possible correlations between cycle timing and these and other distributional factors were discussed by Greenslade (1965) and Lindroth (1949) and are explored further in section 4.22.

Slight differences in timing were frequently observed between members of different conspecific populations. For example, teneral adults of N. eschscholtzii (members of which overwinter as larvae) are found as early as February in coastal parts of northern California, but only later in the spring in the Sierra Nevada. In general, and especially for members of numerous taxa with significant altitudinal and/or latitudinal ranges (e.g. N. obliqua, N. hudsonica, or N. pallipes), activity begins earlier in spring and continues later in autumn in populations at low altitude or latitude than in populations at higher altitude or latitude. Members of populations which differ in

either of these parameters often show slight asynchrony with respect to one another in life cycle timing. Because developmental rates are often temperature-dependent (see above), it is reasonable to suggest that this asynchrony results where different populations are subject to different temperature regimes.

A particularly intriguing example of intraspecific variation in life cycle timing is seen in N. appalachia (see species description for details). From a study of all available material, it appears that individuals have, in past years, overwintered exclusively as adults or as larvae at different localities in the same year or at the same locality in different years. This and other, less-dramatic examples of variation cited above suggest that, in some taxa, significant plasticity in life cycle timing is possible. By recombining numbers of taxa in the overwintering-stage classes used above, I note that 44 Nearctic taxa (65% of the fauna) show little or no plasticity, but that 21 (30.5%) are moderately to very plastic in this character. A potential for flexibility in timing may account, for example, for the large geographical and life zone ranges of N. obliqua and N. gyllenhali castanipes by permitting adaptation of local populations to a variety of local and regional climates. As noted above, the geographical range of N. eschscholtzii, a species with an approximately equivalent life zone range to that of N. obliqua, is nonetheless quite restricted, probably because larval development in members of this species requires activity throughout the winter months.

Nebria living at high altitudes face a unique problem affecting timing of life cycles--namely, the possibility of extreme variation in timing and amount of snowfall, snow accumulation and resultant length

of the snow-free period. For example, members of N. crassicornis crassicornis, N. paradisi and N. vandykei vandykei occupy areas of Paradise Park (Mount Rainier, Washington) which remain completely covered with snow through the summer and autumn in some years. For life in such areas, some level of plasticity in cycle timing would be desirable. In fact, I have found first and third instar larvae, a pupa and adults of N. crassicornis crassicornis and mature adults and third instar larvae of N. paradisi and N. vandykei vandykei all at the same time (early August, 1972) in Paradise Park. In the previous year (1971) snowcover remained intact until late August. It is possible that these examples of asynchrony resulted when development of some individuals was so retarded by unfavorable climatic events that they required more than one year to complete their life cycle. Most members of N. crassicornis crassicornis overwinter as adults; but in years when winter snowfall begins early, individuals may be forced to overwinter as larvae. From field observations, it is apparent that this is not always fatal, but rather that N. crassicornis larvae can pupate in the spring and 'catch up' with other members of the population before the breeding season is over. Similar findings were obtained under laboratory conditions with N. piute individuals. Most members of this species also overwinter as adults. However, development of larvae in culture was slower than in the field, and cultured larvae failed to pupate in autumn. Larvae kept through the winter at 1°C pupated in the following spring, shortly after their transfer to warmer (10°C) conditions. Such plasticity in cycle timing is undoubtedly of significant adaptive value for life at high altitudes.

It follows from the above discussion that in some instances, striking differences in life cycle timing among members of different conspecific populations may be taxonomically insignificant. Slight asynchrony between members of different populations, especially those at different altitudes or latitudes, is probably even less significant if temporal patterns observed conform to those predicted based on differences in "growing seasons" at different altitudes, latitudes, etc. (see above). Therefore, only the broadest possible temporal characterizations of taxa are generally useful; and assignment of high taxonomic significance to slight interpopulational variation in life cycle timing is not justfied.

Control of life cycle, development and reproduction

Temperature and other environmental factors alone cannot account for the strong developmental synchrony observed in members of 69% of Nearctic taxa, nor even for the limited synchrony seen in members of more 'plastic' species (e.g. N. obliqua). Because members of different sympatric taxa often differ grossly in life cycle timing, some intrinsic (inherited) control mechanism must be operative. No such mechanisms have yet been described for Nearctic taxa, but considerable work has been done on life cycle control in N. brevicollis.

Thiele (1969b) found, through laboratory studies, that cold temperatures (2 to -4°C) are required for larval development during the autumn and winter, and that higher spring temperatures trigger pupation. According to Thiele, summer diapause (aestivation) is dependent on photoperiod. However, Penney (1969) reported that diapause occurred under all photoperiod regimes provided

experimentally, but that starvation of adults prevented it. From results of these and other experiments, Penney concluded that body fat content regulates the onset of diapause. Stimulus for termination of diapause is unknown. Penney's findings exclude change in photoperiod from such a role, but implicate decreased daylength as the stimulus for initiation and completion of ovarian development in females and final maturation of testes in males. This interpretation is supported by studies on the neuro-endocrine complex in N. brevicollis (Ganagarajah, 1965). Increased size and activity of the corpora allata, which presumably mediate gonad maturation, are associated with decreased daylength. Thiele (1969b) suggested that decreased temperature was also required for oöcyte maturation.

Some of these same controls may be operative in Nearctic taxa in which members overwinter as larvae; but for those taxa in which adults overwinter, a different set or sequence of controls is required.

Seasonal activity of individuals

Some activities which are apparently restricted to certain seasonal periods and are, in themselves, of interest include: (1) short-range migrations of members of some taxa to and from streambanks; (2) flight; (3) mating; (4) aestivation; and (5) winter activity. Short-range seasonal migrations in riparian Nebria were discussed above (section 3.231). Flight is considered in a following section on locomotion and dispersal. Only two confirmed flight records for Nearctic Nebria are known, both for males of N. crassicornis intermedia Van Dyke in September, 1974.

Mating.--Little is known about mating behavior in Nearctic Nebria. Kavanaugh and Martinko (1972) reported on a nebriine equivalent of 'honeymoon cruises' for members of N. purpurata in New Mexico. Copulating pairs of these beetles were seen leaving the streambank and swimming on the water surface to emergent rocks in midstream. Other pairs, but not individuals, were found resting in tandem on these rocks. The significance of this behavior remains unknown. Other literature notes on mating include only date records for copulation observed in the field (Larochelle, 1972). I have observed copulating pairs representing many different Nearctic taxa (see Table 13A). Most of these were found hiding under cover during daylight hours. Copulating pairs of N. vandykei (both subspecies) were found resting, running and feeding on snow at night.

In laboratory cultures of several taxa studied, males repeatedly attempted copulation with any available individuals, including other males, in the presence of a female during the mating period. Mating activity in males is, therefore, probably stimulated by a female pheromone in members of these and, perhaps, all Nebria taxa. No data on the source, composition or specificity of the proposed pheromone are available.

Copulation is apparently a prolonged activity, unless the beetles are disturbed. As suggested above, pairs found during the day have probably remained in copulo since the previous night. Duration of the period of mating activity under field conditions is unknown for Nearctic taxa. Studies of N. virescens adults in culture indicate a surprisingly long period. A single pair of adults captured in May,

Table 13A. Data on field and laboratory observations on copulation in Nearctic Nebria.

Taxon	Where?[1]	Month	Time
virescens	H	Oct.-Dec.	-----
frigida	H	July	2:00-18:00
crassicornis intermedia	H	July	-----
n. nivalis	H	July	12:00-20:00[2]
n. gaspesiana	H	June	15:00
gouleti	L	Sept.	-----
l. lacustris	St	July-Sept.[3]	-----
l. bellorum	L	Sept.	-----
paradisi	H	Aug.	12:00-15:00
metallica	H	July	11:00-18:00
schwarzi beverlianna	H	Aug.	16:00
piperi	H	Aug.	16:00
v. vandykei	Sn	Aug.	21:30-23:30
v. wyeast	Sn	Aug.	23:30-01:00
piute	H	June	12:00
t. trifaria	H	Aug.	16:00
i. ingens	H	July	15:00
a. acuta	H	Aug.	10:00-18:00
a. arkansana	H	Aug.	10:00-15:00
a. edwardsi	H	July-Aug.	11:00-19:00
f. fragilis	H	Aug.	16:00
f. teewinot	H	Aug.	18:00

Table 13A. (continued)

Taxon	Where?[1]	Month	Time
gregaria	H	July	14:00-19:00
s. sahlbergii	H	July-Sept.	14:00
eschscholtzii	H	Sept.-Oct.	16:00
diversa	H	Sept.-Oct.	-----
suturalis	H	June-July	14:00
pallipes	St	Aug.-Oct.[3]	-----

[1] Code used to denote microhabitat in which copulating specimens were found is as follows: H = hiding under stones, logs, or other cover; L = in laborartory rearing containers; Sn = on surface of snowfield or glacier; St = on open streambank, not under cover.

[2] Data from Larochelle (1972).

[3] Data from Spence (1974).

1971 were first observed in copulo in late September. From that time until late November, 1971, the beetles were found copulating every time their cage was examined. Eggs were first found in mid-November. Mating activity periods for members of all other taxa kept in culture were shorter, in most instances lasting only a few weeks.

Aestivation.--Although aestivation (summer diapause) is well-documented for members of N. brevicollis (see above), it is yet unknown among members of the Nearctic fauna. Very few specimens of N. virescens have been collected during summer months; and life cycle timing among members of this species is similar to that for N. brevicollis members. However, present data are insufficient to support a summer diapause in adults of N. virescens. Aestivation is most unlikely in members of all other Nearctic taxa, based on collection records for adults.

Penney (1969) reviewed previous suggestions on the possible significance of aestivation in N. brevicollis and concluded that it served as a means to avoid energy waste during periods of low food supply. Hågvar and Østbye (1974) have shown that respiration rate (and, therefore, consumption of food reserves) increases significantly with activity in members of N. gyllenhali and N. nivalis. Greenslade's (1965) suggestion that aestivation helps to synchronize breeding and/or delay it until a more favorable period for larval development is also supported by available data. Gilbert's (1958) contention that diapause facilitates gonad maturation, and Tipton's (1960) suggestion that it permits adults to avoid unfavorable periods of low humidity and/or high temperature are contraindicated (Penney, 1969).

Winter activity.--Some of the more intriguing questions about Nebria life history which are yet unanswered concern their activities in winter. Members of taxa which occupy areas at high latitude or altitude must endure winter conditions for more than half of the year. An understanding of the means by which these beetles survive, even thrive, at present is critical for understanding their evolutionary history, at least since pre-Glacial time.

Members of Nearctic taxa which occupy areas with mild winter climate are apparently active through the winter. For example, overwintering larvae of N. eschscholtzii, N. diversa and N. virescens remain active and continue development during winter months. A few active adults of N. eschscholtzii and N. virescens have also been found in winter. However, little is known about the winter activity of Nebria in areas covered by snow. Are these beetles active on the snow surface in winter? Are some active under the snow cover? Do members of some species become inactive, enter a 'cold diapause,' in winter? Is there a significant increase in mortality during this period? None of these questions can be answered at present because virtually no field studies on Nebria have been made in winter.

Overall cold-tolerance in members of Nebria taxa inhabiting high altitude and latitude areas is demonstrated by their ability to remain active in the vicinity of snow and ice during summer months. Some level of cold-tolerance in winter can reasonably be assumed. Østbye and Sømme (1972) observed some freezing tolerance, at least at temperatures above -10°C, in members of another nebriine taxon, Pelophila borealis Paykull. As noted by these authors, microclimate in

sub-nival air-spaces is often milder than above the snowcover, due to insulative properties of the latter. Temperatures under the snowcover are often quite stable, and, even in high altitude areas, may rarely drop below freezing (0°C). Conditions under the snow, therefore, may be favorable for activity of Nebria in winter; but whether or not the beetles are, in fact, active under the snow is unknown. Activity on the snow surface is less likely, except during unseasonally warm periods. The only available field evidence for winter activity among Nearctic Nebria in cold climate is that gathered by John Spence (personal communication) for larvae of N. pallipes and N. lacustris lacustris in Vermont. He collected numerous larvae of these two taxa in pitfall traps after the first winter snowfall and until the traps became deeply buried in snow and, therefore, ceased to function. Unfortunately, he was unable to determine how long this activity persisted because of extreme difficulty in sampling during winter.

3.233 Other aspects of natural history

In this section, I discuss present knowledge of Nebria populations and of the role of these beetles in food chains.

3.2331 Studies on Nebria populations

To date, there have been no studies to determine the size, density, dispersion or sex ratio of Nearctic Nebria populations. Population studies among nebriines have been confined to N. brevicollis in Europe.

Population size.--Greenslade (1964a) used the mark-release-recapture

method (Bailey, 1952) to estimate the size of a population of N. brevicollis in an isolated beech litter plot at Silwood Park (Berkshire, England). His estimates of population size (total number of adults present) during October, 1959 (maximum of 2300 individuals) and October, 1960 (maximum of 200 individuals) differ significantly. He suggested that population size may vary greatly from year to year, with fluctuations dependent on one or more climatic factor(s) (but see below for an alternative interpretation). Changes in population size undoubtedly occur in Nearctic Nebria also. Whether or not Greenslade was actually studying a population as defined by Mayr (1969) is unclear. Most Nebria populations are, however, more broadly extended in space; and their size would therefore be more difficult to estimate.

Population density, dispersion and aggregation.--Density (i.e. number of individuals per unit area) is more easily estimated than size, again using mark-release-recapture techniques. Penney (1966) estimated that density of new-generation N. brevicollis adults at Rossdhu during June, 1962 was 0.945 individuals/m^2. In June, 1963 and 1964, estimated densities were 0.827 and 0.570 individuals/m^2, respectively. Both Penney and Greenslade (1964a) found that dispersion (spatial distribution of individuals) in N. brevicollis populations was non-uniform. As shown by their studies, and in general, individuals tend to be found more commonly in some areas than in others (see above for discussion of microhabitat distribution). For example, I estimated (by hand collecting during daylight hours) that density of N. eschscholtzii adults along a three meter long section of stream bank (Salt Creek, near Oakridge, Oregon) was 83 individuals/m^2 in areas

within one meter of the stream edge, but less than one individual/m^2 in all areas at greater distances from the water.

Similar responses of several individuals to environmental gradients in selecting preferred microhabitats may alone account for many instances of clustering. However, at least in some instances, positive response to the presence of other individuals also leads to aggregation. Greenslade (1963a) determined experimentally with N. brevicollis adults that (1) individuals aggregate, even in a microclimatically uniform area; (2) male locomotory activity is apparently reduced in the presence of females; and (3) crowding appears to inhibit locomotory activity in both sexes. Penney (1969) observed that aggregation often preceded diapause; and I have found unusual aggregations of active N. eschscholtzii and N. arkansana arkansana Casey adults (see below, section 3.43, for details). Greenslade (1963a) suggested several possible advantages obtained from aggregation (see also Kavanaugh, 1977); but its significance in N. brevicollis and in Nearctic Nebria is yet unknown.

Sex ratio.--No data are available on sex ratio for populations of Nearctic Nebria. Some large samples (over 200 adults) I have collected, representing several different taxa, were found to contain, mainly or exclusively, either males or females. The significance of these few random samples is unclear; but they may indicate that, at least for brief periods, sex ratios may depart radically from unity (i.e. from a 1:1 ratio). Greenslade (1964a) found approximately equal numbers of N. brevicollis males and females in the population studied at Silwood Park.

In most instances, I have found the spatial distribution of males and females coincident in Nebria populations. However, at Dutch Harbor, Unalaska Island (Aleutian Islands, Alaska), in July, 1973, males and females of N. gregaria appeared to favor adjacent, but slightly different microhabitats (see species description for details). The significance of this observation is unknown.

3.2332 Trophic relations

In this section, I review what is presently known about trophic relations of Nebria with other biotic components of their environment. Notes from the literature are augmented by my field observations in brief discussions on Nebria feeding and food, and on their predators and parasites.

Feeding and food

Nebria individuals are predators (Evans, 1965a; Lindroth, 1961; and Spence, 1974), feeding on a wide variety of arthropodan and other invertebrate prey. As noted above, larvae are extremely voracious predators and are often cannibalistic (at least in culture). Adults rarely attack hard-bodied prey or each other (except for teneral adults; see above). My field and laboratory observations on members of several taxa suggest, however, that Nebria are also facultative scavengers. Adults of all species kept in culture readily accepted dead arthropods or ground beef as food. Beetles foraging at night on snowfields (e.g. N. vandykei adults) often eat dead and/or frozen arthropods. Feeding is generally associated with nocturnal locomotory activity; but, as noted above, some individuals are found eating in

daytime under cover.

Evans (1965a, 1965b and 1965c) has studied the feeding method of N. brevicollis adults. Sharp, powerful mandibles cut through the prey's body wall and chop it into small pieces. Maxillae rake the bulk food toward the oral cavity, where it is forced down ("bolted") through the esophagus to the crop. The proventriculus grinds food to a smaller size and controls its flow to the midgut. Evans claimed that no external digestion occurs in feeding of N. brevicollis adults; but my laboratory observations on Nearctic Nebria adults and the liquified remains of large prey after feeding suggest otherwise. All other aspects of feeding in Nearctic Nebria appear to agree with Evans' findings.

Because exoskeletal fragments of prey are consumed by Nebria in feeding, analysis of crop contents can help to identify some of the prey taken. This technique was used by Davies (1953 and 1959) and by Penney (1966) in studies of prey preferences of N. brevicollis adults and by Spence (1974) in similar studies on N. pallipes and N. lacustris lacustris adults. Both Davies and Penney reported that collembolans were the preferred prey of N. brevicollis adults, with dipterans, mites, other assorted insects, spiders and earthworms (in that order) less commonly consumed. Spence reported similar prey in similar relative numbers in the apparent diets of both N. pallipes and N. lacustris lacustris adults, the latter favoring collembolans more markedly than the former.

Penney (1966) noted that range in prey size for N. brevicollis adults, as indicated by analysis of crop fragments, was from 0.5 to 4.0 mm. Spence's data also suggest that small-sized prey are

preferred. However, I have repeatedly observed adults of several Nearctic species feeding on large, soft-bodied prey. For example, I have found adults of several taxa (e.g. N. eschscholtzii) eating live stonefly (Plecoptera) adults. One third instar larva of N. gebleri gebleri was found eating a caddisfly (Trichoptera) adult much larger than itself. Adults of N. vandykei will apparently feed on any invertebrate they find on snowfields at night (e.g. large coccinelid adults (genus Anatis), moths, dipterans, and even other (immobilized) carabids). I suggest that crop fragment analysis, although useful, is biased in favor of small-sized prey. Because there must be some limit to the maximum fragment size consumable, and because identifiability of fragments decreases with a decrease in their relative size, recognizable fragments of small prey will be better represented in the crop. Also, Nebria adults (observed in culture) feed discriminately on larger prey, consuming soft, internal parts and avoiding the body wall once it has been opened. Smaller prey can be consumed almost whole. An opportunistic feeding strategy is, therefore, probable for most or all Nearctic Nebria. Small to large and both dead and live invertebrates can be eaten; but diet in a particular instance is dependent on prey availability.

Predators and parasites

Predators.--Little is known about actual predators of Nearctic Nebria. However, because these beetles are often quite abundant, especially in riparian habitats, a variety of nocturnal insectivores could feed on them routinely. Amphibians are likely predator candidates in streamside habitats. R. T. Bell (personal communication) found 13

N. lacustris lacustris adults in the stomach of one toad (Bufo americanus Holbrook) in Vermont; and Larochelle (1976b) found adults of N. gyllenhali castanipes in a toad (same species) in Quebec.

Pratt and Hatch (1938) found remains of N. virescens adults in nests of Black Widow spiders (Latrodectus mactans Fabricius) on Whidby Island (Washington). Spiders are also common predators in riparian and alpine habitats; but none have yet been recorded as preying specifically on Nebria in these areas.

In montane areas, insects flying at low altitudes are often caught by upslope winds and eventually dropped over cold snow and ice areas at high altitude. Unable to fly or even walk at such cold temperatures, they remain stranded there. I have frequently seen birds (identity unknown) eating these insects and other arthropods on the snow surface during the day. In some areas, adults of several Nebria species also forage on these stranded prey, but at night. Nocturnal activity in these beetles may, therefore, aid in avoidance of avian predators. I have not observed potential predators of Nebria active on snowfields at night.

Parasites.--Few endo- and ectoparasites of Nebria have yet been recorded; but, undoubtedly, many remain to be discovered. Just as with other aspects of Nebria natural history, parasitism has been formally studied only in the Palaearctic N. brevicollis.

Phaenoserphus viator (Haliday) (Hymenoptera: Proctotrupidae) has long been known as an endoparasite of N. brevicollis and other carabid larvae (Critchley, 1973; Davies, 1959; Elliott and Morley, 1907-11; Luff, 1976; and Richards, 1946). Luff estimated that 25% mortality in

third instar N. brevicollis larvae was due to parasitism by P. viator and Phaenoserphus pallipes (Latreille) combined in one study area (Silwood Park) in 1966. He noted that, in comparisons among N. brevicollis populations of varied density, mortality due to parasitism appeared density-dependent (i.e. relatively heavier parasite infestations in denser beetle populations). He also suggested that these parasites could significantly affect N. brevicollis population size, and, further, that the ten-fold decrease in the Silwood Park population between 1959 and 1960 noted by Greenslade (1964a) could have been due to parasitism rather than adverse climate.

Luff (1976) also found nematode endoparasites (members of Hexamermis sp. and Mesodiplogaster iheritieri (Maupas)) in N. brevicollis larvae.

To date, there have been no published records of parasitism in Nearctic Nebria; but one can now be reported. Two adult gordian worms (Nematomorpha: Gordioidea: Gordius) emerged through the head of one N. sahlbergii sahlbergii Fischer von Waldheim adult collected on Vancouver Island (British Columbia) by Henri Goulet. Visual comparisons of biomass indicate that interior structure of the beetle must have been almost completely replaced by worms; but the beetle was alive and active when found.

Many adults (both museum specimens and those collected and kept alive), representing many different Nearctic Nebria species, have been found carrying one or more Histiosoma maritimus (Oudemans) (Acarina: Anoetidae) immatures. These mites (Fig. 363) were usually found on the thoracic venter, especially on the prothorax, sometimes clustered in large numbers. Exuviae were also frequently found, still attached

to the venters of some adults. I found no indication that these mites harmed or restricted the activity of their hosts in any way. They are, therefore, probably phoretic rather than ectoparasitic.

3.234 Locomotion and dispersal

My main purpose in presenting data about these topics is to provide a context for evaluation of various zoogeographic hypotheses (section 4.2). Limits to locomotory powers of individuals necessarily place certain constraints on their dispersal and, ultimately, on distributions of their respective taxa. Understanding of distributional shifts or of past, present or potential barriers to dispersal (and distribution) requires at least rudimentary knowledge of locomotory and dispersive capabilities of taxon members.

3.2341 Locomotion

Locomotion (i.e. moving by one's own power) in Nearctic Nebria can be divided into terrestrial (walking and running), aquatic (swimming and walking underwater) and aerial (flight) components. Each of these locomotory modes is discussed separately below. The terrestrial mode is used routinely by members of all Nearctic taxa, the aerial and aquatic modes used to an unknown degree and by members of only some taxa.

Terrestrial locomotion (ambulation)

Evans (1977) recently reviewed ambulation among Adephaga. Using his classification of locomotory types, Nebria can be described as "fast runners/ poor wedgepushers." As suggested by this description, these beetles are capable of relatively rapid movement; but their

delicate stature and long, slender legs provide little pushing power.

As noted above, most ambulatory activity is nocturnal. Beetles observed in the field appear to run rapidly only when disturbed. Normal and maximum gait speeds of various species have not yet been studied experimentally. My crude laboratory estimates of running speeds for members of N. hudsonica and N. gyllenhali castanipes (at 18°C) were, respectively, 55 to 95 mm/sec and 85 to 125 mm/sec. Repeated field observations on disturbed members of single taxa at different temperatures indicate that, within limits, speed increases with temperature. However, as noted above, members of some taxa (e.g. N. vandykei) can run rapidly even at very low (at or near 0°C) temperatures (e.g. on snow or ice at night). I cannot yet suggest a relationship between size and speed (see Evans, 1977), although this could be tested experimentally.

Interspecific differences in speed and other gait characteristics are observable in the field. For example, members of N. darlingtoni and N. gebleri rathvoni, when found together, are distinguished by differences in running stance, although they are otherwise similar in appearance. The former run rapidly with a very low, wide stance, whereas the latter are slightly slower, with an elevated, narrower running stance. In contrast to the swift, agile members of most Nearctic taxa, N. suturalis members run with a clumsy, lurching gait, very similar to that of Diplous (Patrobini) adults. They are, therefore, readily separable in the field from similarly-colored N. gyllenhali lindrothi adults, with which they share alpine talus slopes (Front Range, Colorado).

Although my data are yet too incomplete to evaluate properly, gait characters among Nearctic Nebria may prove to be taxonomically useful, especially for field recognition and discrimination. Unfortunately, these traits appear to be relatively plastic, probably evolve rapidly, and would, therefore, be of little use in demonstrating phylogenetic relationships.

Little is known about ambulatory ranges of Nebria adults. I have found N. vandykei adults on snowfields as far as 100 m from nearest bare rock or soil less than two hours after dusk (when these beetles normally become active). At this pace [average about 14 mm/sec], they could easily cover a linear distance of 400 m in one night; and because they are capable of much faster movement, at least in bursts, their range is probably much greater. Edwards (1975) found a N. crassicornis intermedia adult active on a snowfield in daylight "a half mile from nearest rock or soil." Assuming that the beetle walked rather than flew (see below) to the point where found, it covered at least 800 m, probably in less than 24 hours (beginning early the preceding night). An average speed of 10 to 20 mm/sec would satisfy requirements of this estimate. The above examples suggest that snowfield-prowling Nebria may cover surprisingly large distances when active. In contrast, Greenslade (1964a and 1964b) found that, during their seasonal periods of locomotory activity, N. brevicollis adults moved an average of 3.67 m/night when disturbed (i.e. immediately after being marked for study) and 1.98 m/night when undisturbed. These values may be underestimates of distances normally covered per night because, by using pitfall traps with mark-release-recapture studies, beetles could move only until trapped. However, both the nature and extent of preferred habitat may

affect the speed and distance of movement (Greenslade, 1964b). Woodland beetles, such as N. brevicollis members, may encounter more obstacles and more varied terrain than snowfield-prowling beetles and, therefore, move more slowly and cover less ground.

No data on lifetime ambulatory ranges of adults are available. Such information would be useful in considering their dispersal potential (see below).

Aquatic locomotion

Aquatic locomotion is probably restricted to those taxa whose members occupy riparian habitats. While members of all but one species lack obvious structural adaptations for swimming or other movement in water, they are competent surface swimmers. Swimming activity of copulating N. purpurata pairs was noted by Kavanaugh and Martinko (1972; and see above, section 3.2322). Members of several taxa, notably those of N. zioni Van Dyke, N. meanyi lamarckensis n. ssp. and N. ingens, commonly avoid capture by hurling themselves into cascading streams. I assume that the beetles are subsequently able to swim to safety and resume normal activity.

Members of N. ingens are unique among Nearctic species in having apparent structural adaptations for locomotion underwater. Unique tarsal shape (Fig. 245) and reduced ventral vestiture (Fig. 242) (see also species description) facilitate walking underwater, over even the upper surfaces of submerged stones (Kavanaugh, manuscript preparation). Adults are able to walk upstream underwater even against a strong current. Although members of other species may take refuge underwater when disturbed, they quickly float to the surface or are

swept downstream unless they remain wedged under or between submerged stones.

In summary, riparian Nebria do make use of adjacent streams, at least in some instances. All can swim on the stream surface and some also move over submerged substrates. The implications of this capability for both active and passive dispersal in flowing water are discussed below (see section 3.2341).

Aerial locomotion (flight)

Based on present data, flight is evidently an extremely rare event among Nearctic Nebria. I know of only three proven flight records for Nebria members. Lindroth (1945; see also 1961) reported on the "spontaneous flight" of a N. brevicollis adult [sex unknown] on 4 July 1944 [hour unknown] at Grebbestad, Sweden. G. E. Ball and J. Belicek (personal communication) collected adults of N. crassicornis intermedia in flight on two occasions in Alberta [Prospect Creek, 5.3 miles nw. of Mountain Pass on ne. slope of Prospect Mountain (1670m; 21 September 1974, 17:00; 2 males caught flying along the stream margin); and Pembina River, 30 miles se. of Robb (1300m; 22 September 1974, 12:00 to 15:00; 1 male).

Two essential prerequisites for flight are: wings and functional muscles to power them. Of the 42 Nearctic Nebria species, 16 (38%) have apparently all members with full-sized hindwings and 20 (48%) have all members with hindwings reduced in length, width or both. Six species (14%) have some populations in which all members have full wings and others in which all members have reduced wings.

Any reduction in relative wing size undoubtedly renders an individual

incapable of flight; so only those beetles with full-sized hindwings can be considered potential fliers. Lindroth (1961), citing the work Gislen and Brinck (1950) on Palaearctic N. gyllenhali adults and comments from G. W. Ball (in litt.) on N. metallica adults, suggested that, even in some, if not most, full-winged Nebria, flight muscle may not (or only incompletely) develop, thereby precluding flight. No detailed studies of Nearctic Nebria flight muscle development have yet been made.

Darlington (1936, 1943 and 1971) has demonstrated that, under certain environmental and/or historical conditions, especially in certain habitats (i.e. on islands and mountains), hindwing atrophy has been a frequently and independently repeated transformation among carabid beetles. [Discussions of wing atrophy and associated changes in other structures and of possible selective pressures favoring these changes are presented below, section 4.41]. Because hindwing atrophy is so common, especially among Nebria, I surmise, with Darlington (1936 and 1943) and others, that, in fact, functional hindwings are retained in a lineage through time only at some high 'price,' and that beetles cannot 'afford' wings they do not use, at least occasionally (see below). I therefore assume that, in spite of the paucity of flight records, fully-winged adult Nebria do fly, if only rarely. Data on flight muscle development could be used in testing this assumption, but only if muscle development throughout all of adult life is considered. If, for example, flight in Nebria is only seasonal or climatically opportunistic (see below), flight muscle development may also be seasonal or at least asynchronous with development of other structures (see Carter, 1976, for data on the timing of wing muscle

development in Agonum retractum (LeConte) adults). Muscles may therefore be functional only during a brief part of adult life; and short-term surveys of muscle development might overlook this period completely.

Flight records to date suggest that, although Nebria are normally nocturnal, their flight may be diurnal, perhaps exclusively so. There are no proven nocturnal flight records for Nebria. Edwards (1975) reported on two N. obliqua ("N. obtusa LeConte")adults found "at lights" in Glacier National Park (Montana) on 23 July 1967. However, both were found on the ground; and the lights were located about 30 m from a stream (J. G. Edwards, personal communication). It is therefore unclear whether the beetles walked or flew to the lights. Although a majority of carabids which fly at night are collected at lights, it is still possible that Nebria adults fly at night yet are not attracted to (and therefore not collected at) lights.

Critical minimum body temperatures for flight are undoubtedly universal among flying insects (Chapman, 1969), although intergroup and interspecific differences in threshold temperatures are great. Because Nebria characteristically seek out and occupy cool to cold microhabitats, minimum temperatures for flight may be attained rarely and only in daytime (as suggested by available records). Among Nebria, microhabitat requirements seem to take precedence over flight requirements; and some behavioral shifts may therefore be required for adults to take advantage of their flight capability. A temporary change from nocturnal to diurnal activity may be one such shift, but others may also be involved.

An important question yet unanswered is 'Why do Nebria fly?'. The

flight records for N. crassicornis intermedia (see above) serve to confound rather than clarify. Only three specimens--all males--have been taken in flight. Flights were in late September, when days are shorter and mean maximum daily temperatures much lower than in preceding months. Also, most N. crassicornis intermedia individuals overwinter as larvae; and field data from diverse sources indicate that adults have mated, females have oviposited and larvae have already hatched and developed to second instar stage by September in most years. If the observed events are representative of typical flights by members of this taxon (and they may not be), their significance is unclear. Flight prior to mating could be important for location of mates or in reduction of inbreeding (i.e. among siblings) and maintenance of genetic variability throughout populations. Flight (by females) after mating, but before oviposition, could be important in reduction of crowding and intrapopulational competition through both internal and extralimital dispersal (see below). One possible advantage to flight after the oviposition period would be in exploiting suitable but unoccupied areas (either within or outside the normal range of the population). For this strategy to be effective, however, adults would have to survive, mate and successfully reproduce the following year in the new area. Both males and females would have to disperse, unless females could retain viable sperm for more than a single season. An alternative explanation for flight is that the latter is related to annual runoff cycles and flooding of riparian habitats, purely as an escape mechanism. At present, I have no direct evidence in support of either of these hypotheses (see section 4.41 for

discussion of wing size and flight in relation to habitat and geographical distributions).

3.2342 Dispersal

Udvardy (1969) defines dispersal as "the process whereby an organism is able to spread from its place of origin to another locality." However, embraced by this concept are two classes of events, each of different zoogeographic and evolutionary significance. In the first class are dispersals entirely within the normal range of a population (or a taxon). This type of dispersal is restricted to individuals. It permits outbreeding, gene flow and maintenance of variability throughout populations; and it contributes to the maintenance of geographical distribution by balancing the effects of local extinctions. Platnick (1976) recognized the need for a term to distinguish this type of dispersal and suggested "dispersion" as appropriate. However, as noted by Armstrong (1977), the latter already has a precise (but different) meaning in both ecology and physics (e.g. in gas laws); and its expropriation and redefinition is unjustified. I here use the term internal dispersal for this type of dispersal.

The second type of dispersal, which I term extralimital dispersal, is movement to an area outside the normal range of a population (or taxon). It may refer to the movement of individuals, populations or taxa. Extralimital dispersal of individuals results in at least transient increases in or shifts of the ranges of populations or taxa; and, therefore, these groups can also be said to have undergone extralimital dispersal. The zoogeographic and evolutionary importance of this type of dispersal has long been discussed (see

Darlington, 1957, 1965 and 1971) and is currently under spirited attack by some biogeographers (see Ball, 1976; Croizat, et al., 1974; Nelson, 1975; and Rosen, 1976).

Hypotheses concerning the role of both types of dispersal in the historical development and maintenance of present distributions and distributional patterns among Nearctic Nebria are discussed below (section 4.2). The following discussion summarizes scant available data on both internal and extralimital dispersal and evaluates dispersal potential.

Means of dispersal

Udvardy (1969) noted that "spread or ease of locomotion is in no direct relation to speed or ability of dispersal," and that distributions of taxa and the relative vagility (i.e. the intrinsic ability and tendency to move) of their respective members are not always directly related. For example, taxa (e.g. most birds) with highly vagile members may not occupy ranges as extensive as taxa (e.g. some land snails) in which members have relatively low vagility. Potential relationship between vagility and distribution may be obscured by historical events and because organisms may disperse passively as well as actively. Active (i.e. self-powered) dispersal is, in fact, directly related to locomotory capability; but passive dispersal (i.e. dispersal by means of a carrier) bears no (or perhaps, in practice, some inverse) relationship to locomotory capability. With the discussion above on locomotion as preface, I here attempt to assess the relative and potential importance of different active and passive means of dispersal for Nebria.

Active dispersal.--As noted above, Nebria may use from one to three locomotory modes, including ambulation, natation (including both surface and bottom locomotion) and flight. Each of these modes is potentially of some importance for both internal and extralimital dispersal, although their relative importance is undoubtedly unequal. Ambulation is evidently the predominant locomotory mode for all Nebria; and it seems reasonable to suggest that it is also the most important active means of dispersal. Data presented above indicate that individuals are capable of traveling distances of several hundred meters per day in suitable habitat. Projected over the 'lifetimes' of individuals and of populations, the potential for dispersal through ambulation is tremendous, limited only, it would appear, by the availability and continuity of suitable habitats. Both internal and extralimital dispersal may, therefore, be mainly dependent on ambulation.

Natation itself may, at times, function as a means of dispersal, but only for taxa in which members are (at least in part) riparian. Data available at present indicate that these beetles are able to survive in and navigate on water, traits which are perhaps more important for passive (see below) than active dispersal. Active locomotion in streams is probably limited to efforts toward a return to shore after accidental or intended (see Kavanaugh and Martinko, 1972, and above) stream entry; and its importance is probably confined to internal dispersal (i.e. relocation along streambanks, within the range of a population).

So few details are known about flight among Nebria that its importance is not yet understood; and, consequently, its role in

dispersal cannot yet be estimated directly. However, some pertinent indirect evidence may be cited here. The difference in mean maximum linear extent of range (see Table 6) between taxa with fully-winged members (2150 km) and those with only short-winged members (362 km) is highly significant ($P \geq 0.99$). This suggests that taxa with fully-winged individuals can both attain and successfully occupy greater ranges than taxa with only short-winged members; and differences in both internal and extralimital dispersal capabilities are at least implicated. Of the 22 Nearctic Nebria taxa whose ranges overlap areas which were completely covered by Wisconsinan ice sheets, 20 are represented in these areas by populations with only fully-winged members. The two exceptional taxa are N. diversa and N. kincaidi kincaidi, both of which may have survived the Wisconsinan in coastal refugia (at least in part) very close to their present ranges (see below, section 4.2). Therefore, post-Glacial reinvasion of (i.e. extralimital dispersal to) large, glaciated areas has been achieved almost exclusively by taxa with fully-winged members. A first and most probable conclusion is, therefore, that flight is important for dispersal; and this may well be true. However, there is yet no 'proof' that flight has a role in dispersal. As suggested by B. B. Chiolino (personal communication), fully-winged individuals may simply have a greater intrinsic (behavioral) tendency to disperse than short-winged individuals; and it is still possible that, in fact, they walk rather than fly.

Passive dispersal.--Several classes of carriers may be involved in passive dispersal. Of those discussed by Udvardy (1969), the following may contribute to the dispersal of Nebria: anemochore dispersal (i.e.

dispersal by wind or air currents); anthropochore dispersal (i.e. dispersal by or with man); and hydrochore dispersal (i.e. by moving water). I exclude biochore dispersal (i.e. dispersal by other organisms) because the kinds of interactions with other organisms normally considered prerequisite for this mode of dispersal are unknown among Nebria.

It is doubtful that any foreseeable circumstances would permit Nebria individuals to be picked up off the ground by air currents or wind in the microhabitats they occupy. However, because at least some Nebria adults fly, anemochore dispersal is possible. Nothing is known about flight characteristics of these beetles, however, so that a reasonable estimate of the likelihood of passive aerial dispersal is yet impossible. I find no distributional anomalies among Nearctic Nebria the explanation of which require hypotheses of anemochore dispersal (see section 4.2 below).

Anthropochore dispersal has played no apparent role in the dispersal of Nearctic Nebria. This is not surprising, because members of these species occupy microhabitats not yet extensively exploited by man or containing materials or plants routinely transported by him. [Lindroth (1957 and 1963a) reviewed the characteristics of habitats occupied by carabid beetles frequently transported by man]. It is possible that riparian beetles could be transported (as adults, larvae or eggs) in sands and gravels mined from active stream beds. However, most (and all large-scale) sand/gravel mining operations in North America have worked from quarries (i.e. 'fossil' stream beds) rather than live streams (Kaiser Sand and Gravel representatives, San Francisco; personal communication). Furthermore, successful dispersal

of these riparian beetles would require that materials taken from one stream be deposited in proximity of another. As demonstrated by Lindroth (1957), introductions of riparian carabids are improbable events.

The two N. brevicollis records for North America (see Appendix B and species description) no doubt represent independent accidental ("adventive") introductions by man. N. brevicollis members are highly synanthropic in Europe. Individuals are common in gardens and parks and are totally independent of streams or other water bodies. Transport of adults, larvae or eggs in potted plants or soil, for example, would seem quite possible.

One last, and potentially most important, role for man in aiding and/or directing the dispersal of Nebria may be through his alterations of drainage systems--by diverting streams themselves to new channels, redirecting water flow through aqueducts or canals (thereby possibly linking previously discrete drainage systems) or by constructing bridges (see discussions of trollism above, section 3.2311, and below). These activities may facilitate dispersal, but only indirectly, in concert with ongoing passive dispersal in water.

Because a majority of Nebria taxa have members associated with water systems, including rivers and the creeks, rivulets, springs, snowfields and glaciers which feed them, hydrochore dispersal undoubtedly is and has been an important mode for present and past dispersal in this group. Downstream drift of riparian and, perhaps, perinival beetles is probably (see below for evidence of extralimital dispersal along streams) very common. Profound changes in distribution are possible when passive dispersal in streams is coupled with geologic

and hydrographic events (including those affected by man) which alter the location or direction and volume of stream flow. Classes of natural events of probable present or past importance for Nebria dispersal include orogeny, regional uplift and tilt, embayment (damming) of rivers by lava flows, glaciers or ice sheets (followed by rechannelization) and stream capture (see section 4.2 for discussion of Nebria distributions in relation to these events).

Some of the more classic examples of hydrochore dispersal involve crossings of more extensive water gaps (e.g. stretches of ocean or lake between mainland and islands) and employ various forms of rafting (e.g. ice rafting, rafting on or in logs or other floating debris). Few Nearctic Nebria members are likely to be involved in such dispersals because their habitat preferences provide few or no such opportunities. Members of few taxa (e.g. N. lacustris lacustris) are associated with the shores of large lakes. Only N. diversa and N. gregaria members are common seashore inhabitants and, therefore, likely to participate in and survive extralimital dispersal in or on the surface of seawater. Most Nebria, and all those associated with riparian or sea strand habitats prefer areas free of vegetation and are therefore unlikely to be transported by rafts originating in their areas. The only Nearctic Nebria distribution for which an explanation appears to require oversea dispersal on water is that of N. gregaria (see section 4.2). All members of this species are short-winged; and their presence on various of Aleutian Islands can be most reasonably explained by this passive means, unless present estimates of sea level changes in Pleistocene time are grossly in error (Lindroth, 1963b). A possible role for ice rafting in Nebria dispersal can be neither excluded nor

supported at present. It is, however, unlikely that individuals could survive on such rafts unless soil and rock were present on top of at least part of the raft.

Short-range passive dispersal on or in water or on ice appears to pose no severe behavioral, metabolic or physiological problem for members of many Nebria taxa. As noted above, riparian beetles are competent surface swimmers, and some readily enter water at temperatures near freezing. Perinival beetles can tolerate near-freezing temperatures nightly. Low water temperatures, known to immobilize and/or kill some carabids (e.g. Scaphinotus (Brennus) spp. members, personal observations), may have no negative effect on Nebria members. Many Nebria, therefore, appear to be quite well-adapted for hydrochore dispersal in cool or cold streams.

My own field observations on adults of several Nebria species suggest an additional behavioral characteristic of special advantage for hydrochore dispersal. When suddenly thrown into streams, adults will often float to the surface and assume a compact floating posture (Fig. 364), with all appendages tucked close to the body. They remain motionless (even if floating upside down) until the current propels them against the shore or some emergent stone. The swifter the current, the more likely the beetles are to remain inactive. Some begin swimming actively in calmer water before they reach stones or shore. Such behavior may conserve much energy, thereby permitting longer dispersal and greater chance of survival.

Internal dispersal

Movements of individuals within the distributional limits of their

respective populations or taxa have not yet been studied for any Nearctic Nebria. Greenslade (1964a) used pitfall traps and mark-release-recapture techniques to study movements of N. brevicollis adults within and between each of two beech litter plots at Silwood Park (England). Areas of the two plots were, respectively, 1700 m^2 and 85 m^2; and distance between them was 45 m. He found that, during the seasonal periods of locomotory activity for members of this species, movement within the larger plot was "constant," even for undisturbed (see above) adults, but that exchange of adults between plots was very low (only one percent of undisturbed adults moved from the larger to the smaller plot). This suggests that, where preferred microhabitat areas are discontinuous, although separated by relatively small gaps, movement of individuals may be greatly restricted and confined to small areas. I am at present unable to accurately assess the role of various active and passive dispersal means in internal dispersal, but suggest that ambulation is of primary importance.

Migration is a special kind of internal dispersal. As noted above (section 3.231), migrations presently known among Nearctic Nebria are limited to short-range seasonal movements associated with melting snowfield margins and rising and falling stream levels. I have no data which suggest that Nebria individuals have a "home range" or routinely return to a particular spot after a period of locomotory activity. Movements associated with the above migrations appear to be only ambulatory.

Extralimital dispersal

Carabid beetles which readily fly are frequently found in areas

outside the normal ranges of their populations or even their taxa. Darlington (1943) noted that fully-winged members of several lowland carabid species are sometimes collected at the crest of the Presidential Range (New Hampshire). No such records can yet be cited for Nearctic Nebria members.

Examples of extralimital dispersal among Nebria (except for the apparent anthropochore dispersal of N. brevicollis members to North America from Europe; see above) are more subtle and restricted to downstream drift events (hydrochore dispersal). Spence (1974) occasionally found both adults and larvae of N. pallipes and N. lacustris lacustris along streams at elevations below those normally occupied by members of these species, especially after rains. As noted above (section 3.2311), I have frequently found adults of different Nebria taxa under bridges at elevations well below the altitudinal ranges of their respective taxa. Bridges provide suitably cool, shaded areas in which the beetles can survive after displacement from their normal ranges; and they therefore serve to preserve records of passive extralimital dispersal. As suggested by the surprising frequency of this trollism and the likelihood that only a small percentage of displaced individuals reach these safe shelters, the number of individuals dispersing passively downstream must be very large.

It is interesting to speculate on the potential role of bridges and, therefore, trollism in successful extralimital dispersal of riparian Nebria. On a geologic timescale, bridges are certainly new features of the environment; and no role in past dispersals can reasonably be assigned to them. However, 'natural' equivalents of bridges along streams are few and most are quite small. The closest

equivalent might be an undercut stream bank; but this would be spatially and temporally quite limited and a very dangerous place to be during even minor flooding. As more and larger bridges are built, their cumulative effect on present and future Nebria dispersal may be important. The streambank areas shaded by some existing bridges (especially the new bridges of the interstate highway system which carry six traffic lanes or more) are very large. Some of the areas I have examined under bridges, for example, are more than 3000 m^2. Given even a moderate immigration rate through hydrochore dispersal from areas upstream, large, permanent populations could become established in these areas and, in turn, serve as a source for new colonization under bridges further downstream.

One particular area in North America worth watching in the future for possible effects of trollism is that portion of the Columbia River system which includes the lower Columbia River and the Snake River. From the source of the Snake River in Yellowstone National Park (Wyoming) to the mouth of the Columbia River at the Pacific Ocean, this watercourse passes through and receives drainage from three distinct Nebria faunal regions. Each region is separated from the others by low, arid areas which have evidently served as barriers to dispersal in post-Glacial time (see section 4.2). A recent westward dispersal of eastern elements along this watercourse is not yet strongly indicated in the Nebria fauna; but as more large bridges continue to dot the intervening lowlands, some net westward shift of eastern elements might be expected.

I have not yet observed any special behavior patterns in any Nebria members (except, perhaps, in members of N. ingens; see above,

section 3.2341) which would tend to reverse downstream displacement. One such pattern would be a tendency to walk or fly upstream. If some such mechanism evolves (or, in fact, already exists) among Nebria, then beetles displaced down one stream might reverse direction and actively disperse up a different stream. Aided by downstream drift and suitably positioned microhabitat islands (under bridges), beetles could then disperse across lowland barriers and invade new tributaries and mountain ranges, which in the area discussed above, could lead to extensive faunal mixing.

3.24 Paleontology

The study of fossil specimens and their temporal and spatial distribution may provide valuable data on the evolutionary histories of taxa and biota and on past climate and geography. Hennig (1966) noted that evidence on "phylogeny" of characters (i.e. polarity of character transformations) can, at times, be obtained from stratigraphic sequences (his "paleontological method") (see Matthews, 1970 and 1976 for superb examples). Recently, several proponents of cladistic systematics (e.g. Schaeffer et al., 1972; and Cracraft, 1974) have questioned various traditional uses of paleontological data, especially (1) in the search for actual "ancestors" of extant taxa and (2) in the use of stratigraphic sequence data to determine, a priori, character transformation polarity. There seems to be no doubt, however, that structural, temporal and distributional data from fossils can be extremely important in the testing and reformulation of hypotheses about relationships, character transformations and distributional histories of taxa, if evolutionary theory and knowledge of the inherent limitations (and bias) of these data serve as constraints on interpretation of their significance.

Fossil specimens of any age can be useful in systematics; but those representing extant taxa have added importance. By applying the principle of 'uniformitarianism' and knowledge of the present environmental relations and requirements of members of these taxa to study of these fossils, the latter can be used in reconstructions of past environments. re importantly for the present study, however, such specimens record the loc on and, perhaps, some structural

characteristics of members of an extant taxon at some point in past geologic time (assuming that we can, in fact, assign the specimens to some extant taxon). These data may bear directly on interpretation of past distribution and minimum age of a taxon.

Review of Nebria fossils

The fossil record for Nebria to date is very poor--limited in diversity, distributional representation and geologic time span covered. The oldest fossil clearly representative of some Nebria taxon is of Pliocene age, far too recent to be of any significance in elucidating the early history of the genus. Because specimens were too fragmentary and/or because they could not be distinguished from equivalent specimens representing extant taxa, I obtained no data pertinent to analyses of character transformations or relationships among past or present Nebria faunas. Data pertinent to considerations of the minimum ages and past distributions of extant taxa are discussed with respective species descriptions (section 3.43) and in section 4.23 on historical zoogeography.

Tertiary fossils.--S. H. Scudder described two Nebria species from Tertiary deposits. Nebria paleomelas Scudder (1879:173B; see also 1890:532, 1895a:54 and 1900:17) was described from "Tertiary" beds ("below main coal seam") at Nicola River, British Columbia. Nebria occlusa Scudder (1900:17) is from the Florissant Beds (Florissant, Colorado) of Miocene age. I have not yet studied either of these specimens. However, Scudder's descriptions match details of his drawings for both the N. paleomelas (Scudder, 1890:Pl. 2, Fig. 20) and the N. occlusa (Scudder, 1900:Pl. 1, Fig. 3) specimens. Based on

characters of the elytral striae (including length and position of the scutellar striole and the relationship between the bases of striae 1. and 2.) (see section 3.21 above on comparative morphology for details), I conclude that the specimens described and illustrated do not represent Nebria species. [Both probably represent Amara species.]

The only North American Tertiary fossil presently referable to genus Nebria is that collected by J. V. Matthews, Jr. (see Hopkins et al., 1971; and Matthews, 1977)from the Lava Camp mine (Inmachuk River valley, Seward Peninsula, Alaska). The specimen (Fig. 91) is of Pliocene age (ca. 5.7 million years B. P.), consists of an almost complete left half of a pronotum, and is structurally indistinguishable from the pronotum of a living N. nivalis nivalis adult. Members of N. nivalis (Holarctic distribution) and all other species (all are restricted to the Palaearctic Region) of the nivalis species subgroup (see below, section 3.32) are uniquely characterized by the presence of a small, longitudinal tubercle on the lateral pronotal explanation medial to the midlateral seta. The identity of this specimen, however, as representing N. nivalis nivalis, or some extinct member of the nivalis species subgroup or, more specifically, the stem species of the nivalis species subgroup or any part thereof cannot possibly be established.

Quaternary fossils.--Fortunately, Nebria fossils of Pleistone and post-Glacial age are relatively abundant, from both Eurasia and North America; and the use of modern techniques for recovery of specimens and the expertise and enthusiasm of present investigators (cited below) should help to provide much more material in the future.

Fossil specimens of N. brevicollis are known from various deposits in the British Isles, including some of "Older Dryas" age (ca. 12,500 years B. P.) from North Wales (Coope and Brophy, 1972) and post-Glacial (?) age (ca. 10,000 years B. P.) from England (Ashworth, 1973). Nebria livida (Linnaeus) specimens have been found in Weichselian ("middle Devensian", ca. 38,500 years B. P.) deposits at Four Acres, England (Morgan, 1973). Nebria gyllenhali fossils are known from England (late Weichselian, ca. 10,670 years B. P. or less; Ashworth, 1973) and Scotland (late Allerød interstadial, ca. 11,200 to 10,900 years B. P.; Coope, 1968). Nebria nivalis nivalis specimens have been found in "Younger Dryas" (late Weichselian) deposits in England (Coope, 1970b).

North American Quaternary deposits from which Nebria specimens have been recovered to date are confined to the Toronto (Ontario) area and include the Scarborough Formation ("Scarborough Bluffs"; early Wisconsinan, ca. 70,000 years B. P. (Morgan, 1972)) and the Don Formation ("Don Valley Brickpit"; Sangamon interglacial, ca. 100,000 years B. P. (A. Morgan, personal communication)).

Scudder (1895b:70) based his Nebria abstracta on a single elytron from Scarborough. Although I have seen only the description and illustration (Scudder, 1895b:Pl. 6, Fig. 2) of this specimen, and again based on the pattern of elytral striae (specifically the separate origins of striae 1. and 2. at the basal margin), I conclude that the specimen is non-nebriine (and probably represents an Agonum species).

Scarborough material (received for study from Anne Morgan) included elytral fragments which I have tentatively identified as representing N. suturalis (Figs. 178a,178b) and N. nivalis nivalis (Figs. 180a,180b)

adults. The presumptive N. suturalis elytral specimens are similar (in microsculpture, depth and punctation of striae and shape of the elytral base) to elytra of living members of that species. The combination of character states--size medium; foveate punctures on elytral interval 5. (and, in some members, 7.) present; metallic reflection of elytra absent--is diagnostic for adults of N. nivalis nivalis (Figs. 178a and 178b).

Five elytral fragments (Figs. 179a,179b) (also received from Alan and Anne Morgan) from the Don Valley Brickpit appear to represent members of either N. lacustris lacustris or N. pallipes. Members of these two taxa, and also the fossil specimens, are similar in elytral microsculpture (meshes strongly transverse) and depth of impression of the striae. Because these taxa are broadly sympatric and their members are commonly found together at present, both may be represented among the fossil specimens. Unfortunately, all fragments lack the elytral apical area, to which the only differentiating elytral characters apply.

3.3 Classification

In this section, I discuss classification, especially in relation to evolutionary history, review the history of classification of Nearctic Nebria, and provide a reclassification of the Nearctic taxa.

3.31 Classification: a perspective

Much has been written in the last 20 years on the purposes, principles, and methods of classification. Several contemporary and competing philosophical approaches to classification can be recognized; and these have been called the "pure phenetic", "omnispective", "cladistics", and "evolutionary" approaches, respectively. A superficial review of the literature suggests that great, irreconcilable differences between them must exist. In fact, the approaches have much in common and can be properly distinguished only on more subtle points than are first apparent. All basically agree with Simpson (1961) that classification is "the ordering of [organisms] into groups on the basis of their relationships, that is, of associations by continuity, similarity or both"; and all view classifications as devices for storage and retrieval of information about organic diversity. Differences involve the kinds of relationships that are used or emphasized in formulation of the classifications.

The critical area in which these respective approaches differ is in the relationship advocates of each perceive between classification and evolutionary history. Advocates of the "pure phenetic" (e.g. Sokal and Sneath, 1963) and "omnispective" (see Blackwelder, 1967) approaches

work from the premise that evolutionary history (phylogeny in particular) is unknowable and, therefore, cannot be used as a basis for classification. Advocates of the "cladistic" (i.e. "phylogenetic" of Hennig, 1966) and "evolutionary" (e.g. Mayr, 1969; and Simpson, 1961) approaches contend that testable hypotheses on evolutionary history can be generated through appropriate handling of data on living organisms (and/or fossils); and they agree that hypotheses on evolutionary relationship should serve as the basis for classification.

Because evolutionary theory provides the unifying concept for all biology through a causal explanation of observed diversity, classifications, which are themselves intended as devices for unification and orderly arrangement and storage of information on this diversity, should, if possible, reflect evolutionary relationships. I concur with Whitehead (1972) that classifications must also have predictive value--that is, suggest relationships among members classified in characteristics not yet studied. Such predictions can often be tested directly and therefore serve, themselves, as tests of the classification. Only classifications based on evolutionary relationships can be expected to have this predictive power.

The fundamental rift between cladistic and evolutionary approaches to classification involves a difference in ranking criteria (i.e. the "absolute ranking" of Hennig, 1966) rather than grouping procedures. Griffiths (1974) has provided a conceptual framework in which this distinction is clear (see also Kavanaugh, in press C). He distinguishes between classification (defined above) and systematization, which he defines as "the ordering of organisms according to relations within a

system". He views organic diversity as a hierarchy of element/system relations--an extension of the "levels or organization" concept--and not hierarchy of classes. Systems are unique, individual wholes; and just as single cells are elements of tissues, and tissues elements of organs, populations are elements of species and species elements of a system at the next higher level of organization (e.g. genus). Species are, therefore, elements of a system which exists as an historical reality, independent of our perception of it, generated through the speciational processes of evolution. The important consequences of adopting this perspective are as follows: (1) relationships among the elements (taxa) in this system are historically determined by the branching pattern of phylogeny and are therefore independent of any criterion of similarity; and (2) because systems are themselves wholes, elements are automatically and necessarily parts of them, again without reference to any other criteria. Attempts to discover relationships within the system and to order taxa accordingly can be called "systematization". Classes, on the other hand, are abstractions, and class-membership is dependent on possession of certain essential or contingent attributes. Classification is, therefore, distinct from systematization; but to the extent that a classification mirrors the natural hierarchic system, it can reflect the same objective reality.

In terms of the above concepts, strictly cladistic classifications attempt to mirror exactly the element/system relationships perceived through systematization procedures (see section 4.1 on phylogeny for discussion and details). The formal rank of a taxon in such a classification is determined by its position in the hierarchy (e.g.

"sister" taxa [see section 4.1] are accorded equal rank) and by its geologic age (Hennig, 1966). Degree of phenetic distinctiveness is not used as a criterion for ranking, because its use would necessarily distort element/system relationships. In contrast, this criterion is used extensively in evolutionary classifications. Advocates of this approach consider divergence and novelty as important components of evolutionary history and seek to incorporate these factors in their classifications. Divergence therefore influences formal ranking. Again, as suggested by cladistics, some distortion of element/system relationships normally results from this procedure. Ashlock (1974) acknowledged this in noting the need to consider only "holophyletic" (i.e. "monophyletic", sensu Hennig, 1966) groups in zoogeographic studies.

I concur with Brundin (1966 and 1972), Griffiths (1972, 1974a, and 1974b), and Hennig (1966) that cladistic classifications are to be preferred as general reference classifications. There are, however, practical problems with such classifications. As noted by Crowson (1970) and Mayr (1969) among others, they tend to require larger numbers of categories than more traditional classifications, due to the dichotomous branching format followed in representing hypothetical ancestral relationships. For groups such as Nebria (see cladogram, Fig. 373) which demonstrate markedly unequal diversity in different lines, the resulting cladistic classification is highly asymmetrical and unbalanced with respect to the distribution of taxa in various categories. In such instances, awkwardness of the classification may offset its inherent usefulness.

Nelson (1974) discussed classification as an expression of phylogenetic relationship and presented a convention, called "sequencing", which permits a more manageable arrangement of taxa and judicious use of categories while preserving all the phylogenetic information of a strictly cladistic classification. The convention is as follows: "descendant units may be sequenced [listed] according to the order of branching of their presumed ancestry". The sequence (order) of taxa so listed is critical. A taxon listed under this convention is taken to be the sister group of that group including all the following taxa ranked at the same or lower rank. For example, if three taxa are listed in the order A, B, and C, and each is assigned genus rank, the sequence implies that A is the sister group of B and C together, and that B is the sister group of C. With knowledge of the convention, the reader can reconstruct directly the cladogram on which the classification is based. I have followed this convention in the classification presented below, thereby reducing the number of categories required to express relationship from 10 to 5, with no loss of information on presumed cladistic relationship.

3.32 History of Nearctic *Nebria* classification

LeConte (1878) was first to attempt a classification of Nearctic *Nebria* taxa. He arranged 22 species (19 [86%] of which I recognize as distinct species) in six species groups, based on the following characters: (1) number of pairs of posterior paramedial setae on third through fifth visible sterna; (2) elytral shape; (3) hindwing length; (4) length of the metepisternum; (5) pronotal shape; and (6) degree of

margination of the prosternal intercoxal process.

Casey (1913, 1920, and 1924) described numerous new species, recognized a total of 44 species (22 [49%] of which I recognize as distinct species), and rearranged LeConte's classification to accomodate these new taxa and his divergent views on relationship. He proposed seven species groups (Casey, 1913), only two of which were identical in name and composition with LeConte's (Fig. 365). The other groups differed with LeConte's in either the inclusion of new taxa or the transfer of one or more taxa from one group to another. Characters used by Casey for grouping taxa were less dependable than those used by LeConte and included: (1) elytral shape; (2) elytral convexity; (3) pron al shape; and (4) "habitus". Casey's classification therefore represents no advance in an understanding of the relationships of Nearctic taxa.

E. C. Van Dyke was keenly interested in relationships among Nebria species and used distribution (especially vicariance) patterns among Nebria species he considered related to illustrate certain of his ideas on the origins and distributions of Nearctic insects (see Van Dyke, 1919, 1926, and 1940). Unfortunately, he did not publish his views on relationship in any manner approaching a classification; and what remains of his perspective can be seen only in scattered narrative passages (unsupported by data or analyses) (e.g. Van Dyke, 1919:8).

Following LeConte and Casey, the next classification to include Nearctic taxa was that of Bänninger (1925), who reviewed the world-wide Nebria fauna, but treated Nearctic taxa only superficially. He considered Nebria ovipennis, N. kincaidi, and N. paradisi ("N.

columbiana Casey") as members of subgenus Nebriola Daniel (1903) and arranged the other Nearctic species among five species groups as members of subgenus Nebria (= Paranebria Jeannel, 1937, not Nebria latreille, 1802). He also dealt briefly with relationships among Nearctic taxa in later papers (Bänninger, 1931, 1933, and 1949). In reworking Bänninger's classification, Jeannel (1937) removed all Nearctic taxa from subgenera Paranebria and Nebriola and reassigned them, with several Palaearctic taxa, to his new subgenus Boreonebria.

The most comprehensive classification of Nearctic Nebria to date has been that of Lindroth (1961a). He classified 40 species (36 [90%] of which I recognize as distinct species) into 12 species groups based on a diversity of characters which included: (1) presence or absence of the mid-lateral pronotal seta; (2) pronotal shape; (3) width of the lateral pronotal explanation; (4) number of setae at the base of the hind coxa; (5) presence or absence of setae on second visible abdominal sternum; (6) presence or absence of anterior paralateral setae on third through fifth visible abdominal sterna; (7) elytral shape; (8) continuity of elytral intervals; and (10) structure of the genitalia of males. Lindroth's work represents the major advance in knowledge of relationships within and composition of the Nearctic fauna; and it forms the foundation for my study presented here. It is informative to use Lindroth's classification as a standard with which to compare earlier as well as subsequent classifications. Figs. 365 and 366 graphically illustrate differences in composition of the groups proposed by LeConte and Casey, by later workers noted below, and by me in the classification proposed below, in comparison with Lindroth's

groups. Both great departure from earlier classifications and close approximation to subsequent classifications are evident for Lindroth's classification from this comparison.

Erwin and Ball (1972) revised the trifaria and ovipennis species groups of Nebria and were first to employ cladistic and zoogeographical analyses in the study of relationships among members of the genus. They were also first to use characters of the digestive system and female reproductive system (e.g. bursa copulatrix and associated structures) in a comparative study of Nebria taxa.

The most recent work on Nebria classification is that of Shilenkov (1975a), who revised the genus for Siberia and far-eastern Asia. He proposed several new subgenera, two of which include a majority of the Nearctic taxa. The relationships between his classification (as it applies to Nearctic taxa) and Lindroth's and my own are represented in Fig. 366 . In general, my findings support those of Shilenkov quite closely.

3.33 A reclassification of Nearctic Nebria

I present here a reclassification of the Nearctic Nebria taxa, based on detailed phylogenetic (cladistic) and zoogeographic analyses which are presented in sections 4.1 and 4.2, respectively, below. Every effort was made to maintain independence of these two analyses, so that, in the end, hypotheses generated from zoogeographic analysis could be used in objective tests of hypotheses on relationship generated from cladistic analysis. The resultant compatibility of cladistic and historical zoogeographic reconstructions is discussed in

section 4.3 below.

The cladogram on which the classification is based is presented in Fig. 373 . As noted above, the branching pattern of the cladogram is highly asymmetrical--a bonsai among "family trees". I therefore applied the sequencing convention discussed above to obtain a more balanced distribution of taxa over the categories used, with no loss of cladistic information.

I have refrained from naming or recognizing subgenera at this time, and prefer to wait until a reclassification of the world fauna is possible before doing so. All supraspecific relationships within Nebria are not yet apparent; and there is no need to add to the long list of formal names already proposed for major subdivisions of Nebria. These names are simply listed as synonyms of Nebria Latreille (see section 3.41) and are not discussed further.

I use the informal rank of "lineage" as the most inclusive category within genus Nebria. For reference purposes only, I note that lineages recognized here will probably be ranked either as subgenera or genera when the classification is eventually upgraded to include the world-wide fauna. In fact, Shilenkov (1975a) has already proposed subgenera which correspond almost exactly to the gyllenhali, gregaria, and metallica lineages I recognize; and Habu (1958) has ranked the group comprising the Palaearctic members of the virescens lineage as a distinct genus, Nippononebria Ueno.

Because the criterion of strict monophyly of groups (Hennig, 1966) requires inclusion of all descendants of a common ancestor as well as only them (see below, section 4.1), I examined all

available Palaearctic material in a search for representatives of taxa possibly related to Nearctic forms. A total of 20 such taxa were found represented (and three more taxa, members of which I have not yet examined, may be related to Nearctic taxa). These representatives were included in the cladistic and zoogeographic analyses and appear in the cladogram (Fig. 373). In fact, seven of the 10 species groups recognized have Palaearctic representatives. However, I have omitted the Palaearctic taxa from the classification as outside its scope.

A CLASSIFICATION OF NEARCTIC *NEBRIA* SPECIES

A. The *virescens* lineage

I. The *virescens* group

1. *N. virescens* Horn

B. The *gyllenhali* lineage

I. The *paradisi* group

1. *N. paradisi* Darlington

II. The *hudsonica* group

1. *N. gouleti* Kavanaugh, new species

2. *N. hudsonica* LeConte

3. *N. lacustris* Casey

a. *N. lacustris lacustris* Casey

b. *N. lacustris bellorum* Kavanaugh, new subspecies

III. The *gyllenhali* group

A. The *nivalis* subgroup

1. *N. nivalis* (Paykull)

a. *N. nivalis nivalis* (Paykull)

b. *N. nivalis gaspesiana* Kavanaugh, new subspecies

B. The *gyllenhali* subgroup

1. *N. crassicornis* Van Dyke

a. *N. crassicornis crassicornis* Van Dyke

b. *N. crassicornis intermedia* Van Dyke

2. *N. gyllenhali* (Schönherr)

a. N. gyllenhali castanipes (Kirby)

b. N. gyllenhali lassenensis Kavanaugh, new subspecies

c. N. gyllenhali lindrothi Kavanaugh, new subspecies

3. N. frigida Sahlberg

C. The gregaria lineage

I. The gregaria group

A. The lyelli subgroup

1. N. lyelli Van Dyke

2. N. acuta Lindroth

a. N. acuta acuta Lindroth

b. N. acuta quileute Kavanaugh new subspecies

B. The sahlbergii subgroup

1. N. sahlbergii Fischer von Waldheim

a. N. sahlbergii sahlbergii Fischer von Waldheim

b. N. sahlbergii modoc Kavanaugh, new subspecies

c. N. sahlbergii triad Kavanaugh, new subspecies

C. The gregaria subgroup

1. N. gregaria Fischer von Waldheim

2. N. charlottae Lindroth

D. The arkansana subgroup

1. N. arkansana Casey

a. N. arkansana arkansana Casey

b. N. arkansana edwardsi Kavanaugh, new subspecies

c. N. arkansana oowah Kavanaugh, new subspecies

d. N. arkansana uinta Kavanaugh, new subspecies

2. N. fragilis Casey

a. N. fragilis fragilis Casey

b. N. fragilis teewinot Kavanaugh, new subspecies

3. N. zioni Van Dyke

a. N. zioni zioni Van Dyke

b. N. zioni oasis Kavanaugh, new subspecies

II. The obliqua group

A. The obliqua subgroup

i. The obliqua infragroup

1. N. suturalis LeConte

2. N. obliqua LeConte

ii. The pallipes infragroup

1. N. appalachia Darlington

2. N. pallipes Say

III. The mannerheimii group

A. The mannerheimii subgroup

1. N. darlingtoni Kavanaugh, new species

2. N. mannerheimii Fischer von Waldheim

B. The *eschscholtzii* subgroup

i. The *desolata* infragroup

1. *N. desolata* Kavanaugh

2. *N. navajo* Kavanaugh, new species

ii. The *eschscholtzii* infragroup

1. *N. eschscholtzii* Menetries

2. *N. diversa* LeConte

D. The *metallica* lineage

I. The *ovipennis* group

A. The *gebleri* subgroup

1. *N. gebleri* Dejean

a. *N. gebleri gebleri* Dejean

b. *N. gebleri cascadensis* Kavanaugh, new subspecies

c. *N. gebleri rathvoni* LeConte

d. *N. gebleri siskiyouensis* Kavanaugh, new subspecies

e. *N. gebleri strawberriensis* Kavanaugh, new subspecies

B. The *ovipennis* subgroup

i. The *kincaidi* infragroup

1. *N. carri* Kavanaugh, new species

2. *N. kincaidi* Schwarz

a. *N. kincaidi kincaidi* Schwarz

b. *N. kincaidi balli* Kavanaugh, new subspecies

ii. The *ovipennis* infragroup

1. N. spatulata Van Dyke

a. N. spatulata spatulata Van Dyke

b. N. spatulata sierrae Kavanaugh, new subspecies

2. N. ovipennis LeConte

II. The metallica group

A. The meanyi subgroup

1. N. meanyi Van Dyke

a. N. meanyi meanyi Van Dyke

b. N. meanyi lamarckensis Kavanaugh, new subspecies

c. N. meanyi sylvatica Kavanaugh, new subspecies

B. The metallica subgroup

i. The metallica infragroup

1. N. metallica Fischer von Waldheim

III. The trifaria group

A. The ingens subgroup

1. N. ingens Horn

a. N. ingens ingens Horn

b. N. ingens riversi Van Dyke

2. N. vandykei Bänninger

a. N. vandykei vandykei Bänninger

b. N. vandykei wyeast Kavanaugh, new subspecies

B. The schwarzi subgroup

1. N. piperi Van Dyke

2. N. schwarzi Van Dyke

a. N. schwarzi schwarzi Van Dyke

b. N. schwarzi beverlianna Kavanaugh, new subspecies

C. The trifaria subgroup

i. The purpurata infragroup

1. N. purpurata LeConte

ii. The trifaria infragroup

1. N. trifaria LeConte

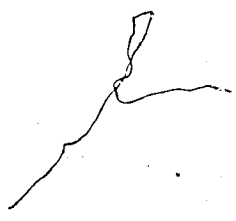
a. N. trifaria trifaria LeConte

b. N. trifaria catenata Casey

c. N. trifaria utahensis Kavanaugh, new subspecies

2. N. coloradensis Van Dyke

3. N. piute Erwin and Ball



3.4 Nomenclature, Description and Identification

3.41 Genus Nebria Latreille

Nebria Latreille, 1802:89. Type species.--Carabus brevicollis Fabricius, 1792:150 (by subsequent designation; Latreille, 1810: 68).

Alpaeus Bonelli, 1810:68. Type species.--Carabus hellwigi Panzer, 1797: 107 (by original designation).

Helobia Curtis, 1826, pl. 103. Type species.--Carabus brevicollis Fabricius, 1792:150 (by original designation).

Eurynebria Ganglbauer, 1891:134. Type species.--Carabus complanatus Linnaeus, 1767:671 (by original designation).

Oreonebria K. Daniel, 1903:159 (as a subgenus of Nebria). Type species. Alpaeus castanea Bonelli, 1810:75 (by subsequent designation; Jeannel, 1937:2).

Nebriola K. Daniel, 1903:164 (as a subgenus of Nebria). Type species.-- Nebria laticollis Dejean, 1826:244 (by subsequent designation; Jeannel, 1937:3).

Epinebriola K. Daniel and J. Daniel, 1904:77 (as a subgenus of Nebria). Type species.--Nebria oxyptera K. Daniel and J. Daniel, 1904:75 (by monotypy).

Spelaeonebria Peyerimhoff, 1911:359 (as a subgenus of Nebria). Type species.--Nebria nudicollis Peyerimhoff, 1911:359 (by monotypy).

Psilonebria Andrewes, 1923a:275 (as a subgenus of Nebria). Type species.--Nebria superna Andrewes, 1923a:273 (by monotypy).

Patrobonebria Bänninger, 1923:131 (as a subgenus of Nebria). Type

species.--Nebria desgodinsi Oberthür, 1883:47 (by subsequent designation; Jeannel, 1937:2).

Eonebria Semenov-Tian-Shanskij and Znojko, 1928:213 (as a subgenus of Nebria). Type species.--Nebria komarovi Semenov-Tian-Shanskij and Znojko, 1928:214 (by original designation).

Eunebria Jeannel, 1937:3 (as a subgenus of Nebria). Type species.--Carabus psammodes Rossi, 1792:85 (by original designation).

Boreonebria Jeannel, 1937:4 (as a subgenus of Nebria). Type species.--Carabus rufescens Strøm, 1768:331 (= Carabus gyllenhali Schönherr) (by original designation).

Paranebria Jeannel, 1937:4 (as a subgenus of Nebria). Type species.--Carabus lividus Linnaeus, 1758:414 (by original designation).

Neonebria Hatch, 1939b:84 (as a subgenus of Nebria). Type species.--Carabus lividus Linnaeus, 1758:414 (by original designation).

Nebriorites Jeannel, 1941:199 (as a subgenus of Oreonebria). Type species.--Alpaeus gagates Bonnelli, 1810:74 (by original designation).

Alpaeonebria Csiki, 1946:166 (as a subgenus of Nebria). Type species.--Nebria fuscipes Fuss, 1850:16 (by original designation).

Nippononebria Ueno, 1953:59 (as a subgenus of Nebria). Type species.--Nebria pusilla Ueno, 1953:59 (by original designation).

Orientonebria Shilenkov, 1975a:833 (as a subgenus of Nebria). Type species.--Nebria coreica Solsky, 1875:254 (by original designation).

Reductonebria Shilenkov, 1975a:834 (as a subgenus of Nebria). Type species.--Nebria ochotica R. F. Sahlberg, 1844:15 (by original

designation).

Catonebria Shilenkov, 1975a:836 (as a subgenus of Nebria). Type species.--Carabus nitidulus Fabricius, 1801:184 (by original designation).

Notes on nomenclature. In his original description of Nebria, Latreille (1802) assigned three species to the genus: Carabus brevicollis Fabricius, Carabus complanatus Linnaeus, and Carabus sabulosus Fabricius (= Carabus lividus Linnaeus). In 1810, he designated C. brevicollis as the type species of Nebria. This was an unfortunate choice, because members of this species are not typical of those of most Nebria species. Several authors (e.g. Bänninger, 1925) refused to accept C. brevicollis as the type species, and referred it instead to subgenus Helobia Stephen (1826) as the type species of that taxon. These authors considered Carabus lividus Linnaeus as the type species of subgenus Nebria. Andrewes (1935) noted this nomenclatural dilemma and suggested that Latreille's (1810) type designation be ignored and C. lividus Linnaeus accepted as type species of Nebria. Both Jeannel (1937) and Hatch (1939b) took issue with this ew, each reaffirmed Latreille's type designation, and each proposed a new subgenus to accomodate C. lividus Linnaeus and its relatives [i.e. Paranebria Jeannel (1937) and Neonebria Hatch (1939b)]. Helobia Stephen is therefore an objective junior synonym of Nebria Latreille, with C. brevicollis the type species of each.

Derivation of genus name.--Greek, nebris = deer skin; probably in reference to the patterned tan and brown coloration of members of two originally included species (N. complanata (Linnaeus) and N. livida (Linnaeus)).

Diagnostic combination.--Head of adults with one pair of supraorbital setae; mandibular scrobe unisetose; maxillae, mentum and submentum without setiferous spiniform processes or ridges; mentum with tooth present, truncate or bifid; elytron with nine complete striae, scutellar striole short, present on basal one-third only, internal plica simple, keel-like, extended to but not across epipleuron; front coxal cavities uniperforate, separate, open posteriorly; front tibia with apex obliquely truncate, both spurs apical, antenna cleaner simple, sulcate; middle coxal cavities disjunct, confluent; basal tarsomeres of middle tarsus (both sexes) without pads of adhesive hairs ventrally; hind coxal cavities conjunct, confluent; metepimeron absent; parameres of male asetose; internal sac without spines, teeth, or plates; common oviduct without sclerites.

Description of form and structure of adults.--Size medium to medium-large, standardized body length 6.7 to 14 mm (in Nearctic species). Form slender, slightly convex; head and pronotum proportionally small, but varied in relative length and width; elytra proportionally large.

Color. Extremely varied; head, pronotum, elytra, and venter usually concolorous (but some individuals of some species with relatively paler elytra; some Palaearctic species with patterned elytra), pale yellow to black; antennae, mouthparts, and legs

concolorous with body or only slightly paler in most adults, but markedly contrasting (paler) in some. Head with or without pale median spot or pair of para-medial spots on frons.

Reflection. Dorsum varied, from entirely non-metallic to markedly metallic (blue, green, violet, or brassy; golden or copper in adults of a few taxa), especially on elytra, on head of members of very few species; venter of adults of most taxa and appendages of those of all taxa non-metallic.

Luster. Dorsum varied, from very dull to very shiny, faintly iridescent in adults of a few taxa.

Microsculpture. Head with isodiametric, unbroken meshes, moderately impressed to effaced, best developed on labrum of most adults; alveolae flat. Pronotum with isodiametric (slightly transverse in some adults), unbroken to slightly broken meshes, in members of some taxa arranged in rows, markedly to faintly impressed, slightly effaced in few adults; alveolae flat to slightly convex. Elytra with isodiametric to markedly transverse, unbroken to moderately broken meshes, in members of some taxa arranged in rows (reduced to dense transverse lines in few adults), markedly to slightly impressed; alveolae flat to slightly convex.

Head. Prognathous frons smooth medially (in few adults sparsely punctulate or punctate), usually faintly rugulose laterally, moderately convex to flattened medially; frontal lobes obsolete; one supraorbital seta positioned just medial to posterior margin of each eye; frontal furrows relatively short (in some adults present only as foveae), vaguely to sharply impressed (absent from a few adults). Genae not to

markedly swollen posterior to eyes. Vertex smooth, convex, with or without very faint medial fovea or more broadly transverse depression. Head not or moderately constricted posterior to eyes. Occiput not to markedly swollen (width across occiput less than to greater than width of head across eyes). Compound eyes moderately to markedly convex (flattened in adults of a few taxa), size medium to small. Antennae length moderate to very long, with basal four antennomeres without pubescence (except at apex of fourth antennomere in very few adults); scape short to long, shape varied (straight to bent, cylindrical to markedly narrowed basally and/or apically), with a single subapical seta on anterodorsal surface; pedicel with a single ventro-apical seta (with one to three additional apical setae in very few adults); second through fourth antennomeres cylindrical (laterally compressed near base in adults of few taxa); fifth through eleventh antennomeres cylindrical (in some adults slightly flattened), relatively short and broad to very elongate and slender. Clypeus with single pair of mid-lateral setae, anterior margin slightly concave (in few adults emarginate) to almost truncate; frontoclypeal suture evident, markedly impressed. Labrum with three pair of setae across apex (except in N. complanata (Linnaeus) adults), shape apical margin varied from slightly concave to slightly convex or bisinuate (deeply emarginate in members of very few taxa). Mandibles with well-developed, unisetose scrobes, laterally slightly to moderately explanate, medial cutting edges basally not or variously toothed (see section 3.212 above for details); apex right mandible narrow, pointed, but not hooked; apex left mandible markedly to very markedly hooked. Maxilla: stipes with all setae not

inserted on ventro-lateral spiniform processes. Labium: ligula longitudinally carinate medioventrally, with one pair of setae apicomedially, apical margin truncate to markedly toothed medially (ligula of N. complanata adults is unique in form and setal pattern); paraglossae adnate, fused to ligula (or distinct, as a very short, dentiform lobe at apicolateral corner of ligula); penultimate labial palpomere bi- or trisetose, length less than or equal to length of terminal palpomere (except in N. complanata adults). Mentum (Fig. 64) deeply emarginate anteriorly (depth of emargination varied, from one-third to one-half total length of mentum), with medioapical tooth of varied shape (bifid to broadly truncate) and length (one-third to one-sixth of depth of emargination), and with three (in few individuals two) pair of setae (one pair at base of mental tooth (M_1), one pair at basolateral angles (or absent) (M_3), and one paramedial pair at or anteriorly removed from base(M_2); each epilobe asetose apically, moderately broad, (narrowed laterally in few adults) with lateral margin smoothly rounded, and with minute to long, well-defined apical tooth. Gula T-shaped, with one to seven pairs of lateral setae not inserted in spiniform processes and zero to two pairs of medial setae not inserted in a raised, transverse medial ridge (Figs. 79 - 81).

Prothorax. Pronotum, shape slightly to very markedly cordate (in members of few taxa semiovoid, not narrowed basally); disc smooth (in few adults faintly punctulate), slightly to markedly convex; apical margin moderately convex to slightly concave medially; lateral margin slightly to markedly arcuate, with basal sinuation absent or shallow to very deep and varied in length; lateral explanation narrow to wide

throughout or anteriorly and/or posteriorly widened or narrowed; basal margin short to long, straight or variously modified; apical angles short to long and projected anteriorly, width broad to narrow, apices broadly ...ded to bluntly pointed; basal angles obtuse to acute, in some ad... ...aterally or posteriorly denticulate or projecting; apical margination markedly to faintly impressed (absent from only few adults), width moderate to narrow, present only in lateral thirds (medial one-third unmargined); lateral bead markedly to faintly impressed, wide to narrow, complete in most adults (but obliterated basally in some), widened apically or basally in many; basal margination absent; anterior transverse impression shallow to deep (absent from very few adults), broad and faintly defined to narrow and sharply defined, smooth to densely punctate; median longitudinal impression shallow to deep, smooth to moderately rugulose, varied in length but complete from apical to basal margin in very few adults; posterior transverse impression deep, narrow (broad in few adults), smooth to densely punctate, straight to anteriorly deflected at middle; basal foveae parallel to posteriorly divergent, deep (in few individuals slightly shallow), broad to narrow, smooth to moderately punctate, not or slightly extended anteriorly onto disc, lateral convexity absent to moderately carinate; a single pair of mid-lateral setae absent or present (positioned lateral to an associated small, longitudinal tubercle in members of few species); single pair of basolateral setae present (absent from adults of two species) at basal angles. Prosternum smooth to moderately punctate; intercoxal process smooth (rarely faintly punctulate or rugulose), asetose ventrally, margination complete to present basally only, shape

sublanceolate to lanceolate (rarely spatulate). Proepisternum smooth to faintly punctate. Proepimeron smooth to densely punctate. Front coxal cavities open, uniperforate, confluent.

Pterothorax. Scutellum small, visible. Elytra with silhouette varied, rectangular to almost petiolate, moderately flat to moderately convex, without pubescence; basal margination short to long, straight to markedly concave, smooth to wavy, deeply impressed and complete; humeral angles variously shaped, bluntly rectangular to markedly rounded (completely obliterated and flattened in members of very few taxa), with or without transverse humeral (epipleural) carina or tooth at the angle; subhumeral lateral sinuation absent to moderately deep; lateral explanation narrow to moderately broad, narrowed basally in most adults; subapical carina varied in length, slightly to markedly developed (absent from very few individuals); apices variously shaped, narrowly to broadly rounded or blunted, medially straight to sinuate; internal plica simple, keel-like, extended to but not across epipleuron; scutellar striole present, short, confined to basal one-third of elytron or less, not fused distally with first stria; eight complete striae, shallowly to deeply impressed (lateral striae in some adults less distinctly so than more medial striae), faintly punctulate to moderately punctate; first and second striae divergent from common stem at some distance from basal margination (in only few individuals divergent from a common point at basal margination or completely independent basally; intervals approximately equal in width, smooth (impunctate), flat to very markedly convex, continuous or faintly to markedly catenate (only third, fifth, seventh, and/or ninth in few adults) intervals interrupted

(in apical half in most instances) by shallow to deep foveae with interfoveal areas nor or moderately tuberculate); discal setiferous pores absent or indistinct to broadly (broader than width of interval) foveate; basal (scutellar) pore absent or present; third interval with one to ten setae (none in N. nudicollis Peyerimhoff adults); fifth and seventh intervals with zero to nine setae each; ninth interval with eight to 22 setae (up to 32 in N. complanata adults) (umbilicate series), not arranged into groups. Metathoracic wing size varied, large and functional with full venation pattern (Fig. 181) to reduced to small scale-like lobe with reduced venation pattern; oblongum cell present (in full to moderately short wings), shape varied (Fig. 197 - 200), broad to narrow, posterior angle slightly to markedly acute, terminated in minute to short stalk; wedge cell (Figs. 201 - 205) single (absent from or double in very few individuals), triangular, truncate proximally (rectangular, open distally in few adults); marginal cell between P + C_2 and E_1 veins (Ward, unpublished manuscript) without sclerotized microtrichial field. Metepisternum smooth to moderately punctate. Metepimeron absent (or at least not visible externally). Middle coxal cavities disjunct, confluent. Hind coxal cavities conjunct, confluent, delimited laterally by metepisternum and first visible abdominal sternum.

Legs. Long and slender in most adults (but varied relatively among species, from long and very slender to short and robust). Front coxa globose, asetose. Middle coxa (Fig. 221) globose, with one (in few adults two) anteromedial seta and one (in few adults two) anterolateral seta subapically. Hind coxa (Figs. 223 - 229) flattened,

transverse, but not extended to lateral margin of venter; coxal ridge complete; plane of lateral wing posterior to coxal ridge 45° to almost 90° (in latter, obscured ventral aspect); one to seven basal setae and and one apical seta (with one or more extra apical setae in members of a few taxa) (Figs.226 - 227). Front and middle trochanters wedge-shaped, each with a single apico-ventral seta. Hind trochanter lobate, asetose. Front tibia with apex (Fig. 236) obliquely truncate (lateral angle displaced proximally), both spurs apical; antenna cleaner (Fig. 236) simple, symmetrical, sulcate. Middle tibia varied dorsally, flat or slightly convex to markedly concave and sulcate (especially in distal half), with slightly to moderately developed longitudinal brush of setae on distal one-third. Front tarsus of male (Figs.241 - 243) with basal three (in adults of few taxa all five) tarsomeres laterally expanded, with pads of adhesive setae (Figs.241 - 243) ventrally on basal two or three tarsomeres (pads rarely in area or entirely absent in adults of few taxa); females with all articles slender (also slightly laterally expanded in adults of few species), without pads. Middle and hind tarsi of both sexes slender in most adults (laterally expanded in few), slightly convex ventrally (adults with all tarsomeres expanded also have them ventrally concave (excavate)). Hind tarsus glabrous to sparsely pubescent dorsally, tarsomeres cylindrical (laterally compressed in few adults); fourth tarsomere (Figs.249 - 252) apically truncate (with ventro-apical setae symmetrical in length and number) or ventro-laterally extended as a short to moderately long lobe (with lateral ventro-apical setae longer and more numerous than medial setae and positioned on the extended lobe). Tarsal claws simple,

slender, evenly arcuate, equal in length.

Abdomen. All sterna with lateral pair of broad, faintly to markedly defined pits (Fig. 253), dorsolaterally carinate, but not otherwise modified as receptor or lock for elytra. Second visible sternum glabrous medially or (in few adults) with one or more scattered setae or sparse to dense patch of setae between hind coxae. Third to fifth visible sterna (Figs. 253 - 258) with one to eight posterior paramedial setae and zero to 15 anterior paralateral setae each side. Sixth visible (or "anal") sternum with one to four posterior paramedial setae (some species sexually dimorphic in number of setae) and no anterior paralateral setae each side.

Male genitalia. Median lobe tubular, complete, enlarged basally, with well-developed internal sac; basal bulb (Figs. 262 - 264) shape varied, globose, rounded and partially closed (basal orifice small, ventrobasal only) to quadrate or wedge-shaped and broadly open (basal orifice large); 'mid-shaft' (see section 3.217 above) (Figs. 262 - 287) very slender to very thick (lateral aspect), circular to laterally compressed in cross-section, cylindrical or tapered (apically or basally), axis markedly, arcuately bent (angle varied, from 90° to 140°), with or without right lateral pouch (Figs. 277 - 280) (slightly to markedly invaginated) or groove (Fig. 272); 'preapical-shaft' (lateral aspect) very long, slender (ventral and dorsal margins almost parallel, with apical orifice broadly open dorsally)to broad, short, (ventral and dorsal margins convergent apically at markedly acute to almost right angles, apical orifice broadly to narrowly open dorsally, dorsoapically or dorsal and right laterally), ventral margin (inner

curvature) straight to markedly recurved dorsally; apex varied in length, symmetry and shape (in dorsal, lateral and apical aspects); internal sac varied in shape, uni- to multi-lobate, without plates, spines, setae or a flagellum (but with microtrichial fields). 'Dorsobasal sclerite' (Figs. 262 - 264) shape varied (entire, mid-dorsal and fin-like or from slightly to broadly split longitudinally, variously fused with or overlapping basal bulb). Parameres asymmetrical (symmetrical in length and shape in males of very few taxa); left paramere short, broad (in few males more elongate and/or narrowed), spatulate or apically narrowed and pointed; right paramere long, slender (in few males short and broad), arcuate, similar in curvature and length to median lobe, with or without a slender, strap-like sclerite ('right medial parameric' sclerite) (Figs. 292, 296) in medial membrane.

Female genitalia. Eighth abdominal sternum (Figs. 300 - 304) divided at middle in form of two hemisterna, each without vestiture except for row of sparse to dense setae on medial one-third of apical margin; basal apodeme moderate in width and length, apically truncate (Fig. 301) or emarginate (in some females very deeply) at middle in form of two distinct heads (with length of lateral head equal to (Fig. 302) or shorter than (Fig. 304) medial head, with lateral head vestigial in few females (Fig. 300)), without longitudinal reinforcing ridge (Figs. 300 - 304). Proctiger heavily sclerotized, shape varied (short, transverse, truncate apically (Fig. 305) to moderately long, hemispheric (Fig. 306)), glabrous. Paraprocts moderately to heavily sclerotized, shape triangular (Fig. 305), glabrous, narrowly to

broadly fused laterobasally with valvifer. Valvifer approximately triangular (Figs. 307 - 311), basal region heavily sclerotized, apicomedial region not to moderately sclerotized (if sclerotized, then not to broadly separated from basal region by membraneous area), with or without scattered setae in apicomedial region; basal apodeme lobate, length moderate (rarely shortened), positioned laterally. Vestige of tenth sternum split medially, each lateral piece pointed, lobate, fused with (or separate from but closely approximated to) medial angle of coxostylus (Figs. 312 - 313). Coxite and stylus fused medially in form of coxostylus, but apparently distinct laterally, ventrally and dorsally (separated by membraneous areas). Stylus region simple, non-segmented, without accessory lobes or teeth, produced apically as slightly to markedly arcuate blade; blade varied in length and shape, dorsolateral surface concave, ventromedial surface convex with one bisetiferous (in few females uni-or trisetiferous) subapical pore (pore absent only from N. complanata females), pore size varied, setae long; medial surface glabrous or sparsely to densely setose basally, medio-dorsal ridge glabrous or with one to six slender or spiniform setae. Coxite region membranous mid-laterally and ventrally to diagonal sclerotized margin, with row of one to 10 slender or spiniform setae (few females without setae) on or near diagonal margin (Figs. 315 - 321), medial surface glabrous or sparsely to densely setose apically. Bursa copulatrix with longitudinal axis varied, 'spermathecal chamber' slightly deflected dorsally (Fig. 315) to sigmoid (Fig. 328) or posterodorsally recurved (Fig. 327); 'vestibular chamber' (Fig. 322) broad, symmetrical, bell-shaped, slightly to markedly flared anterolaterally, dorsal wall

membranous (medially or paramedially sclerotized in few females), anterior wall in form of transverse septum between spermathecal chamber and common oviduct, medially with longitudinal reinforcement rod extended anteriorly in both spermathecal chamber and oviduct; spermathecal chamber shape varied (Figs. 324 - 343), width less than or equal to width vestibular chamber at their juncture, flat to vaulted, elongate-tubular-pointed anteriorly to short-broad-truncate anteriorly, symmetrical or anteriorly deflected left or right, main chamber in females of few taxa with accessory dorsal (Fig. 335) or ventral (Fig. 340) lobes, with or without sclerites (if present, sclerites associated with orifice of spermathecal duct in most females, present and not so associated in only few, shape varied), medial longitudinal reinforcement rod in ventral wall not sclerotized, in few females extended anteriorly as a narrow plate. Spermathecal duct (Figs. 345 - 352) very slightly sclerotized, varied in length (long to very short), diameter (narrow to [illegible] throughout or thick only proximally), and shape (straight to irregular, sinusoidal or helical), point of insertion on spermathecal chamber varied (anterior, dorsal or posterior surface, medial or lateral position). Spermathecal gland absent. Spermatheca very slightly sclerotized, sac-like, shape (Figs. 345 - 352) varied (straight-tubular to ovoid or arcuate-lanceolate). Common oviduct membranous without sclerites; medial longitudinal reinforcement rod in dorsal wa

Sexual dimorphism.--In addition to primary sex differences between male and female reproductive systems (including genitalia), there is sexual dimorphism in several other characters among Nebria species.

Females of all but a few species (e.g. N. ingens) are larger than conspecific males; but, in most species, males have relatively larger eyes and longer antennae and legs than females. At least basal tarsomeres of front legs of males are laterally expanded and bear pads of ventral hairs ventrally. These tarsomeres are slender and without pads in females. Females of most species have two or more pairs of "anal" setae (i.e. posterior paramedial setae on the sixth (last) visible sternum), and males of most species have only one pair.

Sexual dimorphism is also exhibited in one or more other characters by members of one or more Nebria taxa. These characters include: (1) development of elytral reflection (e.g. N. sahlbergii) (2) relative size or width of head (e.g. N. crassicornis or N. ingens); (3) relative width of pronotum (e.g. N. fuscipes Fuss, Palaearctic species); (4) relative length of elytra (e.g. N. ingens); and (5) elytral microsculpture, including depth of impression and shape of alveolae (e.g. N. arkansana) [see species descriptions, section 3.43 for details].

Geographical distribution.--Combined ranges of the several hundred species embraced by the present genus concept almost completely cover the Holarctic Region: Europe and Asia, north to the Arctic coast and southern Arctic islands, south to Taiwan, south slope of the Himalaya Mountains, Syria and Lebanon, west to Iceland, east to Asiatic Beringian islands, North Africa, north of the Sahara Desert, Morocco to Algeria. In the Nearctic Region, combined ranges of the 42 indigenous and one introduced species extend from the Arctic coast and Baffin Island south in mountainous areas to southern California, Arizona,

New Mexico and South Carolina; from North American Beringian islands east to Newfoundland; absent from the central and southern Great Plains and the southern and southeastern Coastal Plain.

Geographical relations with allied genera.--The other genera included in supertribe Nebriitae are generally sympatric with respect to Nebria. The ranges of Leistus, Pelophila, Opisthius and Paropisthius are completely within the geographical limits of Nebria, the last three genera occupying more restricted areas. The range of Notiophilus extends outside that of Nebria only in the southwestern Nearctic and northern Neotropical Regions where its populations reach the highlands of northern Guatemala.

Habitat distribution.--Members of this genus occupy a wide range of habitats in geographical areas with cold to cool-temperate climate and very few habitats (only those which offer cool microclimate) in warmer regions. Most species are markedly hydrophilous, with members living only at the margins of streams, lakes, snowfields or glaciers. A few species are independent of water bodies, with members in forests or in open woodlands and fields; populations of two species inhabit coastal sand dunes and open beaches; and those of one species are restricted to subterranean grottos and caves.

The genus is best represented in mountainous regions. Species exhibit a cumulative altitudinal range extending from sea level to the lower limits of permanent snow. Individual species generally occupy limited altitudinal ranges; and in areas with a diverse Nebria fauna and considerable topographic relief, striking and complex patterns of altitudinal zonation are evident (for details refer to section 4.22).

Dispersal potential.--A high percentage of species have members with reduced hindwings which cannot support flight. Adults with full-sized hindwings are probably capable of at least short-range flight; but, in general, dispersal is by means of ambulatory activity and the dispersive range of individuals is limited (see section 3.235). Dispersal of most taxa is, therefore, limited by relatively narrow zones of unsuitable habitat.

Natural history.--The beetles are nocturnal, opportunistic predator-scavengers, apparently feeding on any fresh (usually invertebrate) prey. They hide under stones or other cover in suitable habitats during the day. Timing of the life cycle, in all species studied, conforms to one of two patterns: a spring or an autumn breeding pattern. The larval stage consists of three instars. [Refer to section 3.23 for more extensive discussion of natural history.]

Fossil record.--Unquestionable representation of the genus in the fossil record is at present confined to samples of Late Tertiary (?Pliocene) and Quaternary age from Eurasia and North America. Few species have been recognized and fragments appear to be indistinguishable from comparable parts of members of extant species (see section 3.24).

3.42 Identification of Nearctic *Nebria*

3.421 Notes on the key and its use

As Simpson (1969:276) stated, the purpose of a key is to "facilitate identification of a specimen". Consequently, the characters a taxonomist uses in his efforts to distinguish and classify biological species are useful in a key only to the extent that they apply to all individuals. Because at least some variation (including sexual dimorphism) in many characters is common to almost all taxa, important taxonomic characters may be useless as key characters. Conversely, apparently trivial characters may be used in a key if they permit simple, rapid and reliable identification. Unfortunately, groups of two or more cryptic species (Smith, 1958) occur in nature, confounding identification by any but more sophisticated means. When differentiation in structural and distributional characters is negligible, there are essentially no good key characters. In such instances, the inability to identify individuals reflects an evolutionary reality (minimal differentiation or convergence) rather than some doubt as to the distinctiveness of the taxa.

Nearctic *Nebria* species and subspecies vary in the phenetic distinctiveness of their members and therefore in the ease with which individuals can be identified. Where possible, characters used in the key conform to the following criteria: (1) Universality: the state of the character is constant for all individuals of each taxon. Characters unique to one sex are avoided unless some character for the opposite sex is included in the couplet. Characters which are highly varied

within one taxon are not used unless the range of variation is essentially non-overlapping with that of the other taxon. (2) Accessibility: ease with which the state of a character is determined. Characters which can be studied only through dissection or which involve data not normally associated with a specimen are avoided if possible. Unfortunately, study of some important taxonomic and (occasionally) key characters (including development of the hindwings and structure of male and female genitalia) requires delicate dissection. Exclusion of genitalic characters prevents, for example, construction of a useful key to the Nearctic species groups because they require polythetic definition involving these characters. (3) Efficiency: speed of identification permitted by use of the character. Characters which are most evident, especially those which do not require use of a microscope (e.g. distributional characters) facilitate rapid progress through a key to an identification.

Organization of individual couplets is such that the most useful character is mentioned first, followed by supplementary characters which should reinforce the reader's initial choice between alternatives. The key assumes familiarity with structure and associated terms or carabid beetles; a few terms are used that are new. However, reference to appropriate discussions in section 3.2 and to the figures suggested in the key provides useful background and explanation. Particular difficulty may be encountered in couplets involving the following characters: form and depth of impression of microsculpture; continuity of elytral intervals (presence or absence of catenations); and absence or presence and intensity of metallic reflection. Preliminary reference

to discussions of these characters is almost essential to effective use of the key.

Extensive use of distributional characters in this key is justified by their efficiency and accessibility. Specimens without associated locality data are, fortunately, rare and seldom worth identifying; and the geographical distributions of most taxa are relatively well known. In two instances (namely, in couplets 64. and 65.), entries contain predictions on the probable occurrence of taxa where they are not yet known to occur (see appropriate species descriptions for present known ranges). Access to a comprehensive geographical atlas on North America is helpful to those without detailed knowledge of the continent.

At a few couplets in the key, dissections are required or suggested. For recommended dissection techniques, refer to section 2.22.

3.422 A Key for Identification of Adults of Nearctic Species and Subspecies of Nebria

i Front tarsus with basal three or four articles dilated, laterally expanded, with pads of adhesive setae ventrally on basal two or three articles .... MALE 1

i' Front tarsus with all articles slender (no broader than articles of middle or hind tarsus), without pads of adhesive setae ventrally .... FEMALE 1

1 (i,i') Midlateral pronotal seta present (Fig. 84) 2

1' Midlateral pronotal seta absent (Fig. 94) 46

2 (1) Head uniformly dark (dark rufous to black) 3

2' Head dark or pale; if dark, then vertex with one pair of pale paramedial spots (or pair fused to form a single median spot (Figs. 4 - 6) 16

3 (2) Metepisternum markedly punctate (Fig. 215); tarsomeres of hind tarsus sparsely pubescent dorsally (Fig. 247) [repeatedly introduced, but not established in Nearctic Region] ..... N. brevicollis (Fabricius) (p. 341)

3' Metepisternum impunctate (Fig. 216); tarsomeres of hind tarsus glabrous dorsally (Fig. 248) 4

4 (3') Pronotum semiovoid (Fig. 84), basal sinuation of lateral margin absent or very short and shallow; fourth tarsomere of hind tarsus truncate ventrally (Fig. 249) with medial and

lateral apicoventral setae symmetrical in length and position; labium with paraglossae distinct as short, pointed apicolateral lobes on ligula (Fig. 61) .... N. virescens Horn (p. 345)

4' Pronotum distinctly cordate (Figs. 86 - 122), basal sinuation of lateral margin moderately to very deep; fourth tarsomere of hind tarsus not truncate (ventrolaterally extended as short to moderately long lobe (Figs. 250 - 252) with lateral apicoventral setae longer than medial setae and displaced toward apex of lobe); labium (Fig. 62) with paraglossae indistinct, fused with ligula 5

5 (4') Pronotum with small, longitudinal tubercle medial to midlateral seta (Fig. 89); fifth elytral interval with one to four setae 6

5' Pronotum without small, longitudinal tubercle medial to midlateral seta; fifth elytral interval without setae (rare individuals with single seta) 7

6 (5) Specimen from Alaska or northern Canada, east to west side of Ungava Bay, Quebec (or on Baffin Island). If locality in Quebec, elytra short, pronotum (Fig. 89) short and broad with basal sinuation of lateral margin moderately deep .... N. nivalis nivalis (Paykull) (p. 362)

6' Specimen from northeastern United States or Canada, from Maine (Mount Katahdin) to east side of Ungava Bay (or on Island of Newfoundland). If locality in Quebec, elytra long, pronotum (Fig. 90) long, narrowed basally with basal

sinuation of lateral margin very deep .....
..... N. nivalis gaspesiana new subspecies (p. 365)

7 (5') Second visible sternum with patch of setae medially (between hind coxae); third to fifth visible sterna each with two to six pairs of posterior paramedial setae 8

7' Second visible sternum glabrous medially; third to fifth visible sterna each with single pair of posterior paramedial setae 9

8 (7) Hind coxa unisetose basally; antennal scape (Figs. 25a, 25b) long, arcuate to bisinuate, narrow basally, broadly truncate apically; elytra slightly dull to moderately shiny, microsculpture moderately impressed, meshes slightly to moderately transverse and irregular; legs dark .....
..... N. hudsonica LeConte (p. 357)

8' Hind coxa bi- or trisetose basally; antennal scape (Fig. 24) moderately long, symmetrically ellipsoid; elytra dull, microsculpture very deeply impressed, meshes isodiametric to very slightly transverse; legs dark or pale .....
..... N. gouleti new species (p. 356)

9 (7') Elytra very shiny (or faintly iridescent), microsculpture of thin, transverse lines without (or with only a few scattered) meshes, intervals markedly convex, striae very deeply impressed; pronotum (Figs. 87 - 88) with apical angles very broad, basal angles slightly to moderately obtuse 10

9' Elytra dull to slightly shiny, microsculpture of isodiametric to moderately transverse meshes, intervals flat to

moderately convex, striae moderately deeply impressed; pronotum (Figs. 92 - 93) with apical angles narrow to moderately broad, basal angles rectangular to acute 11

10 (9) Specimen from eastern North America north of French Broad River (North Carolina) (Fig. 384) .... N. lacustris lacustris Casey (p. 358)

10' Specimen from southeastern United States, south of French Broad River (Fig. 384) .... N. lacustris bellorum new subspecies (p. 359)

11 (9') Head, pronotum and elytra brassy to brilliant metallic green; or, if non-metallic dorsally, pronotal microsculpture very deeply impressed, meshes isodiametric, alveolae slightly convex; penultimate labial palpomere bisetose (trisetose only in very few individuals); third elytral interval clearly catenate (setiferous pores broadly foveate) .... N. frigida R. F. Sahlberg (p. 375)

11' Head, pronotum and elytra non-metallic; pronotal microsculpture faintly to deeply impressed, meshes isodiametric, alveolae flat; penultimate labial palpomere trisetose; third elytral interval continuous or faintly catenate (setiferous pores weakly to moderately foveate) 12

12 (11') Pronotum (Figs. 92 - 93) large, broad, markedly cordate (lateral margin markedly arcuate at middle), dull, microsculpture deeply impressed, meshes isodiametric; head (Figs. 13 - 14) large, very convex, with genae and occiput

broad and eyes slightly reduced in size 13

12' Pronotum (Figs. 93A, 93B) small, slightly narrow, moderately cordate (lateral margin moderately arcuate at middle), slightly dull to moderately shiny, microsculpture moderately to faintly impressed, meshes isodiametric; head (Fig. 14A) moderate in size and convexity, with genae and occiput not broadened and eyes full-sized 14

13 (12) Specimen from the Olympic Peninsula or Cascade Range and adjoining ranges of southwestern British Columbia to central Washington (Fig. 387). Head (Fig. 13) with microsculpture faintly impressed, meshes isodiametric, genae and occiput very broad; pronotum (Fig. 92) markedly narrowed basally, apical angles markedly projected anteriorly, narrowed and bluntly pointed apically .... N. crassicornis crassicornis Van Dyke (p. 366)

13' Specimen from east of the Columbia Basin in Oregon or Washington, east of the Okanagan Valley in southern British Columbia, or in northern British Columbia south to Terrace (Fig. 387). Head (Fig. 14) with microsculpture moderately impressed, meshes isodiametric, genae and occiput moderately broad; pronotum (Fig. 93) moderately narrowed basally, apical angles moderately projected anteriorly, slightly narrowed, rounded .... N. crassicornis intermedia Van Dyke (p. 367)

14 (12') Antennal scape (Figs. 27a, 27b) short, straight, symmetrically ovoid or anteriorly more convex; hindwing

full-sized. Specimen from northern Sierra Nevada of California or the Cascade Range of Oregon (south of Columbia River) (Fig. 388) ..... N. gyllenhali lassenensis new subspecies (p. 374)

14' Antennal scape (Figs. 26, 28) long, straight to slightly arcuate, markedly to moderately narrowed basally; hindwing full or reduced in size and venation pattern. Specimen from north or east of above area (Fig. 388) 15

15 (14') Hindwing (Fig. 192) reduced in length, width and venation. Specimen from southern Rocky Mountains, in Medicine Bow Range or more southerly ranges (Fig. 388) ..... N. gyllenhali lindrothi new subspecies (p. 374)

15' Hindwing (Fig. 191) full-sized. Specimen from more northern area of Rocky Mountain region (south to Laramie Mountains) or from area northeast or northwest (Fig. 388) ..... N. gyllenhali castanipes Kirby (p. 369)

16 (2') Basolateral pronotal seta absent (Fig. 111)..... 17

16' Basolateral pronotal seta present (Fig. 113) 19

17 (16) Specimen from east of Columbia Basin of Washington and Oregon. Penultimate labial palpomere bisetose; mentum (Fig. 72) with M_1 setae absent ..... N. carri new species (p. 413).

17' Specimen from Cascade Range or area further west. Penultimate labial palpomere trisetose; mentum (Fig. 73) with M_1 setae present 18

18 (17') Basal margination of elytron (Fig. 149) very short and wavy, markedly concave. Specimen from Olympic Peninsula, Vancouver Island, or on mainland from Cascade Range of northern Washington or Coast Ranges from southern British Columbia to southeastern Alaska (Fig. 405) .... N. kincaidi kincaidi Schwarz (p. 414)

18' Basal margination of elytron (Fig. 150) moderately long, smooth (or faintly wavy), slightly to moderately concave. Specimen from Cascade Range of central Washington to northern Oregon (Fig. 405) .... N. kincaidi balli new subspecies (p. 415)

19 (16') Specimen from California, extreme western Nevada or extreme southwestern Oregon 20

19' Specimen not from California, western Nevada or southwestern Oregon 28

20 (19) Elytra clearly with moderate to faint metallic (violet, blue or green) reflection 21

20' Elytra without metallic reflection 23

21 (20) Size very large: standardized body length male greater than 12.5 mm, female greater than 11.3 mm; elytral silhouette (Fig. 139) markedly ovoid, narrowed basally .... N. ingens riversi Van Dyke (p. 425)

21' Size moderate: standardized body length male less than 12.0 mm, female 12.3 mm to 9.5 mm; elytral silhouette (Fig. 136) subrectangular, broad basally 22

22 (21') Specimen from southern Sierra Nevada (Fig. 406). Pronotum (Fig. 114) markedly cordate, basal angles acute, projecte posteriorly; basal elytral margination (Fig. 152) straigh to slightly concave .... N. meanyi lamarckensis new subspecies (p. 420)

22' Specimen from Cascade Range (at present known only from Mount Shasta in California). Pronotum (Fig. 113) moderately cordate, basal angles rectangular, denticulate posteriorly; basal elytral margination (Fig. 151) slightly to moderately concave ..... N. meanyi meanyi Van Dyke [in part] (p. 419)

23 (20') Elytral silhouette (Figs. 136 - 137) subrectangular to subovoid; hindwing full-size 24

23' Elytral silhouette markedly ovoid, narrowed basally; hindwing vestigial 25

24 (23) Specimen from Klamath Mountain System of Coast Ranges in northwestern California or southwestern Oregon. Apical angles of pronotum (Fig. 110) moderately narrow; elytral silhouette (Fig. 137) subovoid, relatively short and broad ..... N. gebleri siskiyouensis new subspecies (p. 412)

24' Specimen from Sierra Nevada or extreme southern Cascade Range. Apical angles of pronotum (Fig. 109) moderately broad to slightly narrow; elytral silhouette (Fig. 136) subrectangular, relatively long and narrow .... N. gebleri rathvoni LeConte (p. 411)

25 (23') Size very large: standardized body length male greater than 12.5 mm, female greater than 12.0 mm; elytra black,

moderately shiny, with microsculpture faintly impressed, meshes isodiametric (often broken) .... N. ingens ingens Horn (p. 424)

25' Size moderate: standardized body length male less than 12.0 mm, female less than 12.4 mm; elytra rufous to piceus, very dull, with microsculpture deeply impressed, meshes isodiametric 26

26 (25') Head (Fig. 19) with genae and occiput swollen, very broad, eyes slightly reduced in diameter and convexity, antennal scape (Figs. 33a, 33b) ovoid, symmetrical to more convex anteriorly ..... N. ovipennis LeConte (p. 417)

26' Head (Fig. 20) with genae and occiput not swollen, eyes average in size and convexity, antennal scape (Figs. 34 - 35) cylindrical or narrowed basally and apically truncate 27

27 (26') Antennal scape (Fig. 35) short, straight, cylindrical. Specimen from Great Western Divide (southern Sierra Nevada) (Fig. 403)..... N. spatulata spatulata Van Dyke (p. 416)

27' Antennal scape (Fig. 35) medium length, slightly arcuate, markedly narrowed basally. Specimen from Eastern Divide or more northern Sierra Nevada (Fig. 403) .... N. spatulata sierrae new subspecies (p. 417)

28 (19') Elytral silhouette (Figs. 139, 145) markedly ovoid 29

28' Elytral silhouette subovoid to subrectangular 31

29 (28) Elytra clearly with faint to moderate metallic (violet) reflection; size moderate: standardized body length male

less than 11.5 mm, female less than 12.0 mm .....
..... N. paradisi Darlington (p. 354)

29' Elytra without metallic reflection; size very large: standardized body length male greater than 12.0 mm, female greater than 12.5 mm 30

30 (29') Antennal scape (Fig. 36) cylindrical, straight. Specimen from Olympic Range or Cascade Range north of Columbia River ..... N. vandykei vandykei Bänninger (p. 425)

30' Antennal scape (Fig. 37) narrowed basally, straight or slightly arcuate. Specimen from Cascade Range south of Columbia River .....
..... N. vandykei wyeast new subspecies (p. 426)

31 (28') Head (Fig. 21) large, broad; pronotum (Fig. 116) markedly cordate, broad; elytra with silhouette rectangular to subrectangular, broad, with marked metallic (violet, brassy, or green) reflection, intervals moderately to markedly convex ..... N. metallica Fischer v. Waldheim (p. 421)

31' Combination of character states not as above. If head slightly large and broad (for average proportions see Fig. 18), then pronotum moderately cordate; elytra with silhouette subovoid, without or with only faint metallic reflection, intervals flat to moderately convex 32

32 (31') Specimen from locality in Rocky Mountain Region: south of Peace River (British Columbia), east of Fraser Plateau and Okanagan Valley (British Columbia), east of Columbia Basin and Great Basin 33

32' Specimen from locality northwest or west of above area 42

33 (32) Elytra with marked metallic (violet, blue or green) reflection 34

33' Elytra without or with very faint metallic reflection 38

34 (33) Specimen from Colorado or New Mexico. Pronotum (Fig. 120A) narrow; elytral silhouette (Fig. 138) narrowed basally, lateral margins almost straight posterior to humeral angles ..... N. purpurata LeConte (p. 429)

34' Specimen from north or northeast of Colorado. Pronotum broad; elytral silhouette subrectangular, broad basally 35

35 (34') Size moderate: standardized body length male less than 10.5 mm, female less than 11.0 mm, pronotum (Figs. 107, 110A) moderately cordate, narrowed basally 36

35' Size very large: standardized body length male greater than 12.0 mm, female greater than 12.5 mm; pronotum (Figs. 119 - 120) slightly cordate, broad basally 37

36 (35) Specimen from Strawberry Range of Blue Mountains, eastern Oregon (Fig. 402). Elytra with green metallic reflection; apex median lobe of male as in Fig. 276 ; bursa copulatrix with anteroventral sclerite (Fig. 334) .... N. gebleri strawberriensis new subspecies (p. 413)

36' Specimen not from Strawberry Range. Elytra with violet (in few adults blue or green) metallic reflection; apex median

of male as in Fig. 275 ; bursa copulatrix without anteroventral sclerite (Fig. 333) .... N. gebleri gebleri Dejean [in part] (p. 408)

37 (35') Specimen from Alberta or British Columbia. Pronotum (Fig. 119) moderately convex, slightly narrowed basally; hind coxa (Fig. 226) with two to five basal and two to six apical setae ..... N. schwarzi schwarzi Van Dyke (p. 428)

37' Specimen from Wyoming. Pronotum (Fig. 120) slightly convex to slightly flattened, broad basally; hind coxa (Fig. 227) with four to six basal and usually one (rarely two or three) apical seta .... N. schwarzi beverlianna new subspecies (p. 428)

38 (33') Specimen from Tushar Mountains or Midget Crest, southwestern Utah (Fig. 410). Antennal scape (Fig. 41) arcuate, markedly narrowed basally; elytra with faint metallic violet or blue reflection; apex median lobe of male as in Fig. 285 ; bursa copulatrix with posterodorsal sclerite as in Fig. 336A ..... N. piute Erwin and Ball (p. 433)

38' Specimen not from Tushar Mountains or Midget Crest. Antennal scape (Figs. 38 - 40) slightly arcuate or straight, markedly to slightly narrowed basally; elytra with or without faint metallic reflection 39

39 (38') Pronotum (Fig. 122) with basal sinuation of lateral margin very deep; elytra with faint metallic violet reflection, microsculpture faintly to moderately impressed, meshes isodiametric or broken; apex median lobe of male as in Fig.

284 , apical orifice broad, markedly oblique; bursa copulatrix with posterodorsal sclerite as in Fig. 336 . Specimen from central or northwestern Colorado (Fig. 410) ..... N. coloradensis Van Dyke (p. 432)

39' Pronotum (Figs. 121, 121A) with basal sinuation of lateral margin moderately deep; elytra without (or in few adults with very faint) metallic reflection, microsculpture deeply impressed, meshes isodiametric; apex median lobe of male varied (Figs. 281 - 283), but if specimen from central or northern Colorado, then apical orifice narrow, only slightly oblique 40

40 (39') Specimen from Henry Mountains, southeastern Utah (Fig. 411). Hindwing (Fig. 196) reduced in width and length, truncate distal to stigma; apex median lobe of male as in Fig. 283 ; bursa copulatrix with posterodorsal sclerite as in Fig. 339 ..... N. trifaria utahensis new subspecies (p. 432)

40' Specimen not from Henry Mountains. Hindwing width and length varied 41

41 (40') Specimen from southwestern Colorado, New Mexico, or southeastern Utah (Fig. 411). Antennal scape straight; each epilobe of mentum (Fig. 78) with apical tooth moderately long; elytra with or without very faint metallic violet reflection, intervals moderately convex; apex median lobe of male (Fig. 282) elongate, arcuate; bursa copulatrix as in Fig. 338. ..... N. trifaria catenata Casey (p. 431)

41' Specimen not from above area (Fig. 411). Antennal scape

slightly to moderately arcuate; each epilobe of mentum (Fig. 77) with apical tooth minute; elytra without metallic reflection, intervals flat to slightly convex; apex median lobe of male (Fig. 281) short, bent but not arcuate; bursa copulatrix varied (Figs. 337a-337d) .... N. trifaria trifaria LeConte (p. 430)

42 (32') Elytra (Fig. 144) flat to slightly convex, broad basally, humeral angles smoothly, roundly rectangular, humeral carinae absent; pronotum (Fig. 118) with basal sinuation of lateral margin shallow ..... N. piperi Van Dyke (p. 427)

42' Elytra moderately convex, moderately broad basally, humeral angles faintly to moderately obtuse, humeral carinae present, slightly to markedly developed; pronotum (Figs. 108, 113) with basal sinuation of lateral margin moderately to very deep 43

43 (42') Fifth elytral interval with three to six setae, markedly catenate, striae deeply impressed 44

43' Fifth elytral interval without setae (rarely with one to three setae), not (in few specimens moderately) catenate, striae moderately impressed 45

44 (43) Specimen from Olympic Peninsula, Washington, or Vancouver Island, British Columbia, (Fig. 406). Pronotum (Fig. 115) markedly cordate, basal sinuation of lateral margin very short and deep; elytron with basal margination slightly short, intervals markedly convex .... N. meanyi sylvatica new subspecies (p. 420)

44' Specimen from Cascade Range of Oregon, Washington, or southern British Columbia, or from Coast Ranges of mainland British Columbia or southeastern Alaska (Fig. 406). Pronotum (Fig. 113) moderately cordate, basal sinuation of lateral margin moderately long and deep; elytron with basal margination long, intervals moderately convex .... N. meanyi meanyi Van Dyke [in part] (p. 419)

45 (43') Specimen from Cascade Range of central Oregon to southern British Columbia (Fig. 402). Pronotum (Fig. 108) markedly cordate, basal sinuation of lateral margin very deep; elytral silhouette subovoid, slightly narrowed basally, basal margination [illegible] concave, humeral angles roundly obtuse, humeral carinae moderately to markedly developed .... N. gebleri cascadensis new subspecies (p. 410)

-45' Specimen from north or east of above area (Fig. 402). Pronotum (Fig. 107) moderately cordate, basal sinuation of lateral margin moderately deep; elytral silhouette subrectangular, moderately broad basally, basal margination straight to slightly concave, humeral angles faintly and roundly obtuse, humeral carinae absent or slightly developed ..... N. gebleri gebleri Dejean [in part] (p. 408)

46 (1') Hind coxa (Fig. 228) unisetose basally; third to fifth visible abdominal sterna (Fig. 257) each with single pair of posterior paramedial setae (in very few specimens bisetose unilaterally on one sternum); middle tibia (Fig. 237) dorsally flat to slightly convex throughout, brush of dorsal

setae slightly to moderately developed 47

46' Hind coxa (Fig. 229) bi- or plurisetose basally; third to fifth visible abdominal sterna (Fig. 258) each with two or more pairs of posterior paramedial setae (in very few specimens unisetose unilaterally on one sternum); middle tibia (Figs. 238 - 240) dorsally concave to deeply sulcate (at least near middle, in many specimens also toward apex), brush of dorsal setae moderately to markedly and densely developed 48

47 (46) Size very small: standardized body length male 8.2 mm or less, female 8.8 mm or less; pronotum (Fig. 102) with basal sinuation of lateral margin short, deep, lateral explanation narrow, basal angles rectangular; elytral microsculpture faintly impressed, meshes isodiametric to slightly transverse ..... N. appalachia Darlington (p. 396)

47' Size moderate: standardized body length male greater than 8.4 mm, female greater than 8.8 mm; pronotum (Fig. 103) with basal sinuation of lateral margin absent or shallow, lateral explanation very broad, basal angles obtuse; elytral microsculpture moderately impressed, meshes markedly transverse or in form of dense transverse lines without meshes ..... N. pallipes Say (p. 397)

48 (46') Pronotum (Figs. 105 - 106) with basal angles obtuse, basal sinuation of lateral margin shallow or absent 49

48' Pronotum with basal angles clearly rectangular or acute, basal sinuation of lateral margin shallow to deep 52

49 (48) Elytral silhouette (Fig. 142) ovoid; color body and appendages entirely pale yellow to orange-tan. Specimen from south-central Utah .... N. desolata Kavanaugh [in part] (p. 402)

49' Elytral silhouette subovoid to subrectangular; if subovoid, [illegible] body color and appendages darker (dark rufous to piceus) 50

50 (49') Elytral silhouette (Fig. 137) subovoid, lateral margins clearly rounded; tooth of mentum (Fig. 70) bifid, with notch flat medially; lateral explanation of pronotum (Fig. 105) narrow at middle, broadened apically and basally .... N. mannerheimii Fischer v. Waldheim (p. 400)

50' Elytral silhouette (Figs. 136 - 137) subrectangular, lateral margins faintly rounded or straight (even when elytra narrowed basally); tooth of mentum (Fig. 69) bifid with notch simply V-shaped; lateral explanation of pronotum (Figs. 100 - 101) broadened posteriorly only 51

51 (50') Mandible (Fig. 59) markedly explanate laterally, broad; pronotum (Fig. 101) slightly cordate, broad basally, widest anterior to middle, slightly shiny (microsculpture faintly to moderately impressed, meshes isodiametric), basal margin not or slightly sinuate laterally, lateral bead narrow, obliterated basally in most specimens, basal foveae broad, smooth to faintly rugulose ..... N. obliqua LeConte (p. 394)

51' Mandible (Fig. 58) moderately explanate laterally; pronotum (Figs. 100a,100b) moderately cordate, narrowed basally,

widest near middle, moderately dull (microsculpture moderately to deeply impressed, meshes isodiametric), basal margin markedly sinuate laterally, lateral bead wide, complete to base, basal foveae narrow, faintly punctulate ..... N. suturalis LeConte (p. 392)

52 (48') Elytral silhouette ovoid, markedly narrowed basally, humeral angles markedly rounded and obtuse 53

52' Elytral silhouette rectangular to subovoid, not or moderately narrowed basally, humeral angles not markedly rounded and obtuse 57

53 (52) Fifth and seventh elytral intervals with setiferous pores, slightly catenate (some individuals with setae absent unilaterally from fifth or seventh interval); body and appendages pale yellow. Specimen from sea coast locality, from northern California to central British Columbia (including Vancouver Island or Queen Charlotte Islands) .... N. diversa LeConte (p. 405)

53' Fifth and seventh elytral intervals without setiferous pores (if a single seta present on seventh interval, then specimen from Sierra Nevada, eastern California); body color dark to pale. Specimen from interior locality, California or Utah 54

54 (53') Specimen from Sierra Nevada, California (Fig. 390). Antennal scape (Fig. 29) slightly arcuate, cylindrical; each epilobe of mentum (Fig. 66) with apical tooth very long; pronotum (Fig. 94) with lateral margin slightly

arcuate, sinuate subapically, lateral explanation narrow, slightly broadened apically.... N. lyelli Van Dyke (p. 379)

54' Specimen from Utah. Antennal scape (Figs. 31 - 32) straight to arcuate, ovoid to narrowed basally and truncate apically; each epilobe of mentum (Fig. 71) with apical tooth moderately long; pronotum (Figs. 99, 106) with lateral margin moderately arcuate, not sinuate subapically, lateral explanation broad (or, if narrowed at middle, then broadened basally) 55

55 (54') Pronotum (Fig. 106) with basal sinuation of lateral margin short and shallow, lateral explanation narrow at middle, broadened basally, basal angles rectangular; elytra vaulted, moderately convex; body and appendages pale yellow to orange-tan ..... N. desolata [in part] (p. 402)

55' Pronotum (Fig. 99) with basal sinuation of lateral margin moderately long and deep, lateral explanation moderately and uniformly broad, basal angles rectangular to acute, projected posteriorly; elytra not vaulted, slightly flattened; body and appendages dark to pale 56

56 (55') Antennal scape (Fig. 32) medium length, straight, almost cylindrical, slightly narrowed basally; body and appendages dark (piceus to black). Specimen from Pine Valley Mountains (Fig. 394) .... N. zioni oasis new subspecies (p. 391)

56' Antennal scape (Figs. 31a, 31b) long to medium, slightly arcuate, moderately narrowed basally; body and appendages

dark to pale. Specimen not from above area (Fig. 394) ..... N. zioni zioni Van Dyke (p. 390)

57 (52') Humeral carinae (Fig. 157) markedly developed and projected anterolaterally 58

57' Humeral carinae (Figs. 158a, 158b) absent to moderately developed, not or slightly projected anterodorsally 59

58 (57) Specimen from Olympic Peninsula (Fig. 390). Elytra slightly shiny, microsculpture moderately impressed, meshes isodiametric (broken) or slightly transverse; pronotum (Fig. 96) moderately cordate, basal sinuation of lateral margin moderately short and deep; apex median lobe of male as in Fig. 266 ; bursa copulatrix (Fig. 329) without anterodorsal sclerite ..... N. acuta quileute new subspecies (p. 380)

58' Specimen from northern Sierra Nevada, Cascade Range from northern California to southern British Columbia, or from Coast Ranges of mainland from southern British Columbia to southeastern Alaska (Fig. 390). Elytra moderately dull, microsculpture moderately impressed, meshes isodiametric (unbroken); pronotum (Fig. 95) slightly cordate, basal sinuation of lateral margin moderately long and shallow; apex median lobe of male as in Fig. 265 ; bursa copulatrix (Fig. 328) with anterodorsal sclerite .... N. acuta acuta Lindroth (p. 379)

59 (57') Pronotum (Figs. 104 - 106) with lateral explanation narrow at middle, broadened posteriorly 60

59' Pronotum (Figs. 97 - 98) with lateral explanation broad

throughout 62

60 (59) Legs dark brown to piceus, body black; microsculpture on pronotum and elytra very deeply impressed, meshes isodiametric, alveolae convex. Specimen from California (Fig. 399) ..... N. darlingtoni new species (p. 399)

60' Legs pale yellow, body dark (piceus) to pale (orange-tan); microsculpture on pronotum and elytra moderately impressed, meshes isodiametric, alveolae flat 61

61 (60') Specimen from Arizona (Fig. 400). Hindwing (Fig. 195) short, narrow; apex of fourth tarsomere of hind tarsus with ventrolateral lobe long; apex median lobe of male as in Fig. 273 ..... N. navajo new species (p. 402)

61' Specimen from Pacific Coast states, southern California to northern Washington, or inland from westcentral Idaho or extreme western Nevada (Fig. 400). Hindwing full-sized; apex of fourth tarsomere of hind tarsus with ventrolateral lobe short, only slightly developed; apex median lobe of male as in Fig. 274 ..... N. eschscholtzii Ménétriés (p. 403)

62 (59') Elytral silhouette (Figs. 141 - 142) subovoid AND specimen from Aleutian Islands, Alaska, or Queen Charlotte Islands, British Columbia (Fig. 393); head (Figs. 15 - 16) relatively large and broad 63

62' Elytral silhouette rectangular, subrectangular or subovoid (if subovoid, then specimen from the central or southern Rocky Mountain regions); head size and width average (see Fig. 18) 64

63 (62) Specimen from Aleutian Islands (Fig. 393). Eyes (Fig. 15) protruding, very convex; each epilobe of mentum (Fig. 67) with apical tooth moderately long; prosternal intercoxal process (Fig. 129) sublanceolate, unmargined at apex; elytra (Fig. 141) elongate, narrow, with faint metallic green reflection, humeral carinae slightly to moderately developed, slightly projected anterodorsally ..... N. gregaria Fischer v. Waldheim (p. 385)

63' Specimen from Queen Charlotte Islands (Fig. 393). Convexity of eyes average (see Fig. 16); each epilobe of mentum (Fig. 68) with apical tooth minute; prosternal intercoxal process (Fig. 128) lanceolate, completely margined; elytra (Fig. 142) slightly shortened, moderately broad, without metallic reflection, humeral carinae absent ..... N. charlottae Lindroth (p. 386)

64 (62') Specimen from northern California or extreme southern Oregon 65

64' Specimen from north or east of above area 66

65 (64) Specimen from Klamath Mountain System of the Coast Ranges, northwestern California or southwestern Oregon (Fig. 391). Pronotum (Fig. 98) large, broad, basal sinuation of lateral margin moderate in depth and length, basal angles rectangular, minutely denticulate; proepisternum smooth; elytra moderate in length and basal width, without metallic reflection ..... N. sahlbergii triad new subspecies (p. 384)

65' Specimen from Warner Mountains, northeastern California or southcentral Oregon (Fig. 391). Pronotum (Fig. 97) size moderate, basal sinuation of lateral margin deep and long, basal angles rectangular, not denticulate; proepisternum faintly punctulate anteriorly; elytra slightly short and narrowed basally, in most specimens with very faint metallic green or violet reflection ..... N. sahlbergii modoc new subspecies (p. 383)

66 (64') Hindwing with full reflexed tip (Fig. 182) or truncate (Fig. 193) distal to stigma; if truncate, then wing not also narrowed; elytral silhouette rectangular to subovoid 67

66' Hindwing reduced in length and width (Figs. 188, 194); if truncate, then wing also narrowed (Fig. 194); elytral silhouette subrectangular to subovoid 70

67 (66) Specimen from La Sal Mountains, Utah (Fig. 392). Elytral silhouette subrectangular; hindwing full-sized; apex median lobe of male as in Fig. 269; bursa copulatrix with posterodorsal sclerite as in Fig. 332 ..... N. arkansana oowah new subspecies (p. 388)

67' Specimen not from above area. Hindwing full-sized or truncate distal to stigma 68

68 (67') Specimen from locality in eastern Southern Rocky Mountain Region (Fig. 392): northern New Mexico to southern Wyoming (Medicine Bow and Sierra Madre Ranges) or west in San Juan Mountains of Colorado or Abajo Mountains of southeastern Utah. Elytral silhouette subrectangular to subovoid,

basally narrowed; hindwing truncate distal to stigma or, if reflexed tip present, entire wing slightly miniature .... N. arkansana arkansana Casey (p. 386)

68' Specimen from locality northwest (Fig. 392) of above area. Elytral silhouette rectangular to subrectangular, broad basally; hindwing full-sized or truncate distal to stigma (if truncate, specimen from Aleutian Islands, Alaska) 69

69 (68') Median lobe of male (Fig. 268) broad, with apex short and narrow; bursa copulatrix with posterodorsal sclerite as in Fig. 331 ; elytra slightly to moderately dull, microsculpture with meshes isodiametric to slightly transverse, basal margination (Fig. 147) straight to slightly concave, merged smoothly with lateral margination, humeral carinae absent or very slightly developed .... N. arkansana edwardsi new subspecies (p. 387)

69' Median lobe of male (Fig. 267) narrow, with apex moderately long and broad, deflected ventrally; bursa copulatrix with posterodorsal sclerite as in Fig. 329A ; elytra slightly dull to shiny, microsculpture with meshes slightly to markedly transverse or in form of fine transverse lines without meshes, basal margination (Figs. 158a,158b) slightly to moderately concave, merged with lateral margin at obtuse angle, humeral carinae slightly to moderately developed .... N. sahlbergii sahlbergii Fischer v. Waldheim (p. 381)

70 (66') Specimen from Uinta Mountains or Wasatch Mountains at or

north of Weber River, Utah (Fig. 392). Median lobe of male as in Fig. 270 .... N. arkansana uinta new subspecies (p. 389)

70' Specimen from north or south of above area (Fig. 394). Median lobe of male as in Fig. 271 71

71 (70') Specimen from Wasatch Mountains south of Weber River, Utah (Fig. 394). Elytra dull (microsculpture deeply impressed, meshes isodiametric), without metallic reflection .... N. fragilis fragilis Casey (p. 389)

71' Specimen from westcentral Wyoming (Fig. 39[illegible]. Elytra slightly shiny (microsculpture faintly impressed, meshes irregular isodiametric to slightly transverse), with or without very faint metallic green or violet reflection .... N. fragilis teewinot new subspecies (p. 390)

3.43 Species groups, species, and subspecies

Because of time constraints on completion of this dissertation, I have greatly reduced the coverage and completeness of this section. Material included is intended as a sample of what will appear in the manuscript for publication. Nomenclatural treatment presented (including type designation, synonymies, and bibliographies on each species-group taxon) is complete, covering all Nearctic taxa. Informal synonymies and diagnoses are provided for each of the lineages and species groups represented in the Nearctic fauna. A complete descriptive treatment is provided only for the virescens lineage--this as an example of format and coverage intended for all taxa. All crucial descriptive data can be retrieved, however, from Fig. 372 used in concert with Table 15.

3.431 Introduced species

Apparently only one Nebria species has been introduced into North America--namely, Nebria brevicollis (Fabricius), type species of genus Nebria, native to western Europe, where its members abound in woodlands as well as in parks, gardens, and other synanthropic habitats. Two adults of this species have been collected in North America; but these records are widely separated in space (see Fig. 380) and time (see Appendix B, and Lindroth, 1961a). These adults undoubtedly represented two separate introductions, neither of which has apparently resulted in permanent colonization by this species. For completeness of coverage of the literature on Nebria in the Nearctic region, I offer the following brief nomenclatural treatment.

Nebria brevicollis (Fabricius)

(Figures 60, 125, 133-134, 213, 215, 233-235, 247, 263, 294, 353, 380)

Carabus brevicollis Fabricius, 1792:150. LECTOTYPE (designated by Lindroth, 1961a:78), a male, in ZMKD, labelled: "Lectotypus brevicollis F. design. Lth. 1961." [red label]. TYPE LOCALITY. --Germany.

Nebria brevicollis (Fabricius).--Larochelle, 1975:94.--Lindroth, 1954d:38; 1955a:42; 1961a:78 1963a:12.

Notes on nomenclature and types.--Because N. brevicollis is not a per[illegible]member of the Nearctic fauna, I have listed above only thc[illegible]es which deal with its Nearctic occurrence. Numerous syno[illegible]of see Csiki, 1927:385; Larochelle, 1975:94) and over 100

literature references to N. brevicollis in the Palaearctic Region have been omitted.

3.432 The virescens lineage

This lineage is represented by only three extant species, two of which (N. chalceola Bates and N. pusilla Ueno) are restricted to Japan (Fig. 412). The third species is endemic to western North America. Included in this lineage are taxa previously assigned to Lindroth's (1961a) "virescens" group and genus Nippononebria Ueno (Habu, 1958).

Diagnostic combination.--Adult members of this lineage can be recognized by the following combination of character states: frontal red spot(s) absent; paraglossae distinct, but minute and dentiform; pronotum semiovoid (except slightly cordate in N. pusilla adults), midlateral pronotal setae present; hind coxa with one seta at base; ventroapical margin of fourth hind tarsomere truncate, not projected; second through fifth visible abdominal sterna without anterior paralateral setae; male genitalia: median lobe with basal bulb rounded, globose, partially closed basally, midshaft axis bent 135° or more, apex (ventral aspect) broad, shovel-shaped; dorsobasal piece distinct, in form of an expanded crest in dorsal midline (Fig. 262); female genitalia: basal apodeme of eighth sternum very deeply emarginate, lateral arm reduced to faint lobe or absent; proctiger transverse or hemispheric, membranous apically, heavily sclerotized

basally only; medial area of valvifer moderately sclerotized; coxite with setae of ventral diagonal row spiniform; stylus with setae of mediodorsal row medium length and spiniform (except long in N. virescens females), mediodorsal row diagonal; bursa copulatrix without sclerite in dorsal wall of spermathecal chamber.

Sexual dimorphism.--As described for genus.

Geographical distribution.--The geographical range of this lineage is markedly disjunct--one species restricted to western North America, and two species restricted to Japan.

Geographical relations with allied taxa.--The geographical range of this lineage is broadly sympatric with the respective ranges of each of the other lineages represented in the Nearctic regions, and also with ranges of endemic Palaearctic lines.

Habitat distribution.--Collectively, members of this lineage occupy broad macro- and microhabitat ranges. However, the Palaearctic species are apparently more narrowly restricted than the Nearctic N. virescens (see description below). N. chalceola members live in moist forest habitats (e.g. in leaf litter or loose soil, under moss mats, etc.) (Habu, 1958) at relatively low altitudes. N. pusilla members are restricted to high montane areas (2000 m level or above) (Habu, 1958), where they are found under stones.

Ecophenotypic variation.--See discussion for N. virescens below.

Taxonomic notes.--It could be effectively argued at present that members of this lineage represent such a distinctive monophyletic unit that it should be recognized as a separate genus--as Habu (1958) has already suggested for the Palaearctic species alone (i.e. genus

Nippononebria). At present, however, pending a more complete review of Nebria and related genera on a worldwide basis, I prefer to emphasize relationships both among lineage members and between this lineage and the rest of genus Nebria by including all in a single genus.

Phylogenetic relationships.--If my cladistic analysis of relationships is correct, the virescens lineage represents the sister group of all other extant Nebria (in the broadest sense). However, members of this lineage share a discomforting number of characteristics with members of other nebriine genera, especially Leistus. Although shared character states may be symplesiotypic, alternate interpretations are possible. I plan to investigate these alternatives in a future paper on the Nebriini and related groups.

Dispersal potential.--N. chalceola and N. virescens adults have full-size hindwings and are probably capable of flight. N. pusilla members have highly reduced hindwings. Instances of flight and its significance for dispersal are at present unknown.

Natural history.--N. virescens life history is reviewed below. See Habu (1958) for data relating to life history of Palaearctic taxa.

Fossil record.--There is at present no fossil record for this lineage or any of its members.

3.4321 The virescens group

This group is represented by three extant species, named and discussed above. A single Nearctic species, N. virescens Horn, is described below.

3.43211 Nebria virescens Horn

(Figures 44-45, 54, 57, 61, 84, 155, 162, 182, 214, 225, 240, 249, 262, 290-291, 300, 305, 308, 315, 324, 345, 354, 381)

Nebria virescens Horn, 1870:100. HOLOTYPE, a female, in MCZ, labelled: "Van."/ "Type 652" [red label]/ "N. virescens Horn"/ "Holotype Nebria virescens Horn det. D. H. Kavanaugh 1976" [red label]. TYPE LOCALITY.--Vancouver, British Columbia.--Bänninger, 1925:261; 1949:153.--Beaulne, 1914:29.--Blackwelder and Blackwelder, 1948:2.--Casey, 1913:47; 1924:21.--Csiki, 1927:368.--Hatch, 1939a:120; 1953:56.--Henshaw, 1885:4.--LeConte, 1878:476.--Leng, 1920:47.--Lindroth, 1961a:75; 1975:112.--Pratt and Hatch, 1938:192.--Schaupp, 1878:45.--Van Dyke, 1926:9.

Nebria virescens Chaudoir [an improper assignment of authorship].--Taylor, 1886:35.

Nebria brevis Casey, 1913:55. LECTOTYPE (designated by Lindroth, 1975:112), a male, in USNM, labelled: "Corvallis, Oreg."/ "185"/ "Casey bequest 1925"/ "Lectotype brevis Csy. By C. H. Lindroth." TYPE LOCALITY.--Corvallis, Benton County, Oregon.--Bänninger, 1925:261.--Blackwelder and Blackwelder, 1948:2.--Casey, 1924:21.--Csiki, 1927:368.--Hatch, 1939a:120; 1953:56.--Leng, 1920:47.--Lindroth, 1961a:76; 1975:112.

Diagnostic combination.--Adults of this species can be distinguished from those of all other Nearctic taxa by the combination of character states given for recognition of virescens

lineage members. They can be distinguished from adults of other (i.e. Palaearctic) virescens group members by the following combination of character states: pronotal microsculpture isodiametric, moderately to deeply impressed; elytral microsculpture isodiametric, deeply impressed; penultimate labial palpomere bisetose; M3 setae of mentum present; length of metasternum greater than length of mesocoxal cavity; anterior metasternal process not margined medially; plane of lateral wing posterior to coxal ridge of hind coxa not completely vertical; males with two pairs of paramedial setae on sixth visible sternum; male genitalia: median lobe with mid-shaft (lateral aspect) thick; left paramere long and broad; female genitalia: eighth abdominal sternum apical margin with many long and medium length setae medially, basal apodeme deeply emarginate, lateral arm reduced to short lobe; paraprocts broadly fused with valvifers basally.

Description of form and structure.--Size small to medium, standardized body length males 7.5 to 10.1 mm, females 9.8 to 11.2 mm. Pronotum relatively large and wide, elytra moderately long and wide.

Color. Body uniformly brown or piceus, legs and head appendages slightly paler.

Reflection. Head, pronotum, and elytra moderately to markedly metallic blue or green; prothoracic venter faintly metallic in most members.

Luster. Head moderately dull or slightly shiny; pronotum and elytra dull.

Microsculpture. Dorsum with isodiametric meshes, faintly to moderately impressed on head, deeply impressed on pronotum and elytra.

Head. Frons smooth, frontal furrows linear shallow, broad; eyes moderately convex; antennae with basal four antennomeres without pubescence (except at apex of fourth antennomere in very few individuals), scape medium length, narrowed basally; anterior margin clypeus weakly, evenly concave; anterior margin labrum truncate or slightly bisinuate; penultimate labial palpomere bisetose; M3 setae present at basolateral angles of mentum; submentum with three pairs of lateral and one pair of medial setae across anterior margin.

Prothorax. Pronotum, shape semiovoid, convex; lateral margin markedly arcuate, basal sinuation absent or short and very shallow; lateral explanation broad throughout, slightly widened anteriorly; basal margin long, truncate (straight); apical angles medium length, broad, rounded; basal angles obtuse; anterior margination moderately impressed; lateral bead wide, shallowly impressed, obliterated basally; anterior transverse impression broad, shallow, smooth or faintly rugulose; median longitudinal impression moderately impressed; posterior transverse impression moderately deep, anteriorly deflected at middle; basal foveae broad with or without double etched lines separated by low convexity, carinate or not laterally; prosternum and proepisternum smooth, impunctate; prosternal intercoxal process margined basally only.

Pterothorax. Elytra slightly convex, with silhouette subrectangular; basal margination medium to long, straight to

moderately concave anteriorly; humeri moderately to markedly angulate; humeral carina absent or present as small denticle; subhumeral lateral sinuation shallow; subapical lateral sinuation shallow; apices narrowly rounded, medially straight, apposed in midline; medial striae shallowly or moderately impressed, lateral striae very faintly impressed, densely but minutely punctulate or weakly punctate; intervals flat or very slightly convex; hindwing full-sized; length of metasternum greater than length of mesocoxal cavity; anterior metasternal process not margined medially.

Legs. Plane of lateral wing posterior to coxal ridge of hind coxa not completely vertical; middle tibia deeply sulcate dorsally from base to near apex.

Abdomen. Males with two pairs of paramedial setae on sixth visible sternum; first visible sternum smooth, impunctate.

Male genitalia. Median lobe with mid-shaft (lateral aspect) thick; preapical-shaft (lateral aspect) moderately broad, moderately tapered apically, symmetrical (apical orifice directed dorsally) (apical and dorsal aspects); apex symmetrical, shovel-shaped, without marginal tooth (ventral aspect), short and sharply pointed (lateral aspect); parameres approximately symmetrical, equal in length (i.e. left paramere relatively long and broad, right paramere relatively short and broad).

Female genitalia. Eighth abdominal sternum apical margin with many long and medium length setae medially, basal apodeme width medium, deeply emarginate, lateral arm reduced to short lobe; proctiger hemispheric, membranous apically; paraprocts broadly fused

with valvifers basally; stylus broad, moderately arcuate, spatulate apically (ventral aspect), very broad, broadly rounded apically, straight (lateral aspect); setae in ventral diagonal row on coxite long and spiniform; setae in mediodorsal row on stylus long and spiniform, mediodorsal row diagonal; coxostylus densely setose at middle of medial surface only; bursa copulatrix with main axis slightly deflected do[illegible]y, spermathecal chamber long, thick, with parallel sides (late[illegible]spect).

Sexual dimorphism.--As described for genus.

Geographical distribution.--Fig. 381 ; restricted to Pacific Coast region from southwestern British Columbia to California; south in California only at high altitude in the Sierra Nevada; range extends east across Columbia Plateau to western edge of Rocky Mountain region in westcentral Idaho (see Appendix B for list of localities).

Geographical variation.--Adults in populations in northeastern California (e.g. Modoc County) are, in general, larger and more vividly metallic blue (almost deep purple) than adults from most other areas. See also comments under ecophenotypic variation.

Geographical relations with allied taxa.--Although the geographical range of N. virescens is broadly sympatric with several other Nearctic Nebria taxa (see Table 5), closely related taxa are restricted to Japan, and their ranges are therefore al[illegible]tric.

Habitat distribution.--Macrohabitat range of this species is very broad--from Transition to Arct[illegible]c/Alpine Zone. Members appear to be most abundant in Canadian Zone habitats however. Relationships,

if any, between individuals living in widely different life zones are at present unclear (see below). Microhabitat range of N. virescens is also impressively great. Adults have been collected in moist meadows, forest litter, stream banks, cracks on weathered sea cliffs, talus slopes, and at the edges of snowfields. In general, members of this species do not appear to require association with water bodies; but they do require cool, humid microhabitats.

Ecophenotypic variation.--Adults collected in high-altitude localities are, in every instance, smaller than average. For example, the specimen from Bunker Hill Lookout (Okanogan County, Washington), collected at 2120 m is the smallest known specimen; and the specimen I collected on Mount Baker (Washington) at 1500 m is almost as small. These specimens also differ in having relatively narrowed and shortened elytra (although hindwings in these specimens are full-sized), narrowed pronota in which a basal sinuation of the lateral margin is better developed than in most adults, and a better developed denticle at each humeral angle. Because so few specimens have been collected from high altitude localities (a total of only five, from localities in Washington and the Sierra Nevada of California), I am yet unable to evaluate the status of these specimens. I have found no differences among characters of male or female genitalia by which to distinguish the high and lower altitude forms. Further collecting and study of additional specimens is needed.

Taxonomic notes.--Future review of the worldwide Nebria fauna may indicate that recognition of N. virescens as representing a

distinct group is justified. This taxon is strongly differentiated from its sister group, demonstrating 41 apotypic character states not shared with N. chalceola and N. pusilla (and the latter share 25 apotypic states not also shared with N. virescens). At present, however, I place these three taxa in a single group to emphasize relationships not recognized before.

Phylogenetic relationships--According to my cladistic analysis, this species represents the sister group of N. chalceola and N. pusilla.

Dispersal potential.--N. virescens adults have large, strong, very heavily sclerotized wings; and I have no doubt that they can fly. Whether or not flight is important for dispersal among these beetles is unknown.

Natural history.--Adults of this species have been collected in every month of the year except January (see Table 13). Teneral adults appear in spring (April through June). Adults kept under laboratory conditions for over six months deposited eggs in November and December, a period which, I suggest, corresponds well to the normal oviposition period in the field. Larvae emerge in November through January and overwinter in some larval instar. Some unknown portion of the adult population must also overwinter.

Fossil record.--To date, no specimens referable to this species have been found as fossils.

3.433 The gyllenhali lineage

This lineage is represented by at lea c 15, and perhaps 19 or more, extant species. Five of these species are endemic to North America, three are common to Eurasia and North America, and the remainder are restricted to northern, central, and/or eastern Asia. My uncertainty about total number of included species stems from an insufficient knowledge of the Palaearctic fauna with which to evaluate the status of one or more taxa (see further comments in sections on included species groups). Included in this lineage are taxa previously assigned to Lindroth's (1961a) "pallipes" (in part), "gyllenhali," "hudsonica," and "ovipennis" (in part) groups, or to subgenus Boreonebria Jeannel (1937). Shilenkov's (1975a) concept of subgenus Boreonebria corresponds almost exactly to this lineage as here conceived.

Diagnostic combination.--Adult members of this lineage can be recognized by the following combination of character states: frontal red spot(s) absent (except in all N. paradisi members and in few members of other paradisi group taxa); paraglossae indistinct, completely fused with ligula; pronotum moderately to markedly cordate, midlateral pronotal setae present; hind coxa with one pair of setae at base (except two or more in some N. paradisi and N. gouleti memb s); ventroapical margin of fourth hind tarsomere projected, lobat laterally; second through fifth visible abdominal sterna without anterior paralateral setae; male genitalia: median lobe with basal bulb quadrate, broadly open basally, mid-shaft axis bent less than 135°, apex (ventral aspect) pointed; dorsobasal piece present as

thin collar on basal bulb; female genitalia: basal apodeme of eighth sternum deeply emarginate, lateral arm slightly to moderately shortened; proctiger hemispheric, heavily sclerotized throughout; medial area of valvifer weakly sclerotized or membranous; coxite with setae of ventral diagonal row setiform; stylus with setae of mediodorsal row setiform, mediodorsal row longitudinal; bursa copulatrix without sclerite in dorsal wall of spermathecal chamber.

3.4331 The *paradisi* group

This group is represented by at least three, and perhaps five, extant species, only one of which is a member of (and endemic to) the Nearctic fauna (Fig. 413). The remaining taxa are restricted to Hokkaido (Japan) or the Kuril Islands. Taxonomic status of each of the Palaearctic members of this group (namely, *N. sakagutii* Nakane, *N. shibanaii* Ueno, *N. shiretokoana* Nakane, and *N. gibbulosa* Motschulsky) is yet uncertain; but in section 4.1 on phylogeny, I treat each as a distinct species for comparative purposes. Lindroth (1961a) included *N. paradisi* in his "*ovipennis*" group. Erwin and Ball (1972) recognized the monophyly of that group exclusive of *N. paradisi* and, therefore, removed the latter (but left it unplaced). Shilenkov (1975a) considered only *N. gibbulosa*, and assigned it to subgenus *Boreonebria*.

Diagnostic combination.--Adult members of this group can be recognized by the following combination of character states: relative width pronotum medium or slightly broad; relative width elytra medium; mandibles moderately explanate basolaterally; mentum

with M2 setae moderately distant from basal margin; pronotum with apical angles moderately or very long, basal foveae slightly or moderately divergent basally; elytral silhouette ovoid, humeri markedly or extremely rounded, humeral carinae distinct, sharp, slightly to moderately projected, third, fifth, and seventh intervals uniform, uninterrupted (except faintly catenate in N. paradisi members); hindwing highly reduced, either very thin, elongate, strap-like or very short, scale-like; legs markedly long; male genitalia: median lobe with mid-shaft cylindrical, thickness approximately equal throughout, shape (in cross-section) circular, preapical-shaft (lateral aspect) moderately broad and tapered, apex (ventral aspect) broadly or bluntly pointed; female genitalia: spermathecal duct with distal portion narrow or moderately or extremely thickened, insertion of duct slightly right of midline (except in midline in N. paradisi females) on spermathecal chamber of bursa copulatrix.

3.43311 Nebria paradisi Darlington

(Figures 86, 145, 164, 252, 264, 303, 312, 340, 382)

Nebria columbiana; auctorum (not Casey).--Blackwelder and Blackwelder, 1948:2.--Hatch, 1939a:121; 1953:59.--Lindroth, 1961a:87.--Van Dyke, 1919:8 (in part); 1926:10 (in part).

Nebria kincaidi; auctorum (not Schwarz).--Bänninger, 1925:264; 1933:81; 1949:148.--Blackwelder, 1939:12.--Hatch, 1939a:121; 1953:59.--Lindroth, 1961a:87.--Ueno, 1955:47.

Nebria vandykei Darlington, 1930:104 [preoccupied by Nebria vandykei

Bänninger, 1928:5]. HOLOTYPE, a male, in MCZ, labelled: "Mt. Rainier, Was. VII 18, 27, Darlington"/ "Holotype ♂ Nebria vandykei Darlington" [red label]/ "P. J. Darlington Collection"/ "Nebria paradisi Darl.." Allotype also in MCZ. TYPE LOCALITY. --Parad. Valley (1830m), Mount Rainier National Park, Washington.--Bänninger, 1933:81.--Blackwelder, 1939:12.--Csiki, 1933:630.--Darlington, 1931a:24.--Döbler, 1975:146.--Hatch, 1939a:121; 1953:59.--Leng and Mutchler, 1933:11.--Lindroth, 1961a:87.--de Ruette, 1970:15.--Ueno, 1955:47.

Nebria paradisi Darlington, 1931a:24 [as a replacement name for N. vandykei Darlington].--Bänninger, 1933:81; 1949:148.--Blackwelder, 1939:12.--Blackwelder and Blackwelder, 1948:2.--Csiki, 1933:630.--Erwin and Ball, 1972:81.--Hatch, 1939a:121; 1953:59.--Leng and Mutchler, 1933:11.--Lindroth, 1961a:87.--Mann, 1978:12.--de Ruette, 1970:15.--Ueno, 1955:47.

3.4332 The hudsonica group

This group is represented by three extant species, all endemic to North America (Fig. 415). One is restricted to eastern and the other two to western North America. Taxa included in this group were assigned by Lindroth (1961a) to his "hudsonica" and "pallipes" (in part) groups.

Disgnostic combination.--Adult members of this group can be recognized by the following combination of character states: pronotum and elytra markedly broad in relation to their respective lengths; mandibles broadly explanate basolaterally; mentum with M2

setae near basal margin; pronotum with apical angles moderately long, basal foveae parallel; elytral silhouette rectangular, humeri rectangular, humeral carinae absent or very vague and linear, third, fifth, and seventh intervals uniform, uninterrupted; hindwing full-sized; legs medium length; male genitalia: median lobe with mid-shaft moderately narrowed apically, shape (in cross-section) slightly compressed, preapical-shaft (lateral aspect) narrow, margins almost parallel, apex (ventral aspect) narrowly pointed; female genitalia: spermathecal duct with distal portion narrow, insertion of duct in midline on spermathecal chamber of bursa copulatrix.

3.43321 Nebria gouleti Kavanaugh, NEW SPECIES

(Figures 24, 171, 219, 238, 286, 292, 293, 302, 383)

Nebria gouleti, new species. HOLOTYPE, a male, in CAS, labelled: "U.S., Wash., Asotin Co., Hwy. 129, 10 mi sw. Anatone, Rattlesnake Cr., 3000', 25 August 73 DHKavanaugh Family"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria gouleti Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12504." Allotype (same data as holotype) also in CAS. 514 paratypes (see Appendix B for locality data) are deposited in the following collections: AMNH, ANSP, BFCa, CAS, CUIC, DHKa, DJLa, LRus, MCZ, MSU, OSUO, PURC, RTBe, SJSC, UASM, UIMI, UMMZ, USNM, UWBM, WSU. TYPE LOCALITY.--Rattlesnake Creek (10 miles southwest of Anatone), Asotin County, Washington.

Derivation of taxon name.--I take great pleasure in naming this

species in honor of my good friend and frequent field companion, Henri Goulet, from whom I have learned to observe and appreciate carabid beetles while they are alive!

3.43322 Nebria hudsonica LeConte

(Figures 10,25,49,51,62,65,169,170,199,255,256,325,346,384)

Nebria hudsonica LeConte, 1863b:3. LECTOTYPE (here designated), a male, in MCZ, labelled: "Saskatchewan"/ "Type 643" [red label]/ "N. hudsonica LeC."/ "Lectotype Nebria hudsonica LeConte designated by D. H. Kavanaugh 1976" [red label]. TYPE LOCALITY. --Saskatchewan, Hudson Bay Territory; here restricted to North Saskatchewan River (at Rocky Mountain House), Alberta.--Armin, 1963:91.--Bänninger, 1925:279; 1931:178.--Beaulne, 1914:30.--Blackwelder and Blackwelder, 1948:2.--Csiki, 1927:360.--Edwards, 1975:49.--Erwin and Ball, 1972:78.--Fall, 1926:130.--Fall and Cockerell, 1907:156 (cannot refer to this species, but otherwise uninterpretable).--Gemminger and Harold, 1868:50.--Hatch, 1933:7; 1939a:117; 1953:55.--Henshaw, 1881:206; 1885:4.--Horn, 1870:102.--LeConte, 1863a:2; 1878:476.--Leng, 1920:47.--Lindroth, 1961a:83.--Putnam, 1876a:191.--Schaupp, 1878:45.--Van Dyke, 1925:122; 1926:10.--Wickham, 1893:228.

Notes on nomenclature and types.--In 1863, the area now occupied by the Province of Saskatchewan was part of Hudson's Bay Territory (or the Northwest Territories); and at least up to that date, the name "Saskatchewan" was apparently applied only to the Saskatchewan River system. Therefore, LeConte's use of the term probably refers to the

river system rather than the province. Only the Alberta stretches of the system are within the continuous range of N. hudsonica, although I have seen two specimens from the Province of Saskatchewan. My selection of North Saskatchewan River at Rocky Mountain House as the restricted type locality reflects these facts.

3.43323 Nebria lacustris Casey

Nebria lacustris lacustris Casey

(Figures 12, 87, 165, 384)

Nebria pallipes; auctorum (not Say).--Casey, 1913:56.--LeConte, 1878:477 (as "race 2.").--Leonard, 1928:11 (in part).--Lindroth, 1961a:77.--Wickham, 1909:5.

Nebria lacustris Casey, 1913:56. LECTOTYPE (designated by Lindroth, 1975:112), a female, in USNM, labelled: "Bayfld, Wis, Wickham." / "Casey bequest 1925"/ "Type USNM 46865" [red label]/ "lacustris Csy."/ "Lectotype lacustris Csy. By C. H. Lindroth." TYPE LOCALITY.--Bayfield, Bayfield County, Wisconsin.--Bänninger, 1925:260;1949:147.--Bell, 1955:265 (in part).--Csiki, 1927:362.--Darlington, 1943:60.--Larochelle, 1975:94; 1977:112. --Leng, 1920:47.--Lindroth, 1961a:77; 1963a:76; 1969d:1109; 1975:112.--Spence, 1974:6.--Spence, Bell and Bell, 1976:81.--Spence and Bell, unpublished manuscript.

Nebria expansa Casey, 1913:56. LECTOTYPE (designated by Lindroth, 1975:112, and amended in an addendum to same paper p. 147), a female, in USNM, labelled: "L."/ "Casey bequest 1925"/ "expansa - 2 Paratype USNM 46864" [red label]/ "Lectotype expansa Csy.

By C. H. Lindroth." TYPE LOCALITY.--Indiana; here restricted to Turkey Run State Park, Parke County, Indiana.--Bell, 1955:265.--Csiki, 1927:357.--Larochelle, 1975:94.--Leng, 1920:47.--Lindroth, 1961a:77; 1969d:1109; 1975:112 and 147.--Spence, 1974:12.--Spence and Bell, unpublished manuscript.

Nebria sahlbergi; Leonard, 1928:211.

Nebria suturalis; Leonard (not LeConte), 1928:211.

Notes on nomenclature and types.--The name N. lacustris has priority over N. expansa by precedence of position as well as by action of the first reviser (Bell, 1955:265; see also Lindroth, 1961a:77).

In his original description, Casey recorded expansa from "Texas and Indiana," based on his study of two females. Bell (1955:267) and Lindroth (1961a:77 and 1975:112) accepted the record from Texas. In my judgment, this record is erroneous. Acting on my suggestion, Lindroth (1975:147) amended his lectotype designation (1975:112) and selected the specimen labelled "L.", interpreted by Casey as from Indiana, instead of the "Texas" specimen. The expansa form of N. lacustris lacustris has frequently been collected at Turkey Run State Park, my choice as the restricted type locality.

Nebria lacustris bellorum Kavanaugh, NEW SUBSPECIES

(Figures 88, 309, 384)

Nebria lacustris; Bell, 1955:265 (in part).

Nebria lacustris bellorum, new subspecies. HOLOTYPE, a male, in CAS, labelled: "U.S., Tenn., Great Smoky Mts. N. P., Chimneys Picnic

Area, W. Prong Little Pigeon R., 3000', 24May73 Kavanaugh & HGoulet"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria lacustris bellorum Kavanaugh det. D. H. Kavanaugh 1976: [red label]/ "California Academy of Sciences Type No. 12506." Allotype (same data as holotype) also in CAS. 262 paratypes (see Appendix B for locality data) are deposited in the following collections: CAS, CUIC, DHKa, HoKn, MCZ, RTBe, TCBa, UAFA, UASM, USNM. TYPE LOCALITY.--West Prong Little Pigeon River (at Chimneys Picnic Area), Great Smoky Mountains National Park, Tennessee.

Derivation of taxon name.--I take pleasure in naming this subspecies in honor of Ross and Joyce Bell (Burlington, Vermont), who have long been interested in the systematics of eastern Nebria taxa, and who have generously provided encouragement and information for this study.

3.4333 The gyllenhali group

This group is represented by at least nine, and perhaps 11 or more, extant species. Only one of these species is endemic to North America, three are common to North America and Eurasia, and the remainder are endemic to northern, central, and/or eastern Asia (Fig. 416). The latter include N. subdilatata Motschulsky, N. baicalica Motschulsky, N. uralensis Glasunow, N. biseriata Lutshnik, and N. daisetsuzana Ueno. According to Shilenkov (1975a), N. rubrofemorata Shilenkov and N. sajanica Bänninger (both restricted to central Asia) should also be considered members of this group; but I have not yet

studied specimens representing these species. Except for the addition of the endemic Palaearctic species and a change in status of one taxon, this group is identical (at the species level) to Lindroth's (1961a) "gyllenhali" group.

Diagnostic combination.--Adult members of this group can be recognized by the following combination of character states: relative pronotal width medium to slightly broad (except extremely wide in N. subdilatata members); relative elytral width medium to moderately broad; mandibles moderately explanate basolaterally; mentum with 2 setae near basal margin; pronotum with apical angles medium in length, basal foveae parallel; elytral silhouette varied, rectangular to ovoid, shape of humeri varied, from rectangular to moderately rounded, humeral carinae absent, vague, or distinct but not projected, third, fifth, and/or seventh interval(s) faintly to moderately catenate; hindwing full-sized or variously reduced; legs medium length, slightly short, or slightly long; male genitalia: median lobe with mid-shaft moderately narrowed apically, shape (in cross-section) slightly compressed, preapical-shaft (lateral aspect) narrow or very narrow, margins almost parallel, apex (ventral aspect) broadly or bluntly pointed; female genitalia: spermathecal duct with distal portion slightly to greatly thickened, insertion of duct slightly or markedly right of midline or slightly left of midline on spermathecal chamber of bursa copulatrix.

3.43331 The nivalis subgroup

3.433311 Nebria nivalis (Paykull)

Nebria nivalis nivalis (Paykull)

(Figures 46-47, 89, 320, 344, 385-386)

Carabus nivalis Paykull, 1790:52. LECTOTYPE (here designated), a male, in NRSS, labelled: "Mus. Payk."/"Riksmuseum Stockholm" [green label]/ "Lectotype Carabus nivalis Paykull designated by D. H. Kavanaugh 1976" [red label]. TYPE LOCALITY.--Lule Lappmark, Norrbotten Län, Sweden.--Paykull, 1798:119 (in part). --Schönherr, 1806:197.--Stephens, 1828:61.

Nebria nivalis (Paykull).--Andersen, 1970:89.--Bänninger, 1923:132; 1925:260; 1949:143.--Blair, 1950:220.--Csiki, 1927:364.--Gemminger and Harold, 1868:51.--Hågvar and Østbye, 1974:118.--Hamilton, 1889:93.--Henshaw, 1885:4.--Heyden, 1880-81:14.--Horn, 1870:104.--Horvatovitch, 1973:251.--Jeannel, 1937:4.--Larochelle, 1975:94 (in part); 1977:112 (in part).--Larsson and Gigja, 1959:15.--LeConte, 1863:2; 1878:476.--Leng, 1920:47.--Lindroth, 1939:54; 1961a:81 (in part); 1963a:28, 68 (in part); 1963b:125; 1969a:1109; 1974:30.--Matthews, 1977:302.--Motschulsky, 1846:125; 1850:72; 1865:275.--Poppius, 1905:17; 1910:302.--Sahlberg (J.), 1885:47.--Schaupp, 1878:46.--Shilenkov, 1974:50; 1975a:839; 1975b:61; 1976:117.--Van Dyke, 1940:256.

Nebria bifaria Mannerheim, 1853:120. LECTOTYPE (here designated), a male, in ZILR, labelled: "38"/ "Nebria carbonaria Esch. Insel.

Paul"/ "Lectotype ?" [red label]/ "Lectotype Nebria bifaria Mannerheim det. D. H. Kavanaugh 1977" [red label]. TYPE LOCALITY.--Saint Paul Island, Alaska.--Bänninger, 1923:132; 1925:260; 1949:144.--Beaulne, 1914:30.--Brown, 1937:107.--Casey, 1913:51.--Coope, 1970b:154.--Csiki, 1927:357.--Fall, 1926:130.--Gemminger and Harold, 1868:48.--Hamilton, 1889:93; 189[illegible].--Hatch, 1939a:119.--Henshaw, 1885:4.--Heyden, 1880-81:13.--Horn, 1870:102.--Jeannel, 1937:5.--Larochelle, 1975:94.--LeConte, 1860:10; 1863:2; 1878:476.--Leng, 1920:46.--Lindroth, 1954c:366; 1961a:81 (in part).--Motschulsky, 1865:275.--Poppius, 1910:303.--Schaupp, 1878:45.--Shilenkov, 1975a:839; 1976:120.--Van Dyke, 1921:158; 1924:4; 1940:256.--Wickham, 1923:5.

Nebria carbonaria; auctorum (not Eschscholtz).--Beaulne, 1914:30.--Csiki, 1927:357.--Gemminger and Harold, 1868:48.--Hamilton, 1889:93; 1894:7.--Henshaw, 1885:4.--Heyden, 1880-81:13.--Larochelle, 1975:94.--LeConte, 1860:10.--Lindroth, 1961a:81.--Mannerheim, 1852:293; 1853:120.--Motschulsky, 1850:72 (in part); 1859:224.--Van Dyke, 1921:158.

Nebria femoralis Motschulsky, 1859:224 [preoccupied by Nebria femoralis Chaudoir, 1843:749]. LECTOTYPE (designated by Shilenkov, 1975a:389), in ZILR, not seen. TYPE LOCALITY.--Yakutsk, Yakutskaya A.S.S.R., U.S.S.R..--Bänninger, 1923:132; 1925:260.--Csiki, 1927:357.--Gemminger and Harold, 1868:49.--Heyden, 1880-81:13.--Jeannel, 1937:4.--Lindroth, 1955a:40; 1961a:82.--Motschulsky, 1865:275.--Poppius, 1910:303.--Shilenkov, 1975a:839; 1976:120.

Nebria femorata Motschulsky, 1865:275 [as a replacement name for N. femoralis Motschulsky].--Bänninger, 1923:132; 1925:260; 1949:144.--Csiki, 1927:358.--Gemminger and Harold, 1868:49.--Heyden, 1880-81:13.--Jeannel, 1937:4.--Larochelle, 1975:94.--Lindroth, 1955a:40; 1961a:82.--Sahlberg (J.), 1885:47.--Shilenkov, 1975a:839; 1976:120.

Nebria molbis Motschulsky, 1865:274 [an incorrect original spelling]. LECTOTYPE (here designated), sex undetermined [specimen incomplete, badly damaged], in ZMUM, labelled: "A. borealis" [green label]/ "Nebria mollis Motsch. Am. arct. cont." [green label]/ [red rectangle]. TYPE LOCALITY.--Alaska.--Csiki, 1927:389.--Lindroth, 1961a:82.

Nebria mollis Motschulsky [a justified emendation].--Csiki, 1927:389.--Gemminger and Harold, 1868:51.--Henshaw, 1885:4.--Horn, 1870:104.--Larochelle, 1975:94.--LeConte, 1878:473.--Leng, 1920:47.--Lindroth, 1961a:82.--Schaupp, 1978:46.--Shilenkov, 1976:120.

Nebria nivalis bifaria Mannerheim.--Lindroth, 1955a:39 (in part).

Notes on nomenclature and types.-- The specimen chosen as lectotype of Carabus nivalis is one of three specimens in NRSS from the Paykull Collection identified as nivalis. The other two specimens are actually individuals of N. gyllenhali gyllenhali (Schönherr). Because all three specimens bear identical labels and have been considered syntypes, the two gyllenhali gyllenhali specimens could perhaps be considered paralectotypes. Paykull (1798:119) subsequently described "variety β" of Carabus nivalis, which is clearly

synonymous with N. gyllenhali gyllenhali and was based on specimens from a different collector and locality. The original description of nivalis does not fit the two hetero-specific specimens, but the description of "variety β" does. I conclude that these specimens are probably not part of Paykull's original type series of nivalis; but they may be specimens now described as "variety β."

I have seen no published statement by Motschulsky indicating that his Nebria "molbis" was a misspelling. However, the type specimen is labelled "mollis"; and from as early as 1868, every subsequent citation of the name has been as "mollis." This suggests early recognition, possibly initiated (privately) by Motschulsky himself, of an original error. The first clear indication of an intended emendation is that of Csiki (1927:389).

Nebria nivalis gaspesiana Kavanaugh, NEW SUBSPECIES

(Figures 90, 251, 385-386)

Nebria suturalis; Leng (not LeConte).--Leng, 1920:47 (in part).--Lindroth, 1955a:39.

Nebria nivalis bifaria Mannerheim.--Lindroth, 1955a:39 (in part).

Nebria nivalis; auctorum.--Larochelle, 1972:62 (in part); 1976:48; 1977:12 (in part).--Lindroth, 1961a:81 (in part); 1971:1459.

Nebria bifaria; Lindroth, 1961:81 (in part).

Nebria nivalis gaspesiana, new subspecies. HOLOTYPE, a male, in CAS, labelled: "Can., Que., Peninsule de Gaspe, Mt. Albert, Ruisseau du Diable, 3200'-3500', 11-12 June 73 DHKavanaugh & HGoulet"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria

nivalis gaspesiana Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12510." Allotype (same data as holotype) also in CAS. 287 paratypes (see Appendix B for locality data) are deposited in the following collections: ALar, CAS, CNC, DBUM, DHKa, MCZ, RTBe; UASM, USNM. TYPE LOCALITY.--Ruisseau du Diable (980m-1070m), Mont Albert, Parc de La Gaspésie, Comté de Gaspé-Ouest, Québec.

Derivation of taxon name.--This subspecies is named for the Gaspé Peninsula, on which the type locality is found.

3.43332 The gyllenhali subgroup

3.433321 Nebria crassicornis Van Dyke

Nebria crassicornis crassicornis Van Dyke

(Figures 13, 92, 217, 326, 387)

Nebria crassicornis Van Dyke, 1925:121. HOLOTYPE, a male, in CAS, labelled: "Paradise Park Alt. 6000 ft."/ "Mt. Rainier Wash. VII, 14-31, 05"/ "Coll. by Van Dyke"/ "Van Dyke Collection"/ "Type Nebria crassicornis Van Dyke" [red-tipped label]/ "California Academy of Sciences Type No. 1627." Allotype (same data as holotype) also in CAS (California Academy of Sciences Type No. 1628). TYPE LOCALITY.--Paradise Park, Mount Rainier National Park. Washington.--Bänninger, 1928:6; 1931:178.--Blackwelder, 1939:12.--Blackwelder and Blackwelder, 1948:2.--Csiki, 1927:388; 1933:631.--Hatch, 1939a:119; 1953:56.--Leng and Mutchler, 1933:10.--Lindroth, 1961a:80.--Mann, 1978:20.--Van Dyke, 1926:10.

Nebria crassicornis intermedia Van Dyke, NEW STATUS

(Figures 14, 93, 352, 387)

Nebria labradorica; auctorum (not Casey).--Bänninger, 1928:6 (in part); 1931:178 (in part).--Hatch, 1939a:119 (in part); 1953:56.--Van Dyke, 1925:122 (in part); 1926:10 (in part).

Nebria intermedia Van Dyke, 1949:49. HOLOTYPE, a male, in CAS, labelled: "Logan Pass Glac. Nat. Pk VII-*-1938"/ "Van Dyke Collection"/ "Holotype No. 6008 Nebria intermedia Van Dyke" [red-tipped label]/ "California Academy of Sciences Type No. 6008." Allotype (same data as holotype) also in CAS (CAS Type No. 6009). TYPE LOCALITY.--Logan Pass, Glacier National Park, Montana. NEW STATUS.--Edwards, 1975:49.--Hatch, 1953:56.--Lindroth, 1961a:80.

3.433322 Nebria gyllenhali (Schönherr)

Nebria gyllenhali gyllenhali (Schönherr)

Carabus gyllenhali Schönherr, 1806:196. LECTOTYPE (here designated), a male, in NRSS, labelled: "♂"/ [triangular blue label]/ "Lectotype Carabus gyllenhali Schönherr designated by D. H. Kavanaugh 1976" [red label]. Five paralectotypes (same data as lectotype) also in NRSS. TYPE LOCALITY.--Lake Vänern, Sweden.

Nebria gyllenhali (Schönherr).--Csiki, 1927:358.--Lindroth, 1939:59; 1955a:41; 1961a:78.

Notes on nomenclature and types.--N. gyllenhali gyllenhali is

restricted to the Palearctic Region. The literature on this subspecies is extensive and numerous synonyms have been recognized (see Jeannel, 1937:4; Lindroth, 1939:54). I have omitted a listing of synonymy and most references in this treatment both because they are inappropriate here and because there is still some question on the status of several of the proposed synonyms.

One nomenclatural problem must be considered, however, because it affects the validity of the species epithet and thereby the names of the three Nearctic subspecies. The name Carabus rufescens Strøm (1768:331) did not appear in the literature between the date of its original description and 1880, when Schøyen (1880:183) revived its use. Jeannel (1937:4) accepted N. rufescens (Strøm) as the senior synonym of Nebria gyllenhali (Schönherr); and following him, a number of authors have subsequently applied the name rufescens to this species (Blair, 1950:220; Friden, 1971:30; Greenslade, 1968:41; Horvatovitch, 1973:252; Luff, 1972:174; Luff and Davies, 1972:47; Nakane, 1963:18 and 1971:180; Ueno, 1953:59 and 1955:47). The combination N. rufescens gyllenhali has sporadically appeared (Jeanne, 1966:12; Jeannel, 1937:4 and 1941:19) as has the unfortunate combination N. gyllenhali rufescens, where rufescens referred variously to a subspecies, race, variety, or aberration of gyllenhali (Andrewes, 1939:161; Bänninger, 1925:345 and 1960:261; Csiki, 1927:359; Munster, 1933:267; Reitter, 1908:93).

Lindroth (1939:59, 1954b:121, and 1961:78) and Bänninger (1949:144) have refused to recognize N. rufescens as the valid name for this species. For the reasons they have cited, because no type

specimen has been found or perhaps ever existed, and because Strŏm's original description "cannot be interpreted (not even as a Nebria)" (Lindroth, personal communication), I agree that the name gyllenhali (Schŏnherr) should be conserved as the valid name for the species. Any future use of the epithet rufescens should be discouraged; and the name Carabus rufescens Strŏm should be listed as a nomen dubium.

Nebria gyllenhali castanipes (Kirby)

(Figures 14A, 26, 93A, 191, 289, 319, 356, 388)

Helobia castanipes Kirby, 1837:2[illegible]. LECTOTYPE (here designated), a female, in BMNH, labelled: "Type" [red-trimmed disc]/ "70"/ "N. Amer. " [pale blue disc with "569 " on underside]/ "apparently Type of castanipes Kby. Lindroth 1952"/ "Lectotype Helobia castanipes Kirby designated by D. H. Kavanaugh 1976" [red label]. TYPE LOCALITY.--Nipigon, Lake Superior, Thunder Bay District, Ontario (designated by Lindroth, 1961a:78).--Horn, 1876:128.--Lindroth, 1953a:169.

Nebria castanipes (Kirby).--Bänninger, 1925:279.--Csiki, 1927:367.--Hamilton, 1894:7.--Henshaw, 1881:206.--Horn, 1870:102.--Larochelle, 1975:94.--LeConte, 1848:447; 1850:209; 1863a:[illegible] 1873:322.--Leng, 1920:46.--Lindroth, 1961a:78.--Melsheimer, 1853:11.--Provancher, 1877:148.--Schaupp, 1878:46.

Nebria moesta LeConte, 1850:209. LECTOTYPE (here designated), a male, in MCZ, labelled: [light green disc]/ "Type 645" [red label]/ "N. moesta LeC."/ "N. castanipes Kby."/ "Lectotype Nebria moesta LeConte designated by D. H. Kavanaugh 1976" [red

label]. One male and two female paralectotypes (same data as lectotype) also in MCZ. TYPE LOCALITY.--Lake Superior, Ontario. --Bänninger 1925:279.--Casey, 1913:51.--Csiki, 1927:367.--Darlington, 1943:60.--Fall, 1926:130.--Gemminger and Harold, 1868:51.--Hamilton, 1894:7.--Hatch, 1939a:120; 1953:58.--Henshaw, 1881:206.--Horn, 1870:102.--Larochelle, 1975:94.--LeConte, 1863a:2; 1863b:3; 1869:370; 1873:322.--Leng, 1920:46.--Leng and Mutchler, 1933:10.--Lindroth, 1939:61; 1953a:169; 1954b:121; 1954c:366; 1955a:40; 1961a:78; 1963a:28.--Mank, 1934:74.--Melsheimer, 1853:[illegible].--Motschulsky, 1865:274.--Provancher, 1877:148.--Schaupp, 1878:46.

Nebria sahlbergii; auctorum (not Fischer von Waldheim).--LeConte, 1853:400; 1878:479 (in part).--Packard, 1872:92; 1888:144.

Nebria sahlbergi; auctorum.--Beaulne, 1914:30 (in part).--Blackwelder and Blackwelder, 1948:2.--Blatchley, 1910:52.--Bowditch, 1896:2.--Casey, 1913:51; 1920:149.--Criddle, 1922:61.--Csiki, 1927:367 (in part).--Fall and Cockerell, 1907:156.--Hamilton, 1894:7 (in part).--Harrington, 1890:139, 190.--Hatch, 1939a:120 (in part).--Henshaw, 1881:206 (in part); 1885:4 (in part).--Horn, 1870:102; 1876:128 (in part); 1885:4 (in part).--Leng, 1920:46 (in part).--Leonard, 1928:211 (in part.--Lindroth, 1954c:366 (in part); 1955a:40; 1961a:78 (in part).--Poppius, 1910:303 (in part).--Schaupp, 1878:45 (in part).--Scudder, 1879:178B; 1890:532: 1895a:54.--Sherman, 1910:177(in

part).--Wickham, 1893:298.

Nebria gyllenhalii Motschulsky, 1865:274 [a misspelling].

Nebria elias Motschulsky, 1865:275. NOMEN DUBIUM? Type specimen destroyed (See discussion below); only labels survive: "Am. bor. occ. cont." [green label]/ "Nebria elias Motsch. Am. b. occ." [green label]/ [red rectangle]/ "Type specimen lost. Consider: Nomen Dubium designated by D. H. Kavanaugh 1977" [red label]. TYPE LOCALITY.--Alaska.--Bänninger, 1925:279.--Csiki, 1927:388.--Gemminger and Harold, 1868:49.--Henshaw, 1885:4.--Horn, 1870:104.--LeConte, 1878:473.--Leng, 1920:47.--Lindroth, 1961a:78.--Schaupp, 1878:46.

Nebria stahlbergi Knobel, 1895:9 [a misspelling].

Nebria labradorica Casey, 1920:151. LECTOTYPE (designated by Lindroth, 1975:112), a female, in USNM, labelled: "W. St. Modest [illegible]"/ "Casey bequest 1925"/ "Type USNM 46855" [red label]/ [illegible]abradorica Csy." "Lectotype labradorica Csy. By C. H. Lindroth." TYPE LOCALITY.--West Saint Modest, Labrador, Newfoundland.--Bänninger, 1925:261; 1928:6 (in part).--Blackwelder and Blackwelder, 1948:2.--Brown, 1930:232.--Casey, 1924:20.--Csiki, 1927:360.--Hatch, 1939a:119 (in part); 1953:55.--Jeannel, 1937:5.--Larochelle, 1975:94.--Leng and Mutchler, 1927:8.--Lindroth, 1939:61; 1953a:169; 1954b:122; 1954c:366; 1955a:40; 1961a:78; 1975:112.--Van Dyke, 1924:5; 1925:122 (in part); 1926:10 (in part); 1949:49.

Nebria prominens Casey, 1920:151. LECTOTYPE (designated by Lindroth, 1975:112), a female, in USNM, labelled: "N.H. Mt. W."/ "195/

"Casey bequest 1925"/ "Type USNM 46867" [red label]/ "prominens Csy."/ "Lectotype prominens Csy. By C. H. Lindroth." TYPE LOCALITY.--Mount Washington, Coos County, New Hampshire.--Csiki, 1927:389.--Larochelle, 1975:94.--Leng and Mutchler, 1927:8.--Lindroth, 1954b:122; 1954c:366; 1955a:40; 1961a:78; 1975:112.

Nebria curtulata Casey, 1924:20. LECTOTYPE (designated by Lindroth, 1975:112), a male, in USNM, labelled: "W. St. Modest Labr."/ "♂"/ "Casey bequest 1925"/ "Type USNM 46856" [red label]/ "curtulata Csy."/ "Lectotype curtulata Csy. By C. H. Lindroth." TYPE LOCALITY.--West Saint Modest, Labrador, Newfoundland.--Csiki, 1927:360.--Larochelle, 1975:94.--Leng and Mutchler, 1927:8.--Lindroth, 1954b:122; 1954c:366; 1961a:78; 1975:112.

Nebria gyllenhali; auctorum.--Bänninger, 1928:6 (in part).--Edwards, 1975:49.--Kirk and Balsbaugh, 1975:15.--Larochelle, 1972:62; 1975:94; 1976a:48; 1976b:130; 1977:112.--Lindroth, 1961a:78; 1963a:28; 1969d:1109; 1975:112.

Nebria gyllenhali labradorica Casey.--Bänninger, 1931:128 (in part).

Nebria rufescens gyllenhali Schönherr.--Jeannel, 1937:4 (in part).

Nebria curtulana Jeannel, 1937:5 [a misspelling].

Nebria sahlbergi moesta LeConte.--Hatch, 1939a:120.--Lindroth, 1955a:40.

Nebria gyllenhali castanipes (Kirby).--Larsson and Gigja, 1959:14.--Lindroth, 1954c:366; 1955a:40.

Notes on nomenclature and types.--The lectotype of Helobia castanipes bears no labels in Kirby's hand. However, according to P. M. Hammond (personal communication), the number "5699" on the

underside of one label refers to an entry in manuscript catalogs of the Coleoptera in BMNH. An original label in Kirby's hand is pasted in the catalog at this entry and reads: "73. 1. ♀?/ castanipes." The fate of the second of the two specimens mentioned by Kirby in his original description is unknown.

The type specimen of N. elias has been completely destroyed and only its pin and labels remain (in ZMUM). Motschulsky's original description is too vague to permit certainty that N. elias and N. gyllenhali castanipes are synonymous. The occurrence of the latter in Alaska (the type area of N. elias) is relatively rare and local, which casts further uncertainty on the identity of N. elias. I therefore refrain from designation of a neotype and list N. elias as as a nomen dubium, but tentatively as a synonym of N. gyllenhali castanipes, following Lindroth (1961a:78).

Nebria gyllenhali lindrothi Kavanaugh, NEW SUBSPECIES

(Figures 28, 93B, 192, 356, 388)

Nebria sahlbergi; Wickham, 1902:232.

Nebria gyllenhali; auctorum.--Armin, 1963:90.

Nebria gyllenhali lindrothi, new subspecies. HOLOTYPE, ♂ a male, in CAS, labelled: "U.S., Wyo., Albany Co., Medicine Bow Mts., Snowy Range, Brooklyn Lk., 10500', 11July 72 DHKavanaugh"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria gyllenhali lindrothi Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12512." Allotype (same data as holotype) also in CAS. 1387 paratypes

(see Appendix B for locality data) are deposited in the following collections: AMNH, ANSP, CArm, CAS, CNC, CUB, CUIC, DHKa, DRWh, EAMa, FMNH, ICCM, KSUC, KUSM, MCZ, MSU, PADA, PMCh, PMNH, PURC, RCGr, RDav, RTBe, SDSU, UAFA, UASM, USNM, UWBM, UWL, ZMLS. TYPE LOCALITY.--Brooklyn Lake (3200m), Albany County, Wyoming.

Notes on nomenclature and types.--This subspecies is the form noted by Lindroth (1969d:1109) as an undescribed species related to N. gyllenhali.

Derivation of taxon name.--I take great pleasure in naming this subspecies in honor of Carl H. Lindroth, a friend whose knowledge of and studies on Holarctic Carabidae have been a guiding light in this study, and who first called my attention to the distinctiveness of members of this taxon.

Nebria gyllenhali lassenensis Kavanaugh, NEW SUBSPECIES

(Figures 27, 388)

Nebria gyllenhali lassenensis, new subspecies. HOLOTYPE, a male, in CAS, labelled: "U.S.A., Calif., Lassen Volcanic N. P., Cascade Range, s. slope Mt. Lassen, Emerald Lk., 2450m, 22Aug.74 D.H. Kavanaugh Coll."/ "Holotype Nebria gyllenhali lassenensis Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12511." Allotype (same data as holotype) also in CAS. 34 paratypes (see Appendix B for locality data) are deposited in the following collections: CAS, DHKa, FMNH, USNM. TYPE LOCALITY.--Emerald Lake, Mount Lassen

(south slope), Lassen Volcanic National Park, California.

Derivation of taxon name.--This subspecies is named for Mount Lassen, on the south slope of which the type locality is found.

3.433323 Nebria frigida R. F. Sahlberg

(Figures 156, 197, 253-254, 327, 347, 389)

Nebria frigida R. F. Sahlberg, 1844:11. LECTOTYPE (designated by Lindroth, 1961:81), a female, in UMTF, labelled: "♀"/ [violet disc]/ "Ochotsk"/ "Coll. Sahlb."/ "Lectotypus frigida F. R. Sahlb. design. Lindroth" [red label]. TYPE LOCALITY.--Ochotsk (Marekan ["in monte Morikan"]), Khabarovskiy Kray, U.S.S.R..--Bänninger, 1923:133; 1925:261; 1949:;153.--Beaulne, 1914:30.--Csiki, 1927:358.--Gemminger and Harold, 1868:49.--Hamilton, 1894:7. Henshaw, 1887:1; 1895:1.--Heyden, 1880-81:14; 1893:12.--Leng, 1920:47.--Lindroth, 1961a:81; 1961b:442; 1963b:125; 1969a:1109; 1975:112.--Motschulsky, 1850:73; 1859:224.--Poppius, 1910:303.--Sahlberg (J.), 1885:47.--Shilenkov, 1975a:839.

Nebria viridis Hörn, 1870:101. LECTOTYPE (here designated), a male, in MCZ, labelled: "R. [superscript "M"] A."/ "Type No. 1027-" [red label]/ "N. viridis Horn"/ "Lectotype Nebria viridis Horn designated by D. H. Kavanaugh 1976" [red label]. One male paralectotype (same data as lectotype) also in MCZ. TYPE LOCALITY.--Saint Michael, Alaska.--Bänninger, 1928:6; 1949:147.--Beaulne, 1914:29.--Blackwelder and Blackwelder, 1948:2.--Csiki, 1927:368.--Fall, 1926:130.--Hamilton, 1894:7.--Hatch, 1939a:119; 1939b:45; 1953:55.--Henshaw, --1885:4.--LeConte, 1878:476.--Leng,

1920:46.--Lindroth, 1961a:81; 1961b:442.--Poppius, 1910:303.--Schaupp, 1878:45.--Van Dyke, 1921:158; 1924:4.

Nebria parvula J. Sahlberg, 1885 (1887, according to Lindroth, 1969d:1109):47. LECTOTYPE (designated by Lindroth, 1961a:81), a female, in NRSS, labelled: "Porte Clarence"/ "Exped. Vega."/ "Spec. typ."/ "192" [yellow label]/ "Typus" [red label]/ "Nebria parvula J. Sahlb."/ "N. frigida F. Sbg. v. obscurata Popp. teste Poppius"/ "89 59" [red label]/ "Lectotypus parvula J. Sahlb. design. Lindroth" [red label]/ "Riksmuseum Stockholm" [green label]. TYPE LOCALITY.--Port Clarence, Alaska.--Bänninger, 1923:133; 1925:261.--Beaulne, 1914:30.--Blackwelder and Blackwelder, 1948:2.--Casey, 1913:51.--Csiki, 1927:358.--Hamilton, 1894:7.--Hatch, 1939a:119.--Henshaw, 1887:1; 1895:1.--Heyden, 1893:13; 1896:7.--Leng, 1920:46.--Lindroth, 1961a:81; 1969d:1109.--Poppius, 1910:303.--Van Dyke, 1924:5.

Nebria reducta Casey, 1920:150. LECTOTYPE (designated by Lindroth, 1975:112), a female, in USNM, labelled: "'Al"/ "Casey bequest 1925"/ "Type USNM 46866" [red label;/ "reducta Csy."/ "Lectotype reducta Csy. By C. H. Lindroth." TYPE LOCALITY.--Saint Paul Island, Pribilov Islands, Alaska.--Blackwelder and Blackwelder, 1948:2.--Csiki, 1927:389.--Hatch, 1939a:119.--Leng and Mutchler, 1927:8.--Lindroth, 1961a:81; 1975:112.--Van Dyke, 1921:158; 1924:5.

Notes on nomenclature and types.--In Horn's original description of N. viridis, only two specimens are mentioned. In MCZ, there are now three specimens (one from the Horn Collection, two from the

LeConte Collection). I have designated the Horn specimen as lectotype and the first LeConte specimen as the paralectotype. The second LeConte specimen (labelled "viridis 2") has no type status. All three specimens bear identical first labels; but LeConte may have received his second specimen directly from Ulke (see Horn, 1870:14), his first specimen from Horn.

I see no reason to doubt the record of N. frigida from St. Paul Island (type locality of N. reducta), although Lindroth's (1961a:21, 81 and 1975:112) comments on the general reliability of some older records from that area must be considered.

3.434 The gregaria lineage

This lineage is represented by 23 extant species, five of which (N. carbonaria Eschscholtz, N. snowi Bates, N. angustula Motschulsky, N. altaica Gebler., and N. ochotica Sahlberg) are restricted to eastern and/or central Asia. [I am not yet convinced that N. ochotica and N. japonica Bates are conspecific, and I therefore treat these as separate species in section 4.1 on phylogeny.] Included in this lineage are taxa previously assigned to Lindroth's (1961a) "gregaria," "obtusa," "mannerheimi," "pallipes," (in part) and "appalachia" groups or to subgenus Reductonebria Shilenkov (1975a).

Diagnostic combination.--Adult members of this lineage can be recognized by the following combination of character states: frontal red spot(s) present; paraglossae indistinct, completely fused with ligula; pronotum moderately to faintly cordate, midlateral pronotal setae absent; hind coxa with two or more pairs of setae at base;

ventroapical margin of fourth hind tarsomere projected, lobate; second through fifth visible abdominal sterna without anterior paralateral setae; male genitalia: median lobe with basal bulb quadrate, broadly open basally, mid-shaft axis bent less than 135°, apex (ventral aspect) pointed; dorsobasal piece present as thin collar on basal bulb; female genitalia: basal apodeme of eighth sternum deeply emarginate, lateral arm not or moderately shortened; proctiger hemispheric, heavily sclerotized throughout; medial area of valvifer weakly sclerotized; coxite with setae of ventral diagonal row setiform; stylus with setae of mediodorsal row setiform, mediodorsal row longitudinal; bursa copulatrix with sclerite, varied in size and shape, in dorsal wall of spermathecal chamber.

3.4341 The gregaria group

This group is represented by 11 extant species, three of which (N. carbonaria, N. snowi, and N. angustula) are restricted to extreme eastern Asia (specifically, to Kamchatka and/or the northern Kuril Islands). The remaining species are restricted to western North America (Fig. 414). Except for the addition of the Palaearctic species, this group is identical (at the species level) in composition to Lindroth's (1961a) "gregaria" group.

Diagnostic combination.--Adult members of this group can be recognized by the following combination of character states: head faintly shiny; pronotum with basal sinuation of lateral margin moderately long, width of lateral explanation medium (except narrow in N. lyelli members); male genitalia: median lobe with mid-shaft

cylindrical or slightly narrowed basally, shape (in cross-section) slightly compressed (except markedly compressed in N. angustula males), ventral margin of preapical-shaft (lateral aspect) straight or evenly concave, or abruptly deflected ventrally near apex, apex (ventral aspect) broadly pointed (except narrowly pointed in N. snowi, N. carbonaria, and N. lyelli males); female genitalia: bursa copulatrix with spermathecal chamber (dorsal aspect) spatulate or broadly cordate, insertion of spermathecal duct posterior/ventral.

3.43411 The lyelli subgroup

3.434111 Nebria lyelli Van Dyke

(Figures 29, 66, 94, 189, 310, 390)

Nebria lyelli Van Dyke, 1925:120. HOLOTYPE, a male, in CAS, labelled: "Mt. Lyell, Yosemite Pk. Cal. VII-13-1921"/ "Van Dyke Collection"/ "Type Nebria lyelli Van Dyke" [red-tipped label]/ "California Academy of Sciences Type No. 1626." TYPE LOCALITY.--Mount Lyell (3350m), Yosemite National Park, California.--Blackwelder, 1939:12.--Csiki, 1927:388; 1933:631.--Darlington, 1930:105.--Kavanaugh, 1971:44.--Leng and Mutchler, 1933:10.--Lindroth, 1961a:72.--Van Dyke, 1926:11.

3.434112 Nebria acuta Lindroth

Nebria acuta acuta Lindroth

(Figures 95, 157, 265, 328, 390)

Nebria acuta Lindroth, 1961a:71. HOLOTYPE, a male, in MCZ, labelled:

"Alaska. 16 mi. E. Valdez. 439 20.VIII.1958 Lindroth"/ "M.C.Z. Type 30428" [red label]/ "Holotypus acuta Lth." [red label]. TYPE LOCALITY.--Snowslide Gulch (16 miles east of Valdez), Alaska.--de Ruette, 1970:15.

Nebria acuta quileute Kavanaugh, NEW SUBSPECIES

(Figures 95, 266, 329, 390)

Nebria acuta Lindroth, 1961a:71 (in part).

Nebria acuta quileute, new subspecies. HOLOTYPE, a male, in CAS, labelled: "U.S., Wash., Olympic N. P., Olympic Mts., Boulder Cr. at Olympic Hot Springs, 2000', 20July71 DHKavanaugh & EAMartinko"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria acuta quileute Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12494." Allotype (same data as holotype) also in CAS. 132 paratypes (see Appendix B for locality data) have been distributed among the following collections: CAS, CNC, DHKa, LACM, MCZ, UASM, UIMI, USNM, UWBM. TYPE LOCALITY.--Boulder Creek (at Olympic Hot Springs), Olympic National Park, Washington.

Derivation of taxon name.--This subspecies is named for the people native to the area including the type locality, the Quileute tribe.

3.43412 The sahlbergii subgroup

3.434121 Nebria sahlbergii Fischer von Waldheim

Nebria sahlbergii sahlbergii Fischer von Waldheim

(Figures 158, 267, 329A, 391)

Nebria sahlbergii Fischer von Waldheim, 1828:254. LECTOTYPE (here designated), a male, in UMHF, labelled: "♂"/ "Eschsch."/ "Sitka"/ "Lectotype Nebria sahlbergii Fischer v. Wald. designated by D. H. Kavanaugh 1977" [red label]/ "Lectotype Nebria violacea Motsch. designated by D. H. Kavanaugh 1977" [red label]. TYPE LOCALITY.--Sitka, Baranof Island, Alaska.--LeConte, 1960:10; 1878:479 (in part).--Melsheimer, 1853:11.--Motschulsky, 1850:72.

Nebria sahlbergii Eschscholtz [an improper assignment of authorship].--Dejean, 1831:576.--Fischer von Waldheim, 1828:254.--Mannerheim, 1843:189.--Motschulsky, 1865:274.

Nebria sahlbergi Eschscholtz [unjustified emendation and an improper assignment of authorship].--Menetries, 1844:54.

Nebria violacea Motschulsky, 1850:73. LECTOTYPE (here designated), a male, in UMHF, labelled: "♂"/ "Eschsch."/ "Sitka"/ "Lectotype Nebria sahlbergii Fischer v. Wald. designated by D. H. Kavanaugh 1977" [red label]/ "Lectotype Nebria violacea Motsch. designated by D. H. Kavanaugh 1977 [red label]. TYPE LOCALITY.--Sitka, Baranof Island, Alaska.--Csiki, 1927:367.--Gemminger and Harold, 1868:52.--Leng, 1920:46.--Lindroth, 1961a:68.

Nebria sahlbergi; auctorum [unjustified emendation].--Bänninger,

1925:259; 1949:147.--Beaulne, 1914:30 (in part).--Blackwelder and Blackwelder, 1948:2 (in part).--Clark, 1948:25.--Csiki, 1927:367 (in part).--Eschscholtz, 1833:23.--Fall, 1926:129.--Gemminger and Harold, 1868:52.--Hamilton, 1894:7 (in part).--Hardy, 1927:C22.--Hatch, 1939a:120 (in part); 1953:58.--Henshaw, 1881:206 (in part); 1885:4 (in part).--Horn, 1870:102 (in part); 1876:128 (in part).--Jeannel, 1937:4.--LeConte, 1878:476.--Leng, 1920:46 (in part).--Lindroth, 1954b:121; 1961a:68; 1963b:123.--Poppius, 1910:303 (in part).--Schaupp, 1878:45 (in part).--Sherman, 1910:177 (in part).--Van Dyke, 1919:8; 1924:5; 1925:120; 1926:9.--Venables, 1913:268.

Nebria gregaria; Schwarz, 1900:524 (in part).

Nebria aleuta Van Dyke, 1924:5. HOLOTYPE, a male, in CAS, labelled: "Mt. Makushin, Unalaska I. Alaska VII-3-1907"/ "E. C. Van Dyke Collector"/ "Van Dyke Collection"/ "Type Nebria aleuta Van Dyke" [red-tipped label]/ "California Academy of Sciences Type No. 3342." TYPE LOCALITY.--Mount Makushin, Unalaska Island, Aleutian Islands, Alaska.--Blackwelder and Blackwelder, 1948:2.--Hatch, 1939a:120.--Leng and Mutchler, 1933:11.--Lindroth, 1961a:68.

Nebria violaceus Fall, 1926:129 [a misspelling].

Notes on nomenclature and types.--Fischer's description of N. sahlbergii was based on study of Eschscholtz's material (Fischer, 1828:254). I have found only two specimens probably representing the original type series--one in the Fischer collection (ZMUM), the other in the Mannerheim collection (UMHF). I have chosen the UMHF specimen

as lectotype because, first, the original description better fits this specimen, and second, the Fischer specimen is, in fact, a representative of N. gyllenhali (Schönherr) rather than N. sahlbergii as the latter name has been applied (Lindroth, 1961a). The Fischer specimen must be considered a paralectotype of N. sahlbergii in spite of its identity. In fact, the strange misuse of the name N. sahlbergii by numerous North American authors in referring to N. gyllenhali castanipes (Kirby) (see synonymy under this latter name) can only now be explained--that is, if these authors considered the Fischer specimen as the type for N. sahlbergii.

An additional result of the mixed nature of Fischer's type series is as follows. Mannerheim obtained one of Eschscholtz's specimens, probably studied the other specimen in Fischer's collection, and then noted (1843:189) that two 'varieties' existed. He called the form represented by the Eschscholtz specimen in his possession "var. B." Motschulsky (1850:73), referring to Mannerheim's brief description of variety "B," named this form N. violacea. Consequently, the specimen now in UMHF appears to be the specimen upon which both N. violacea and N. sahlbergii are based! I have, therefore, designated (and so labelled) the specimen as lectotype for both names.

Nebria sahlbergii modoc Kavanaugh, NEW SUBSPECIES

(Figures 97, 124, 203, 330, 391)

Nebria sahlbergii modoc, new subspecies. HOLOTYPE, a male, in CAS, labelled: "U.S., Calif., Modoc Co., Warner Mts., 4 mi. e. New Pine Creek, Pine Cr., 5700', 22May71 DHKavanaugh & EAMartinko"/

"D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria sahlbergii modoc Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12513." Allotype (same data as holotype) also in CAS. 11 paratypes (see Appendix B for locality data) have been distributed among the following collections: CAS, DHKa, UASM, USNM. TYPE LOCALITY.--Pine Creek (4 mmles east of New Pine Creek), Modoc County, California.

Derivation of taxon name.--This subspecies is named for the county which includes the type locality, as well as for the people native to the region.

Nebria sahlbergii triad Kavanaugh, NEW SUBSPECIES

(Figures 98, 391)

Nebria sahlbergii triad, new subspecies. HOLOTYPE, a male, in CAS, labelled: "U.S.A., Calif., Trinity Co., Trinity Alps, S. F. Salmon R. at Big Flat Cmpgd., 1490m, 18July75 D.H. & B.A. Kavanaugh Stop #75-36"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria sahlbergii triad Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12514." Allotype (same data as holotype) also in CAS. 212 paratypes (see Appendix B for locality data) have been distributed among the following collections: CAS, DHKa, FMNH, MCZ, PUCA, UASM, USNM. TYPE LOCALITY.--South Fork Salmon River (at Big Flat Campground), Trinity County, California.

Derivation of taxon name.--This subspecies is named for the Trinity Alps, in which the type locality is found. I use a synonym

of 'trinity' for this purpose.

3.43413 The gregaria subgroup

3.434131 Nebria gregaria Fischer von Waldheim

(Figures 11, 15, 53, 67, 129, 141, 186, 311, 393)

Nebria gregaria Fischer von Waldheim, 1821:72. LECTOTYPE (here designated), a male, in ZMUM, labelled: "47. gregaria Fisch."/ "Lectotype Nebria gregaria Fischer v. Wald. designated by D. H. Kavanaugh 1977" [red label]. TYPE LOCALITY.--Unalaska, Unalaska Island, Aleutian Islands, Alaska.--Bänninger, 1925:259; 1928:2; 1949:147.--Beaulne, 1914:29.--Blackwelder and Blackwelder, 1948:2.--Casey, 1913:47.--Csiki, 1927:358.--Dejean, 1931:575.--Eschscholtz, 1823:101.--Gemminger and Harold, 1868:49.--Hamilton, 1894:6.--Hatch, 1938:145; 1939a:120.--Henshaw, 1885:4.--Horn, 1870:100.--Jeannel, 1937:4.--LeConte, 1860:10.--Leng, 1920:46.--Lindroth, 1961a:66; 1963b:123; 1975:111.--Melsheimer, 1853:11.--Schaupp, 1878:45.--Van Dyke, 1925:121.

Nebria gregaria Eschscholtz [an improper assignment of authorship].--Dejean, 1826:232.--Fischer von Waldheim, 1821:72; 1828:250.--Mannerheim, 1843:189.--LeConte, 1863:2; 1878:473.--Motschulsky, 1846:128; 1850:72; 1860:98.--Sturm, 1826:173.

Alpaeus gregarius (Fischer von Waldheim).--Motschulsky, 1865:273.

Nebria cuneata Casey, 1913:50. LECTOTYPE (designated by Lindroth, 1975:111), a male, in USNM, labelled: "Alask"/ "Casey bequest 1925"/ "Type USNM 46851" [red label]/ "cuneata Csy."/ "Lectotype cuneata Csy. By C. H. Lindroth." TYPE LOCALITY.--

Alaska; here restricted to Unalaska Island, Aleutian Islands, Alaska.--Csiki, 1927:357.--Leng, 1920:46.--Lindroth, 1961a:66; 1975:111.

Nebria gregaris Van Dyke, 1924:4 [a misspelling].

Notes on nomenclature and types.--Fischer (1821:73) indicated that his description of N. gregaria was based on material in his own and Eschscholtz's collections. I have been unable to locate any Eschscholtz specimens of N. gregaria from among those in UMHF. Apparently, the single Fischer specimen (ZMUM) chosen as lectotype is the only survivor from the type series.

3.434132 Nebria charlottae Lindroth

(Figures 16, 68, 128, 142, 185, 393)

Nebria charlottae Lindroth, 1961a:67. HOLOTYPE, a male, in CNC, labelled: "Q. C. I. Kean"/ "Holotypus charlottae Lth." [red label]/ "Holotype No. 7611" [red label]. TYPE LOCALITY.--Queen Charlotte Islands, British Columbia.--de Ruette, 1970:15.

3.43414 The arkansana subgroup

3.434141 Nebria arkansana Casey

Nebria arkansana arkansana Casey

(Figures 193, 392)

Nebria eschscholtzii; auctorum (not Menetries).--Armin, 1963:89.--Wickham, 1902:232.

Nebria arkansana Casey, 1913:52. LECTOTYPE (designated by Lindroth,

1975:11), a male, in USNM, labelled: "Ind"/ "Casey bequest 1925"/ "Type USNM 46858" [red label]/ "arkansana Csy."/ "Lectotype arkansana Csy. BY C. H. Lindroth." TYPE LOCALITY:-- Valley of the Upper San Juan River, Archuleta County, Colorado (designated by Lindroth, 1961a:70).--Armin, 1963:88.--Casey, 1924:21.--Csiki, 1927:367.--Leng, 1920:47.--Lindroth, 1961a:70 (in part); 1975:11.

Nebria sahlbergi; auctorum.--Armin, 1963:94.--Hatch, 1939a:120 (in part).--Lavigne, 1977:46.

Notes on nomenclature and types.--Lindroth was certainly correct in denying the validity of Casey's records for Arkansas and Indiana; and his choice for the new type locality is quite reasonable. The specimens in Casey's series are labelled "Ind" and "S. Ark"; and it is at least possible that the latter refers to the South Arkansas River (a quite suitable locality in Chaffee County, Colorado) rather than to the State of Arkansas as supposed by Casey.

Nebria arkansana edwardsi Kavanaugh, NEW SUBSPECIES

(Figures 147, 250, 268, 307, 331, 392)

Nebria sahlbergi; auctorum.--Edwards, 1975:48.--Mank, 1934:74.

Nebria arkansana; Lindroth, 1961a:70 (in part).

Nebria arkansana edwardsi, new subspecies. HOLOTYPE, a male, in CAS, labelled: "U.S., Mont., Glacier N. P., Livingstone Range, Logan Pass Area, ne. slope Mt. Clements, 7100', 17July72 DHKavanaugh & JGEdwards"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria arkansana edwardsi Kavanaugh det.

D. H. Kavanaugh" [red label]/ "California Academy of Sciences Type No. 12495". Allotype (same data as holotype) also in CAS. 1861 paratypes (see Appendix B for locality data) are deposited in the following collections: AMNH, ANSP, BFCa, CAS, CNC, CUIC, DBUM, DHKa, DJLa, FMNH, INHS, JSch, JVMa, KUSM, LRus, MCZ, MSU, OSUO, PMNH, PURC, ROM, RTBe, SJSC, UAFA, UASM, UBC, UIMI, USNM, UWBM. TYPE LOCALITY.--Logan Pass, Glacier National Park, Montana.

Derivation of taxon name.--I take great pleasure in naming this subspecies in honor of J. Gordon Edwards, whose interest in life at high altitudes has fostered my own.

Nebria arkansana oowah Kavanaugh, NEW SUBSPECIES

(Figures 269, 332, 392)

Nebria arkansana oowah, new subspecies. HOLOTYPE, a male, in CAS, labelled: "U.S., Utah, Grand Co., LaSal Mts., Mill Cr. at Oowah Lk., 8800', 2August71 DHKavanaugh & EAMartinko"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria arkansana oowah Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12496". Allotype (same data as holotype) also in CAS. 75 paratypes (see Appendix B for locality data) have been distributed among the following collections: CAS, DHKa, MCZ, UASM, USNM. TYPE LOCALITY.--Mill Creek (at Oowah Lake) Grand County, Utah.

Derivation of taxon name.--This subspecies is named for the small, sheltered lake at the type locality.

Nebria arkansana uinta Kavanaugh, NEW SUBSPECIES

(Figures 30, 132, 194, 270, 392)

Nebria arkansana uinta, new subspecies. HOLOTYPE, a male, in CAS, labelled: "U.S., Utah, Summit Co., Uinta Mts., Hwy. 150, Lost Lk., 9800', 14Aug71 DHKavanaugh"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria arkansana uinta Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12497". Allotype (same data as holotype) also in CAS. 92 paratypes (see Appendix B for locality data) have been distributed among the following collections: CAS, DHKa, MCZ, UASM, USNM. TYPE LOCALITY.--Lost Lake, Summit County, Utah.

Derivation of taxon name.--This subspecies is named for the Uinta Mountains, in which the type locality is found.

3.434142 Nebria fragilis Casey

Nebria fragilis fragilis Casey

(Figures 126, 188, 224; 271, 394)

Nebria mannerheimii; Putnam (not Fischer von Waldheim), 1876b:199.

Nebria fragilis Casey, 1924:21. LECTOTYPE (designated by Lindroth, 1975:112), a male, in USNM, labelled: "North Fork Provo Cañon IX-1 [?] Spalding"/ "Casey bequest 1925"/ "type USNM 46857" [red label]/ "Lectotype fragilis Csy. By C. H. Lindroth". TYPE LOCALITY.--North Fork Provo Canyon, Utah County, Utah.--Csiki, 1927:367.--Leng and Mutchler, 1927:8.--Lindroth, 1961a:72;

1975:112.

Nebria fragilis teewinot Kavanaugh, NEW SUBSPECIES

(Figures 209, 394)

Nebria fragilis teewinot, new subspecies. HOLOTYPE, a male, in CAS labelled: "U.S., Wyo., Teton N. P., Teton Mts., Mt. Teewinot, stream on se. slope, 7100'-9000', 3Aug.73 DHKavanaugh Family"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria fragilis teewinot Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12500". Allotype (same data as holotype) also in CAS. 377 paratypes (see Appendix B for locality data) have been distributed among the following collections: CAS, DHKa, KUSM, MCZ, SJSC, UASM, USNM. TYPE LOCALITY.--Mount Teewinot (southeast slope), Grand Teton National Park, Wyoming.

Derivation of taxon name.--This subspecies is named for the type locality.

3.434143 Nebria zioni Van Dyke

Nebria zioni zioni Van Dyke

(Figures 31, 80, 99, 321, 394)

Nebria zioni Van Dyke, 1943:20. HOLOTYPE, a male, in CAS, labelled "Zion Canon, V-29-1935 Ut."/ "Van Dyke Collection"? "Holotype No. 5299 Nebria zioni Van Dyke" [red-tipped label]/ "California Academy of Sciences Type No. 5299". Allotype (same data as

holotype) also in CAS (California Academy of Sciences Type No. 5300). TYPE LOCALITY.--Zion Canyon, Zion National Park, Utah.--Blackwelder and Blackwelder, 1948:2.--Lindroth, 1961a:72. --Tanner, 1928:269 (as "Nebria sp.").

Nebria zioni oasis Kavanaugh, NEW SUBSPECIES

(Figures 32, 212, 287, 394)

Nebria zioni oasis, new subspecies. HOLOTYPE, a male, in CAS, labelled: "U.S., Utah, Washington Co., Pine Valley Mts., Leeds Cr. at Oak Grove Cmpgd., 6300'-6500', 20June71 DHKavanaugh & EAMartinko"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria zioni oasis Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12518". Allotype (same data as holotype) also in CAS. 46 paratypes (see Appendix B for locality data) have been distributed among the following collections: CAS, DHKa, MCZ, UASM, USNM. TYPE LOCALITY.--Leeds Creek (at Oak Grove Campground), Washington County, Utah.

Derivation of taxon name.--This subspecies is named for the oasis-like nature of the type locality--a spot of green, as it were, in an otherwise dry land.

3.4342 The obliqua group

This group is represented by six extant species, two of which (N. altaica and N. ochotica [including, for the present, N. japonica]) are restricted to central and eastern Asia, respectively. The

remaining species are endemic to North America--two restricted to eastern North America, one to the West, and one shared between both areas. (Fig. 420) The group includes taxa previously assigned to Lindroth's (1961a) "obtusa", "pallipes" (in part), and "appalachia" groups.

Diagnostic combination.--Adult members of this group can be recognized by the following combination of character states: head markedly shiny; pronotum with basal sinuation of lateral margin moderately long (except short in N. suturalis adults), width of lateral explanation medium or broad (except narrow in N. appalachia members); male genitalia: median lobe with mid-shaft markedly narrowed apically, shape (in cross-section) moderately or markedly compressed, ventral margin of preapical-shaft (lateral aspect) moderately recurved, apex (ventral aspect) narrowly pointed; female genitalia: bursa copulatrix with spermathecal chamber (dorsal aspect) round, insertion of spermathecal duct posterior/middle.

3.43421 The obliqua subgroup

3.434211 The obliqua infragroup

3.4342111 Nebria suturalis LeConte

(Figure 100, 159, 180, 313, 398)

Nebria suturalis LeConte, 1850:209. LECTOTYPE (here designated), a male, in MCZ, labelled: [light green disc]/ "Type 650" [red label]/ "suturalis 3"/ "Lectotype Nebria suturalis LeConte designated by D. H. Kavanaugh 1976" [red label]. Two female

paralectotypes (same data as lectotype) also in MCZ. TYPE LOCALITY.--Islands at mouth of Black Bay, Lake Superior, Ontario.--Banninger, 1925:259.--Beaulne, 1914:30.--Blatchley, 1910:52.--Bowditch, 1896:2.--Casey, 1920:150.--Csiki, 1927:367. --Darlington, 1943:60.--Evans, 1906:96 (cannot refer to this species, but otherwise uninterpretable).--Gemminger and Harold, 1868:52.--Hatch, 1953:59.--Henshaw, 1881:206; 1885:4.--Horn, 1870:101.--Knobel, 1895:9.--Larochelle, 1975:95; 1977:112.-- LeConte, 1863a:2; 1878:476.--Leng, 1920:47 (in part).--Lindroth, 1954b:122; 1961a:73; 1963a:76; 1975:112.--Melsheimer, 1853:11-- Schaupp, 1878:45.

Nebria longula Le Conte, 1878:478. HOLOTYPE, a male, in MCZ, labelled: "Col."/ "Type 644" [red label]/ "N. longula LeC."/ "Holotype Nebria longula LeConte det. D. H. Kavanaugh 1976" [red label]. TYPE LOCALITY.--Colorado; here restricted to Longs Peak, Rocky Mountain National Park, Colorado. NEW SYNONYMY.--Armin, 1963:92 (in part).--Casey, 1920:150.--Csiki, 1927:364.--Henshaw, 1881:206; 1885:4.--Leng, 1920:47.-- Lindroth, 1961a:73; 1969d:1109.--Schaupp, 1878:45.--Wickham, 1902:232.

Nebria nimbosa Casey, 1920:150. HOLOTYPE, a female, in USNM, labelled: "Lake of the Clouds Mt. Washington"/ "Casey bequest 1925"/ "Type USNM 46860" [red label]/ "nimbosa Csy."/ "Holotype nimbosa Csy. By C. H. Lindroth". TYPE LOCALITY.--Lake of the Clouds, Mount Washington, Coos County, New Hampshire.-- Banninger, 1925:259.--Csiki, 1927:367.--Larochelle, 1975:95.--

Leng and Mutchler, 1927:8.--Lindroth, 1954b:122; 1961a:73; 1975:112.

Nebria obtusa; Harwald (not LeConte), 1951:691 (in part).

3.4342112 Nebria obliqua Le Conte

(Figures 69, 101, 200, 216, 220-221, 343, 357, 395)

Nebria obliqua Le Conte, 1866:363. LECTOTYPE (here designated), a male, in MCZ, labelled: "Col."/ "Type 646" [red label]/ "Nebria obliqua Lec. Lewis Col."/ "obliqua 2"/ "Lectotype Nebria obliqua LeConte designated by D. H. Kavanaugh 1976" [red label]. One female paralectotype (same data as lectotype (also in MCZ. TYPE LOCALITY.--Colorado; here restricted to North Fork South Platte Canyon (at Santa Maria), Park County, Colorado.--Armin, 1963:92.--Casey, 1913:47.--Csiki, 1927;364.--Fall and Cockerell, 1907:156.--Gemminger and Harold, 1968:51.--Henshaw, 1881:206; 1885:4.--Horn, 1870:100.--Kirk and Balsbaugh, 1975:14.--Lavigne, 1977:46.--LeConte, 1878:476; 1879:500.--Leng, 1920:47.--Lindroth, 1961a:73; 1975:112.--Schaupp, 1878:45.--Van Dyke, 1926:10.--Wickham, 1902:231.

Nebria obtusa LeConte, 1878:478. HOLOTYPE, a male, in MCZ labelled: "6-7,000 ft. Green River City, Wyo. July 2-27, 1[illegible] "Type 647" [red label]/ "N. obtusa LeC."/ "Holotype Nebria obtusa LeConte det D. H. Kavanaugh 1976" [red label]. TYPE LOCALITY.--Green River City, Sweetwater County, Wyoming. NEW SYNONYMY.--Armin, 1963:92.--Banninger, 1925:259; 1947:147.--Beaulne, 1914:29.--Blackwelder and Blackwelder, 1948:2.--Casey, 1913:53.--Csiki,

1927:364.--Edwards, 1975:49.--Hatch, 1933:7; 1939:121; 1953:59. --Haubold, 1951:691 (in part).--Henshaw, 1881:206; 1885:4.-- Kirk and Balsbaugh, 1975:14.--LeConte, 1879:500.--Leng, 1920:47. --Lindroth, 1961a:72; 1975:112.--Schaupp, 1878:45.--Spence, 1974:7.--Van Dyke, 1926:10.--Wickham, 1902:231.

Nebria mannerheimii; Wickham (not Fischer von Waldheim), 1902:231.

Nebria incerta Casey, 1913:53. LECTOTYPE (designated by Lindroth, 1975:112), a female, in USNM, labelled: "Col."/ "Casey bequest 1925"/ "Type USNM 46859" [red label]/ "incerta Csy."/ "Lectotype incerta Csy. By C. H. Lindroth". TYPE LOCALITY.-- Colorado: here restricted to North Fork South Platte Canyon (at Santa Maria), Park County, Colorado.--Csiki, 1927:360.-- Leng, 1920:47.--Lindroth, 1961a:73; 1975:112.

Nebria testaceipes Casey, 1913:54. HOLOTYPE, a male, in USNM, labelled: Glenora, B. C. Wickham."/ "Casey bequest 1925"/ "Type USNM 46861" [red label]/ "testaceipes Csy."/ "Holotype testaceipes Csy. By C. H. Lindroth". TYPE LOCALITY.--Glenora, British Columbia.--Beaulne, 1914:31.--Csiki, 1927:367.--Fall, 1926:130.--Hatch, 1953:59.--Leng, 1920:47.--Lindroth, 1961a:72; 1975:112.

Nebria texana Casey, 1913:54. HOLOTYPE, a male, in USNM, labelled: "Tex."/ "Casey bequest 1925"/ "Type USNM 46863" [red label]/ "texana Csy."/ "Holotype texana Csy. BY C. H. Lindroth". TYPE LOCALITY.--Texas.--Csiki, 1927:367.--Leng, 1920:47.--Lindroth, 1961a:73; 1975:112.

Nebria eschscholtzii; Beaulne (not Menetries), 1914:30.

Nebria escholtzi; auctorum.--Clark 1948:25.--Hatch, 1933:7.

Nebria longula; Armin (not LeConte), 1963:92 (in part).

Notes on nomenclature and types. The type locality of N. obliqua, as originally stated, was Colorado. LeConte subsequently (1878:478) listed "North Fork of South Platte Cañon (7,000 to 8,000 ft.)" as a locality for the species; and Lindroth (1961a:73) accepted this as the type locality. I here formally restrict the type locality to this area.

My interpretation of LeConte's original description of N. obtusa (1878:478-479) is that it is based on a single specimen (see p. 479, lines 7-8). I therefore list the type specimen as a holotype.

The holotype of N. texana bears the label "Tex", interpreted by Casey as referring to the State of Texas (a highly improbable record). It is more probable the specimen was collected in Colorado, perhaps at Texas Creek (on the Arkansas River), Fremont County, Colorado. However, I have chosen not to amend or restrict the type locality pending further field search in the mountainous regions of western Texas.

3.434212 The pallipes infragroup

3.4342121 Nebria appalachia Darlington

(Figures 9, 17, 59, 102, 127, 183, 228, 257, 397)

Nebria appalachia Darlington, 1931b:153. HOLOTYPE, a male in MCZ, labelled: "Smoky Mts. N.C.-Tenn. Newfound Gap 5,000-5,200 ft."/ "Aug. 30, 1930 Darlington"/ "Holotype Nebria appalachia Darl.

M.C.Z. 16433" [red label]. Allotype (same data as holotype) also in MCZ. TYPE LOCALITY.--Newfound Gap (naer 1520m), Great Smoky Mountains National Park, Tennessee.--Bell, 1955:265.--Csiki, 1933:631.--Fattig, 1949:12.--Leng and Mutchler, 1933:79.--Lindroth, 1961a:77.--de Ruette, 1970:15.

3.43421222 Nebria pallipes Say

(Figures 50, 103, 166, 201, 237, 351, 396)

Nebria pallipes Say, 1823:78. NEOTYPE (selected by Lindroth and Freitag, 1969:333), a male, in MCZ, labelled: "C. H. Frost Monterey"/ "Mass. Aug. 1, '20"/ "pallipes Say ♂"/ "C. A. Frost Collection 1962"/ "Neotypus Nebria pallipes Say design. Lth." [red label]. TYPE LOCALITY.--Massachusetts, Boston (county unspecified) (designated by Lindroth, 1961a:76).--Banninger, 1925:260; 1949:147.--Beaulne, 1914:30.--Bell, 1955:265; 1967:104.--Blatchley, 1910:53.--Bowditch, 1896:2.--Casey, 1913:47.--Chagnon, 1914:167.--Csiki, 1927:365.--Darlington, 1931b:154.--Dillon and Dillon, 1961:67.--Fattig, 1949:12.--Gemminger and Harold, 1868:51.--Henshaw, 1885:4.--Horn, 1870:104.--Jeannel, 1937:4.--Kirk, 1970:9.--Knobel, 1895:9.--Larochelle, 1975:74; 1977:112.--LeConte, 1848:447; 1850:209; 1863a:2; 1878:477 (in part).--Leng, 1920:47.--Leonard, 1928:211.--Lindroth, 1954a:301; 1961a:76; 1963a:65; 1969:1149d.--Lindroth and Freitag, 1969:333.--Loding, 1945:12.--Melsheimer, 1853:11.--Provancher, 1877:148.--Schaupp, 1878:45.--Scudder, 1900:17.--Smith, 1910:200.--Spence, 1974:6.--Spence, Bell, and

Bell, 1976:81.--Spence and Bell, unpublished manuscript.--Sturm, 1843:16.--Ulke, 1902:6.

Nebria mühlenbergii Sturm, 1826:173 [here emended to Nebria muehlenbergii Sturm]. NOMEN NUDUM.--Csiki, 1927:365.--Gemminger and Harold, 1868:51.--Sturm, 1843:16.

Notes on nomenclature and types.--Lindroth (1969a:1149, and in Lindroth and Freitag, 1969:326) discusses the problem of establishing the actual publication date of Say's paper in which the original description of N. pallipes appeared. His comments support the date presented above rather than 1825 (as presented in Lindroth, 1961a:76).

Sturm (1843:16) cited N. muehlenbergii Sturm as a synonym of N. pallipes, thereby providing the only clue to his application of the name to a taxon.

3.4343 The mannerheimii group

This group is represented by six extant species, all endemic to western North America (Fig. 417). With exception of the three new or recently described species, the group is identical to Lindroth's (1961a) "mannerheimi" group.

Diagnostic combination.--Adult members of this group can be recognized by the following combination of character states: head moderately dull; pronotum with basal sinuation of lateral margin short, width of lateral explanation narrow; male genitalia: median lobe with mid-shaft markedly narrowed apically, shape (in cross section) moderately or markedly compressed, ventral margin of preapical-shaft (lateral aspect) faintly to moderately recurved,

apex (ventral aspect) narrowly pointed; female genitalia: bursa copulatrix with spermathecal chamber (dorsal aspect) spatulate or ovoid (slightly elongate longitudinally), insertion of spermathecal duct posterior/ventral.

3.43431 The mannerheimii subgroup

3.434311 Nebria darlingtoni Kavanaugh, NEW SPECIES

(Figures 7, 104, 202, 316, 341, 399)

Nebria darlingtoni, new species. HOLOTYPE, a male, in CAS, labelled: "U.S.A., Calif., El Dorado Co., Sierra Nevada, S. F. American R., 3 mi. w. of Riverton, 910m, 16July75 D.H. & B.A. Kavanaugh Stop #75-29"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria darlingtoni Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12499". Allotype (same data as holotype) also in CAS. 170 paratypes (see Appendix B for locality data) are deposited in the following collections: AMNH, CAS, DHKa, ICCM, KSUC, KUSM, MCZ, UASM, USNM. TYPE LOCALITY.--South Fork American River (3 miles west of Riverton), El Dorado County, California.

Derivation of taxon name.--I take great pleasure in naming this species in honor of Philip J. Darlington, Jr., biogeographer, student of carabid evolution, and friend, whose work and encouragement have provided inspiration in this study.

3.434312 Nebria mannerheimii Fischer von Waldheim

(Figures 70, 105, 399)

Nebria mannerheimii Fischer von Waldheim, 1828:253. LECTOTYPE (here designated), a male, in ZMUM, labelled: "Sitcha"/ "48. mannerheimii Fisch"./ "Lectotype Nebria mannerheimii Fischer v. Wald. designated by D. H. Kavanaugh 1977" [red label]. One male paralectotype in UMHF. TYPE LOCALITY.--Sitka, Baranof Island, Alaska.--Eschscholtz, 1833:23.--Hamilton, 1894:7.--Harrington, 1890:139.--Hatch, 1953:58.--Henshaw, 1885:4.--Horn, 1870:103.--LeConte, 1860:10; 1878:475.--Melsheimer, 1853:11.--Provancher, Schaupp, 1878:45.--Schwarz, 1900:524.--Taylor, 1886:35.--Van Dyke, 1919:4.--Wickham, 1893:213, 228.

Nebria mannerheimii Eschscholtz [an improper assignment of authorship]. --Dejean, 1831:575.--Fischer von Waldheim, 1828:253.--LeConte, 1863a:2; 1869:370.--Mannerheim, 1843:189.--Motschulsky, 1846:126; 1850:73.

Nebria mannerheimi; auctorum [unjustified emendation].--Banninger, 1925:259.--Bates, 1883:218.--Beaulne, 1914:30.--Blackwelder and Blackwelder, 1948:2.--Casey, 1913:48; 1924:20.--Csiki, 1937:364. --Gemminger and Harold, 1868:51.--Hatch, 1933:7 (cannot refer to this species but otherwise uninterpretable); 1939a:120.--Jeannel, 1937:4.--Kavanaugh, 1971:44.--Leng, 1920:46.--Lindroth, 1961a:74; 1975:112.--Menetries, 1844:55.--Van Dyke, 1926:9; 1943:21.

Nebria sahlbergi; Keen, 1895:166.

Nebria gregaria; Schwarz (not Fischer von Waldheim), 1900:524 (in part).

Nebria oregona Casey, 1913:52. LECTOTYPE (designated by Lindroth, 1975:112), a male, in USNM, labelled: "Clackamas Co. Oreg."/ "Casey bequest 1925"/ "Type USNM 46853" [red label2/ "oregona Csy."/ "Lectotype oregona Csy. By C. H. Lindroth". TYPE LOCALITY.--Clackamas Co., Oregon; here restricted to Zigzag River (at Rhododendron), Clackamas County, Oregon.--Csiki, 1937:364.--Hatch, 1953:58.--Leng, 1920:46.--Lindroth, 1961a:74; 1975:112.

Nebria corvallis Casey, 1924:20. LECTOTYPE (designated by Lindroth, 1975:112), a male, in USNM, labelled: "Corvallis Or 7-4-12"/ "Casey bequest 1925"/ "Type USNM 46854" [red label]/ "corvallis Csy."/ "Lectotype corvallis Csy. By C. H. Lindroth". TYPE LOCALITY.--Corvallis, Benton County, Oregon.--Csiki, 1937:357. --Hatch, 1953:58.--Leng and Mutchler, 1927:8.--Lindroth, 1961a:74; 1975:112.

Nebria hippisleyi Casey, 1924:21. HOLOTYPE, a male, in USNM, labelled: "B. C. Terrace Hippisley"/ "Casey bequest 1925"/ "Type USNM 46868" [red label]/ "hippisleyi Csy."/ "Holotype hippisleyi Csy. By C. H. Lindroth". TYPE LOCALITY.--Terrac British Columbia.--Blackwelder and Blackwelder, 1948:2.--Clark, 1948:25.--Csiki, 1937:388.--Hatch, 1939a:121; 1953:58.--Leng and Mutchler, 1927:8.--Lindroth, 1961a:74; 1975:112.

Notes on nomenclature and types.--Both specimens I recognize as comprising the type series of N. mannerheimii Fischer v. Wald. were

probably those collected by Eschscholtz (Fischer, 1828:253). The specimen chosen as lectotype is from the Fischer collection (ZMUM), the paralectotype is from the Mannerheim collection (UMHF) and bears an "Eschsch." label.

3.43432 The eschscholtzii subgroup

3.434321 The desolata infragroup

3.4343211 Nebria desolata Kavanaugh

(Figures 48, 71, 106, 143, 229, 272, 342, 400)

Nebria desolata Kavanaugh, 1971:41. HOLOTYPE, a male, in CAS, labelled: "Utah, Garfield Co., 11 mi. sw Boulder, The Gulch 5600' 16July69"/ [white dot]/ [red dot]/ [orange dot]/ "D. H. Kavanaugh Collector"/ "Holotype ♂ Nebria desolata D. Kavanaugh det. D. H. Kavanaugh 1969" [red label]/ "California Academy of Sciences Type No. 11388". Allotype (same as holotype) also in CAS. TYPE LOCALITY.--The Gulch (11 miles southwest of Boulder), Garfield County, Utah.

3.4343212 Nebria navajo Kavanaugh, NEW SPECIES

(Figures 195, 273, 400)

Nebria navajo, new species HOLOTYPE, a male, in CAS, labelled: "Kayenta Ariz. 19 mi sw VI-18-33"/ "Navajo Co. Alt. 6500 ft."/ "Ansel F Hall Exp. 1933"/ "H N Hultgren Collector"/ "Holotype Nebria navajo Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12509". One paratype (same data as holotype) also in CAS. TYPE LOCALITY.--Kayenta

(19 miles southwest), Navajo County, Arizona.

Derivation of taxon name.--This species is named for the people native to the region including the type locality.

3.434322 The eschscholtzii infragroup

3.4343221 Nebria eschscholtzii Menetries

(Figures 248, 274, 362, 400)

Nebria eschscholtzii Menetries, 1844:55. LECTOTYPE (here designated), a female, in ZILR, labelled: [gold-coated square]/ "California" [pink label]/ "Eschscholtzii Menet. Californ."/ "Syntypus" [red label]/ "Lectotype Nebria eschscholtzii Menetries designated by D. H. Kavanaugh 1976" [red label]. One paralectotype also in ZILR. TYPE LOCALITY.--California; here restricted to South Fork American River (3 miles west of Riverton), El Dorado County, California.--Hamilton, 1894:7 (in part; records from Alaska and British Columbia cannot refer to this species, but are otherwise uninterpretable).--Hatch, 1953:58.--Henshaw, 1881:206; 1885:4. --Horn, 1870:103.--LeConte, 1860:10; 1863a:2; 1878:475.-- Motschulsky, 1846:128; 1850:72.--Schaupp, 1878:45.

Nebria castanipes; auctorum (not Kirby).--Hamilton, 1894:7.--Henshaw, 1881:206.--Horn, 1870:103 (in part).--LeConte, 1863:2 (in part). --Schaupp, 1878:46.

Nebria eschscholtzi; auctorum [unjustified emendation].--Banninger, 1925:259; 1949:147.--Blackwelder and Blackwelder, 1948:2.-- Casey, 1913:48; 1920:152.--Csiki, 1927:357.--Gemminger and

Harold, 1868:49.--Hatch, 1939:121.--Kavanaugh, 1971:44.--LaRivers, 1946:138.--Leng, 1920:46.--Lindroth, 1961a:75; 1975:112.--Van Dyke, 1926:9; 1943:21.

Nebria tenuipes Casey, 1913:51. LECTOTYPE (designated by Lindroth, 1975:112), a female, in USNM, labelled: "Alameda Co. Cal."/ "Casey bequest 1925"/ "Type USNM 468 3" [red label]/ "tenuipes Csy."/ "Lectotype tenuipes Csy. BY C. H. Lindroth". TYPE LOCALITY.--Alameda County, California; here restricted to Niles Canyon, Alameda County, California.--Blackwelder and Blackwelder, 1948:2.--Csiki, 1927:367.--Hatch, 1939a:121; 1953:58.--Leng, 1920:46.--Lindroth, 1961a:75; 1975:112.

Nebria transversa Casey, 1920:152. HOLOTYPE, a female, in USNM, labelled: "Corvallis Or. 5-30-98"/ "Casey bequest 1925"/ "Type USNM 46869" [red label]/ "transversa Csy."/ "Holotype transversa Csy. By C. H. Lindroth". TYPE LOCALITY.--Corvallis, Benton County, Oregon.--Blackwelder and Blackwelder, 1948:2.--Casey, 1924:21.--Csiki, 1927:389.--Hatch, 1939a:121; 1953:58.--Leng and Mutchler, 1927:8.--Lindroth, 1961a:75; 1975:112.

Nebria formalis Casey, 1920:153. LECTOTYPE (designated by Lindroth, 1975:112), a female, in USNM, labelled: "Wawawai Wash"/ "Casey bequest 1925"/ "Type USNM 46870" [red label]/ "formalis Csy."/ "Lectotype formalis Csy. By C. H. Lindroth". TYPE LOCALITY.--Wawawai, Whitman County, Washington.--Blackwelder and Blackwelder, 1948:2.--Csiki, 1927:388.--Hatch, 1939a:121; 1953:58.--Leng and Mutchler, 1927:8.--Lindroth, 1961a:75; 1975:112.

Nebria pallidissima Casey, 1924:19. LECTOTYPE (designated by Lindroth, 1975:112), a male, in USNM, labelled: "Wawawai Wash"/ "Casey bequest 1925"/ "Type USNM 46845" [red label]/ "pallidissima Csy."/ "Lectotype pallidissima Csy. By C. H. Lindroth". TYPE LOCALITY.--Wawawai, Whitman County, Washington.--Csiki, 1927:365.--Hatch, 1953:58.--Leng and Mutchler, 1927:8.--Lindroth, 1961a:75; 1975:112.

Nebria pugetana Casey 1924:19. LECTOTYPE (designated by Lindroth, 1975:112), a female, in USNM, labelled: "Wawawai Wash"/ "Casey bequest 1925"/ "Type USNM 46847" [red label]/ "pugetana Csy."/ "Lectotype pugetana Csy. By C. H. Lindroth". TYPE LOCALITY.--Wawawai, Whitman County, Washington.--Csiki, 1927:365.--Hatch, 1953:58.--Leng and Mutchler, 1927:8.--Lindroth, 1961a:75; 1975:112.

Nebria escholtzi Van Dyke, 1926:9 [a misspelling].

Nebria eschholtzi Jeannel, 1937:4 [a misspelling].

3.4343222 Nebria diversa LeConte

(Figures 8, 230-232, 306, 360, 401)

Nebria livida LeConte, 1859a:84 [preoccupied by Carabus lividus Linnaeus, 1758:414]. LECTOTYPE (here designated), a male, in MCZ, labelled: [blue disc]/ "Type 642" [red label]/ "N. diversa ‖C. livida‖ LeC."/ "Lectotype Nebria livida LeConte designated by D. H. Kavanaugh 1976" [red label]. One paralectotype male (same data as lectotype) also in MCZ.

LOCALITY.--Cape Flattery, Clallam County, Washington.--

Csiki, 1927:357.--Gemminger and Harold, 1868:49.--Hatch, 1953:59.--Henshaw, 1881:206.--LeConte, 1859b:287: 1863:2.--Leng, 1920:47.--Lindroth, 1961a:75.

Nebria diversa LeConte, 1863a:2 [as a replacement name for N. livida LeConte].--Bänninger, 1925:260.--Beaulne, 1914:29.--Blackwelder and Blackwelder, 1948:2.--Casey, 1913:47: 1924:19.--Fletcher, 1906:100.--Gemminger and Harold, 1868:49.--Hatch, 1939:121; 1953:58.--Henshaw, 1881:206; 1885:4.--Horn, 1870:99.--Kavanaugh, 1971:45.--Keen, 1895:166.--LeConte, 1878:474.--Leng, 1920:47.--Lindroth, 1961a:75: 1975:112.--Schaupp, 1878:45.--Spence and Bell, unpublished manuscript.--Van Dyke, 1919:9; 1926:9.--Wickham, 1903:50.

Nebria townsendi Casey, 1924:19. LECTOTYPE (designated by Lindroth, 1975:112), a female, in USNM, labelled: "Port Townsend, Wash."/ "Casey bequest 1925"/ "Type USNM 46846" [red label]/ "townsendi Csy."/ "Lectotype townsendi Csy. By C. H. Lindroth". TYPE LOCALITY.--Port Townsend, Jefferson County, Washington.--Csiki, 1927:389.--Hatch, 1953:59.--Leng and Mutchler, 1927:8.--Lindroth, 1961a:75; 1975:112.

Nevria diversa Guppy, 1947:51 [a misspelling].

3.435 The metallica lineage

This lineage is represented by 18 extant species, three of which (namely, N. mellyi Gebler, N. nitidula (Fabricius), and N. aenea Gebler) are restricted to central and/or eastern Asia. The remaining species are endemic to western North America. Included in this lineage are taxa previously assigned to Lindroth's (1961a) "metallica," "trifaria," "ingens," and "ovipennis" groups, or to subgenus Catonebria Shilenkov (1975a).

Diagnostic combination.--Adult members of this lineage can be recognized by the following combination of character states: frontal red spot(s) present; paraglossae indistinct, completely fused with ligula; pronotum moderately to markedly cordate, midlateral pronotal setae present; hind coxa with two or more pairs of setae at base; ventroapical margin of fourth hind tarsomere projected, lobate; second through fifth visible abdominal sterna each with one or more pairs of anterior paralateral setae (except for N. ovipennis members); male genitalia: median lobe with basal bulb quadrate, broadly open basally, mid-shaft axis bent less than 135°, apex (ventral aspect) pointed; dorsobasal piece present as thin collar on basal bulb; female genitalia: basal apodeme of eighth sternum moderately to deeply emarginate, lateral arm not, moderately, or markedly shortened; proctiger hemispheric, heavily sclerotized throughout; medial area of valvifer membranous; coxite with setae of ventral diagonal row setiform; stylus with setae of mediodorsal row setiform, mediodorsal row longitudinal; bursa copulatrix with or without sclerite in dorsal wall of spermathecal chamber.

3.4351 The ovipennis group

This species group is represented by six extant species, one of which (N. mellyi) is restricted to the Altai Mountains (central Asia) and vicinity (Fig. 419). The group includes taxa previously assigned to Lindroth's (1961a) "metallica" (in part only) and "ovipennis" (excluding N. paradisi) groups.

Diagnostic combination.--Adult members of this group can be recognized by the following combination of character states: overall size medium or small; tooth of epilobe of mentum minute; second visible abdominal sternum with a pair of paramedial setae or with sparsely scattered setae medially; male genitalia: right dorsal face of median lobe mid-shaft faintly indented or more or less deeply invaginated to form a pouch; right medial parameric sclerite absent; female genitalia: spermathecal chamber (except in N. carri members) with a single, short to long and slender accessory lobe in midline on dorsum, ventral to spermathecal duct insertion; spermathecal duct medium length, loosely and unevenly convoluted.

3.43511 The gebleri subgroup

3.435111 Nebria gebleri Dejean

Nebria gebleri gebleri Dejean

(Figures 18, 107, 275, 318, 333, 402)

Nebria gebleri Dejean, 1831:573. HOLOTYPE, a female, in MHNP, labelled: "Sitka"/ "Gebleri Eschs"/ "Ex Musaeo Mniszech"/ "Holotype Nebria gebleri Dejean det. D. H. Kavanaugh 1976" [red

label]. TYPE LOCALITY.--shores of Sitka Sound ["Norfolk Sound"], Baranof Island, Alaska.--Bänninger, 1925:258.--Beaulne, 1914:29.--Blackwelder and Blackwelder, 1948:2.--Casey, 1913:51.--Csiki, 1927:358.--Edwards, 1975:49.--Erwin and Ball, 1972:89.--Eschscholtz, 1833:23.--Fall, 1926:130.--Fletcher, 1904:95.--Gemminger and Harold, 1868:49.--Hamilton, 1894:7.--Hatch, 1939a:118 (in part); 1949:115; 1953:57.--Henshaw, 1885:4.--Horn, 1870:101.--Jeannel, 1937:4.--Kavanaugh and Martinko, 1972:147.--LeConte, 1860:10; 1863a:2; 1878:476.--Leng, 1920:46.--Lindroth, 1955b:12; 1961a:83 (in part).--Mank, 1934:74.--Melsheimer, 1853:11.--Schaupp, 1878:45.--Van Dyke, 1925:119 (in part); 1926:10 (in part).--Venables, 1913:268.

Nebria gebleri Eschscholtz [an improper assignment of authorship].--Dejean, 1831:573.--LeConte, 1860:10.--Mannerheim, 1843:188.--Motschulsky, 1850:73.

Nebria purpurata; auctorum (not LeConte).--Hatch, 1939a:119 (in part); 1953:58 (in part).--Lindroth, 1961a:86 (in part).--Mank, 1934:74.

Nebria melanaria Hatch, 1949:115. HOLOTYPE, a male, in UWBM, labelled: "G.N.P., Going-to-the-Sun Chalet, Aug. 26, 1939, M. H. Hatch"/ "Type ♂ Nebria melanaria M.H. Hatch 1948." TYPE LOCALITY.--Going-to-the-Sun Chalet, Glacier National Park, Montana.--Hatch, 1953:57.--Lindroth, 1961a:83.

Notes on nomenclature and types.--It is clear from his original description that the specimen of N. gebleri seen by Dejean was at that time complete. Lindroth (1955b:12), in his review of the

Dejean types, noted that the head and prothorax of the type specimen had been lost. In my study of the type, I now find it to be complete again. Unfortunately, the parts replaced are not only from a different specimen but from one representing a different species [=Nebria picicornis (Fabricius)]. There is no doubt, however, that the pterothorax and abdomen (through which the pin passes) are the remains of the valid type specimen.

I have not seen the specimen from Boulder County, Colorado, which Armin (1961:89) identified as N. gebleri. The record is most improbable; and the specimen could have been either a small specimen of N. pupurata LeC. or an unusually brilliant specimen of N. arkansana arkansana Casey.

Nebria gebleri cascadensis Kavanaugh, NEW SUBSPECIES

(Figures 108, 402)

Nebria gebleri; auctorum.--Hatch, 1939a:118 (in part).--Lindroth, 1961a:83 (in part).--Van Dyke, 1925:119 (in part); 1926:10 (in part).

Nebria gebleri cascadensis, new subspecies. HOLOTYPE, a male, in CAS, labelled: "U.S., Wash., Mt. Rainier N. P., Paradise R. above Narada Falls, 4580'-4800', 8Aug72 DHKavanaugh & HGoulet"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria gebleri cascadensis Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12502." Allotype (same data as holotype) also in CAS. 1688 paratypes (see Appendix B for locality data) are deposited in the

following collections: AMNH, ANSP, BFCa, CAS, CNC, CUIC, DHKa, DJLa, FMNH, ICCM, INHS, JSch, KSUC, KUSM, LRus, MCZ, MSU, NMDo, ODa, OSUC, OSUO, PURC, ROM, RTBe, SDSU, SJSC, UAFA, UASM, UCB, UCR, UIMI, UMMZ, USNM, UWBM, UWEM, WSU. TYPE LOCALITY.--Paradise River (above Narada Falls), Mount Rainier National Park, Washington.

Derivation of taxon name.-- This subspecies is named for the Cascade Mountain Range, in which populations of this taxon are widely distributed.

Nebria gebleri rathvoni LeConte, NEW STATUS

(Figures 109, 402)

Nebria rathvoni LeConte, 1853:400. HOLOTYPE, a male, in MCZ, labelled: "6465 ft. Lake Tahoe, Cal. May 24, 1879"/ [light green square]/ "79." [red-tipped label]/ "N. rathvoni LeC."/ "Type 7403" [red label]/ "Holotype Nebria rathvoni LeConte det. D. H. Kavanaugh 1976" [red label]. TYPE LOCALITY.--Sacramento, California; here amended to Truckee River (at Truckee), Nevada County, California. NEW STATUS.--Bänninger, 1925:258.--Casey, 1913:51.--Csiki, 1927:367.--Gemminger and Harold, 1868:52.--Henshaw, 1881:206; 1885:4.--Horn, 1870:103.--LeConte, 1860:10; 1863:2.--Leng, 1920:46.--Lindroth, 1961a:83; 1969d:1109.--Schaupp, 1878:45.--Van Dyke, 1925:122.

Nebria rathvonii LeConte, 1878:475 [a misspelling].

Notes on nomenclature and types.--There is little reason to doubt that the specimen recognized above as the holotype is actually

the specimen seen by LeConte, although the specimen locality and date ("1879") label would indicate otherwise. It is the only specimen found in the LeConte Collection (MCZ). Because data on the first label conflict with the date (1853) and data of LeConte's original description, and because the label itself appears to be relatively new, I suspect that it has been more recently added to the original type specimen.

LeConte's type locality, Sacramento, is well outside the habitat range of the subspecies; so the type was surely not collected there. Truckee, as the amended type locality, is about at the midpoint of the habitat and geographical ranges of the subspecies.

Nebria gebleri siskiyouensis Kavanaugh, NEW SUBSPECIES

(Figures 110, 402)

Nebria gebleri siskiyouensis, new subspecies. HOLOTYPE, a male, in CAS, labelled: "U.S.A., Calif., Trinity Co., Trinity Alps, S. F. Salmon R. at Big Flat Cmpgd., 1490m, 18July75 D. H. & B. A. Kavanaugh Stop #75-36"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria gebleri siskiyouensis Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12503." Allotype (same data as holotype) also in CAS. 33 paratypes (see Appendix B for locality) are deposited in the following collections: CAS, DHKa, FMNH, UASM, USNM. TYPE LOCALITY.--South Fork Salmon River (at Big Flat Campground), Trinity County, California.

Derivation of taxon name.--This subspecies is named for the Siskiyou Mountains, in which members of this taxon were first

collected.

Nebria gebleri strawberriensis Kavanaugh, NEW SUBSPECIES

(Figures 110A, 276, 334, 402)

Nebria gebleri strawberriensis, new subspecies. HOLOTYPE, a male, in CAS, labelled: "U.S., Ore., Grant Co., Blue Mts., Strawberry Cr., 5800' 28 May 1971, DHKavanaugh & EAMartinko"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria gebleri strawberriensis Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12501." Allotype (same data as holotype) also in CAS. 27 paratypes (see Appendix B for locality data) have been distributed among the following collections: CAS, DHKa, UASM, USNM. TYPE LOCALITY.--Strawberry Creek (1770m), Grant County, Oregon.

Derivation of taxon name.--This subspecies is named for the Strawberry Range of the Blue Mountains, to which it is apparently geographically restricted.

3.43512 The ovipennis subgroup

3.435121 The kincaidi infragroup

3.4351211 Nebria carri Kavanaugh, NEW SPECIES

(Figures 72, 111, 239, 277, 304, 405)

Nebria carri, new species. HOLOTYPE, a male, in CAS, labelled: "U.S.,Ida.,Blaine Co., Sawtooth Mts., Smoky Range, 2 mi. e. Dollarhide Summit, N. F. Warm Springs Creek, 7700'-7900',

21 Aug.73 DHKavanaugh Family"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria carri Kavanaugh, det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12498." Allotype (same data as holotype) also in CAS. 151 paratypes (see Appendix B for locality data) have been distributed among the following collections: BFCa, CAS, CNC, DHKa, FMNH, MCZ, UASM, USNM. TYPE LOCALITY.--Dollarhide Summit, Blaine County, Idaho.

Derivation of taxon name.--I take great pleasure in naming this species in honor of John and Betty Carr (Calgary, Alberta), who first collected specimens of same, and who have offered help and encouragement to me and other students in our respective studies.

3.4351212 Nebria kincaidi Schwarz

Nebria kincaidi kincaidi Schwarz

(Figures 73, 112, 149, 278, 335, 405)

Nebria kincaidi Schwarz, 1900:525. HOLOTYPE, a male, in USNM, labelled: "Farragut Bay, Alaska 6-5-99"/ "Harriman Expedition '99 T. Kincaid, Collector"/ "Nebria kincaidi Sz."/ "Type No. 56138 ♂ U.S.N.M." [red label]/ "Nebria kincaidi Schw. det. Schwarz Holotype." TYPE LOCALITY.--Farragut Bay, Alaska.--Bänninger, 1933:81; 1949:148.--Blackwelder, 1939:12.--Blackwelder and Blackwelder, 1948:2 (in part).--Csiki, 1927:369; 1933:630.--Darlington, 1930:104.--Erwin and Ball, 1972:85 (in part).--Hatch, 1939a:121 (in part); 1953:59.--Leng, 1920:46.--Lindroth, 1961a:88 (in part); 1975:113.--Perrault, 1972:62.--

Ueno, 1955:47.--Van Dyke, 1919:8 (in part); 1926:10.

Nebria columbiana Casey, 1913:48. LECTOTYPE (designated by Lindroth, 1975:113), a male, in USNM, labelled: "Inverness, B. Col."/ "Casey bequest 1925"/ "Type USNM 46848" [red label]/ "columbiana Csy."/ "Lectotype columbiana Csy. by C. H. Lindroth." TYPE LOCALITY.--Inverness, British Columbia.--Bänninger, 1925:265; 1933:81; 1949:148.--Beaulne, 1914:31.--Blackwelder, 1939:12.--Csiki, 1927:368; 1933:630.--Darlington, 1930:104.--Erwin and Ball, 1972:85.--Hatch, 1939a:121 (in part); 1953:59.--Leng, 1920:46.--Lindroth, 1961a:88; 1975:113.--Ueno, 1955:47.--Van Dyke, 1919:8 (in part); 1926:10 (in part).

Nebria paradisi; Clark (not Darlington), 1948:25.

Nebria kincaidi balli Kavanaugh, NEW SUBSPECIES

(Figures 150, 210, 405)

Nebria kincaidi; auctorum.--Blackwelder and Blackwelder, 1948:2 (in part).--Erwin and Ball, 1972:85 (in part).--Hatch, 1939:121 (in part).--Lindroth, 1961a:88 (in part).--Van Dyke, 1919:8 (in part).

Nebria columbiana; auctorum (not Casey).--Hatch, 1939a:121 (in part).--Van Dyke, 1919:8 (in part).

Nebria kincaidi balli, new subspecies. HOLOTYPE, a male, in CAS, labelled: "U.S., Wash., Mt. Rainier N. P., Paradise R. above Narada Falls, 4580'-4800', 8Aug72, DHKavanaugh & HGoulet"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria kincaidi balli Kavanaugh det. D. H. Kavanaugh 1976" [red label]/

"California Academy of Sciences Type No. 12505." Allotype (same data as holotype) also in CAS. 358 paratypes (see Appendix B for locality data) have been distributed among the following collections: AMNH, CAS, CNC, CUIC, DHKa, FMNH, LACM, LRus, MCZ, MSU, ODA, OSUO, SJSC, UASM, USNM, UWBM, WSU. TYPE LOCALITY.--Paradise River (above Narada Falls), Mount Rainier National Park, Washington.

Derivation of taxon name.--I take great pleasure in naming this subspecies in honor of George E. Ball, my mentor and friend.

3.435122 The ovipennis infragroup

3.4351221 Nebria spatulata Van Dyke

Nebria spatulata spatulata Van Dyke

(Figures 20, 34, 74, 403)

Nebria spatulata Van Dyke, 1925:119. HOLOTYPE, a female, in CAS labelled: "Franklin Lake, Sept. 8"/ "M"/ "Type ♀ Nebria spatulata Van Dyke" [red-tipped label]/ "California Academy of Sciences Type No. 1625." TYPE LOCALITY.--Franklin Lake, Tulare County, California.--Blackwelder, 1939:12.--Csiki, 1927:389; 1933:631.--Darlington, 1930:105.--Erwin and Ball, 1972:83 (in part).--Leng and Mutchler, 1933:10.--Lindroth, 1961a:87.

Nebria fusiformis Van Dyke, 1926:11. NOMEN NUDUM.

Nebria spatulata sierrae Kavanaugh, NEW SUBSPECIES

(Figures 35, 190, 279, 403)

Nebria spatulata; Erwin and Ball, 1972:83 (in part).

Nebria spatulata sierrae, new subspecies. HOLOTYPE, a male, in CAS labelled: "U.S.A., Calif., Mono Co., Sierra Nevada Mts., ne. face White Mt., along streams in cirque above Big Horn Lake, 3290m-3480m, 21 July74 D.H.Kavanaugh Collector"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria spatulata sierrae Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12516." Allotype (same data as holotype) also in CAS. 58 paratypes (see Appendix B for locality data) have been distributed among the following collections: CAS, DHKa, MCZ, RPPa, UASM, UCB, USNM. TYPE LOCALITY.--White Mountain (east slope) above Big Horn Lake, Mono County, California.

Derivation of taxon name.--This subspecies is named for the Sierra Nevada, to which its geographical range is restricted.

3.4351222 Nebria ovipennis LeConte

(Figures 19, 33, 75, 243, 246, 280, 295, 404)

Nebria ovipennis LeConte, 1878:477. HOLOTYPE, a male, in MCZ, labelled: "Sierra Nev. Cal."/ "Type 648" [red label]/ "N. ovipennis LeC."/ "Holotype Nebria ovipennis LeConte det. D. H. Kavanaugh 1976" [red label]. TYPE LOCALITY.--Sierra Nevada, California; here restricted to Mount Conness (east slope, above Greenstone Lake), Mono County, California.--Bänninger, 1925:264;

1949:148.--Casey, 1913:47.--Csiki, 1927:370.--Darlington, 1930:104.--Erwin and Ball, 1972:81.--Henshaw, 1881:206; 1885:4.--Leng, 1920:46.--Lindroth, 1961a:87.--Papp, 1978:126.--Schaupp, 1878:45.--Schwarz, 1900:525.--Van Dyke, 1919:8; 1925:120; 1926:10.

Notes on nomenclature and types. The type specimen of N. ovipennis is representative of populations north of Mount Lyell, Yosemite National Park but not south of that point in the Sierra Nevada. The restricted type locality is therefore both more precise and appropriate for the form represented by the type specimen.

3.4352 The metallica group

This species group is represented by four extant species--two (namely, N. aenea Gebler and N. nitidula (Fabricius))restricted to eastern and/or central Asia, and two restricted to western North America (Fig. 421). Lindroth (1961a) assigned the Nearctic species to his "metallica" group.

Diagnostic combination.--Adult members of this group can be recognized by the following combination of character states: overall size medium; tooth of epilobe of mentum moderately long; second visible abdominal sternum asetose medially; male genitalia: right dorsal face of median lobe mid-shaft unmodified, convex; right medial parameric sclerite present; female genitalia: spermathecal chamber without dorsal accessory lobe(s) in midline; spermathecal duct slightly shortened, sinusoidal (i.e. evenly, regularly convoluted [Fig. 350]).

The only character in the above list by which all members of this group can be distinguished from members of the following (trifaria) group is, unfortunately, overall size. I have no doubt that this group is both a monophyletic assemblage and the sister of the trifaria group. However, the distribution of character states among members of these two groups is so complex that even simple combinations of characters by which respective group members can be distinguished (=polythetic definitions) cannot be recognized at present. Such problems in definition can be expected occasionally when ranking is based on phylogenetic relationship rather than phenetic similarity. Review of data presented in Fig. 372 will demonstrate that recognition of this group as monophyletic and distinct from the trifaria group provides the simplest explanation for the cumulative distribution of states of all characters.

3.43521 The meanyi subgroup

3.435211 Nebria meanyi Van Dyke

Nebria meanyi meanyi Van Dyke

(Figures 113, 151, 167, 406)

Nebria meanyi Van Dyke, 1925:118. HOLOTYPE, a male, in CAS, labelled: "Nesqually Riv. below glacier"/Mt. Rainier Wash. IX-5-1912"/ "Coll. by Elliott"/ "Van Dyke Collection"/ "Type ♂ Nebria meanyi Van Dyke" [red-tipped label]/ "California Academy of Sciences Type No. 1623." Allotype (same data as holotype) also in CAS (California Academy of Sciences Type No. 1624). TYPE LOCALITY.--Nisqually River (below toe of Nisqually Glacier),

Mount Rainier National Park, Washington.--Bänninger, 1931:178.--Blackwelder, 1939:12.--Blackwelder and Blackwelder, 1948:2.--Csiki, 1927:388; 1933:631.--Hardy, 1927:C22.--Hatch, 1939a:118 (in part); 1953:57.--Leng and Mutchler, 1933:10.--Lindroth, 1961a:84.--Van Dyke, 1926:10.

Nebria meanyi lamarckensis Kavanaugh, NEW SUBSPECIES

(Figures 114, 152, 211, 406)

Nebria meanyi lamarckensis, new subspecies. HOLOTYPE, a male in CAS, labelled: "U.S., Calif., Inyo Co., Sierra Nevada, Lamarck Cr. above Upper Lamarck Lk., 10700'-11000' 6July71 DHKavanaugh & EAMartinko"/ "71-248" [orange label]/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria meanyi lamarckensis Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12507." Allotype (same data as holotype) also in CAS. 21 paratypes (see Appendix B for locality data) have been distributed among the following collections: CAS, DHKa, UASM, USNM. TYPE LOCALITY.--Lamarck Creek (above Upper Lamarck Lake), Inyo County, California.

Derivation of taxon name.--The name for this subspecies refers to the type locality, Lamarck Creek, which in turn refers to Jean Baptiste Pierre Antoine Lamarck, the noted French naturalist and pioneer evolutionist.

Nebria meanyi sylvatica Kavanaugh, NEW SUBSPECIES

(Figures 115, 406)

Nebria meanyi; Hatch, 1939a:118 (in part).

Nebria meanyi sylvatica, new subspecies. HOLOTYPE, a male, in CAS, labelled: "U.S.A., Wash., Olympic N. P., Olympic Mts., Boulder Cr., at Olympic Hot Springs, 610m, 15Aug.74 D. H. Kavanaugh"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria meanyi sylvatica Kavanaugh det. by D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12508." Allotype (same data as holotype) also in CAS. 177 paratypes (see Appendix B for locality data) are deposited in the following collections: CAS, CNC, CUIC, DHKa, ICCM, JSch, UASM, USNM, UWBM. TYPE LOCALITY.--Boulder Creek (at Olympic Hot Springs), Olympic National Park, Washington.

Derivation of taxon name.--This subspecies name is derived from the Latin word, sylvaticus, meaning "of the forest," and referring to the deep forest habitat occupied by taxon members.

3.43522 The metallica subgroup

3.435221 The metallica infragroup

3.4352211 Nebria metallica Fischer von Waldheim

(Figures 21, 116, 172, 222, 407)

Nebria metallica Fischer von Waldheim, 1821:71.

LECTOTYPE (here designated), a male, in ZMUM, labelled: "Unalaschka. F."/ "73 metallica Fisch."/ "Lectotype Nebria metallica Fischer v. Wald. designated by D. H. Kavanaugh 1977" [red label]. Two paralectotypes, one male and one female, are

in UMHF. TYPE LOCALITY.--Unalaska, Unalaska Island, Aleutian Islands, Alaska.--Bänninger, 1925:258; 1928:5; 1931:178; 1949:147.--Beaulne, 1914:29.--Blackwelder and Blackwelder, 1948:2.--Bush, 1914:59.--Casey, 1913:47.--Chaudoir, 1850:424.--Criddle, 1922:61.--Csiki, 1927:364; 1933:631.--Dejean, 1831:574.--Eschscholtz, 1823:100, 1833:23.--Fall, 1826:129.--Gemminger and Harold, 1868:51.--Hamilton, 1894:6.--Hatch, 1938: 145; 1939a:118.--Henshaw, 1885:4.--Horn, 1870:100.--Jeannel, 1937:4.--LeConte, 1860:10; 1863:2; 1878:476.--Leng, 1920:46.--Lindroth, 1961a:84; 1963b:123.--Melsheimer, 1853:11.--Perrault, 1972:62.--Schaupp, 1878:45.--Schwarz, 1900:524.--Van Dyke, 1924:4; 1925:117; 1926:9; 1943:20.--Wickham, 1893:223, 228.

Nebria metallica Eschscholtz [an improper assignment of authorship].--Dejean, 1826:229.--Eschscholtz, 1823:100.--Fischer von Waldheim, 1821:71; 1828:245.--Mannerheim, 1843:188.--Motschulsky, 1850:73; 1865:273.--Sturm, 1826:173.

Nebria pacifica Chaudoir, 1850:424. HOLOTYPE, a female, in MHNP, labelled: "Otahiti ???"/ "pacifica Chaudoir"/ "Muséum Paris 1952 Coll R. Oberthür"/ "Holotype Nebria pacifica Chaudoir det. D. H. Kavanaugh 1976" [red label]. TYPE LOCALITY.--Tahiti, Society Islands, French Polynesia [doubtful record].--Bänninger, 1931:178.--Csiki, 1927:389; 1933:631.--Gemminger and Harold, 1868:51.--Lindroth, 1961a:85.

Nebria metallica metallica Fischer von Waldheim.--Hatch, 1953:57.

Notes on nomenclature and types.--Fischer's description of metallica was based on material in his own and in Eschscholtz's

collections (Fischer, 1821:72). Specimens from the latter, identified as such, are now in UMHF as part of the Mannerheim collection. I have chosen the Fischer specimen as lectotype, the two Eschscholtz specimens as paralectotypes. A fourth specimen, in the Fischer collection (ZMUM), bears a "Kadjak" [Kodiak] label and is thus excluded from the type series.

3.4353 The trifaria group

This species group is represented by eight extant species, all endemic to western North America (Fig. 418). Species included in this group were previously assigned to Lindroth's (1961a) "metallica," "ingens," and "trifaria" groups.

Diagnostic combination.--Adult members of this group can be recognized by the following combination of character states: overall size large or very large; tooth of epilobe of mentum moderately to very long; second visible abdominal sternum asetose medially; male genitalia: right dorsal face of median lobe mid-shaft unmodified, convex; right medial parameric sclerite present (except in trifaria infragroup members); female genitalia: spermathecal chamber without dorsal accessory lobe(s) in midline; spermathecal duct slightly shortened, sinusoidal (i.e. evenly, regularly convoluted [Fig. 350]). Refer to comments in section 3.4352 concerning the phenetic distinction between this and the metallica species group.

3.43531 The *ingens* subgroup

3.435311 *Nebria ingens* Horn

Nebria ingens ingens Horn

(Figures 22, 43, 52, 63, 76, 117, 154, 242, 245, 408)

Nebria ingens Horn, 1870:98. LECTOTYPE (here designated), a female, in MCZ, labelled: "Cala."/ "TypeNo. 1026" [red label]/ "Nebria ingens Horn"/ "Lectotype Nebria ingens Horn designated by D. H. Kavanaugh 1976" [red label]. One female paralectotype, also in MCZ, labelled: "Cala."/ "Type 8127" [red label]/ "N. ingens Horn." TYPE LOCALITY.--Sierra Nevada Mountains east of Visalia, California; here restricted to Franklin Lake, Tulare County, California.--Casey, 1913:47.--Csiki, 1927:369.--Darlington, 1930:105.--Erwin and Ball, 1972:80.--Henshaw, 1885:4.--LeConte, 1878:474.--Leng, 1920:46.--Lindroth, 1961a:87 (in part).--Schaupp, 1878:45.--Schwarz, 1900:525.--Van Dyke, 1919:8; 1925:116; 1926:11; 1953:102.

Nebria raveni Van Dyke, 1953:102. HOLOTYPE, a female, in CAS, labelled: "stream from snow runoff, Mt. Darwin, 13600ft."/ Fresno Co. Calif. VIII-9-1952, Coll. by P. Raven"/ "Holotype ♀ Nebria raveni Van Dyke" [red-tipped label]/ "California Academy of Sciences Type No. 8163." TYPE LOCALITY.--Mount Darwin (4150m), Fresno County, California.--Lindroth, 1961a:87.

Notes on nomenclature and types.--In his original description, Horn mentioned two specimens, a male and a female. The MCZ specimen seen by Lindroth (his "allotype," 1961:87) is a female. The other

specimen, from the Horn Collection (formerly at ANSP, now at MCZ), is also a female; so Horn did not actually see a male. The lectotype chosen for N. ingens is the specimen from the Horn Collection.

Nebria ingens riversi Van Dyke, NEW STATUS

(Figures 130, 408)

Nebria riversi Van Dyke, 1925:115. HOLOTYPE, a male, in CAS, labelled: "Mt. Lyell, Yosemite Pk. Cal. VII-13-1921"/ "Van Dyke Collection"/ "Type ♂ Nebria riversi Van Dyke" [red-tipped label]/ "California Academy of Sciences Type No. 1619." Allotype (same locality data as holotype) also in CAS (Type No. 1620). TYPE LOCALITY.--Mount Lyell (3440m), Yosemite National Park, California.--Allen, 1967:82.--Blackwelder, 1939:12.--Csiki, 1927:389; 1933:631.--Darlington, 1930:105.--Döbler, 1975:138.--Leng and Mutchler, 1933:10.--Lindroth, 1961a:87.--Van Dyke, 1926, 1926:11; 1953:102.

Nebria ingens; Lindroth, 1961a:87 (in part).

3.435312 Nebria vandykei Bänninger

Nebria vandykei vandykei Bänninger

(Figures 36, 55, 160, 288, 408)

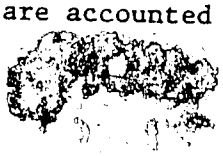
Nebria trifaria; Van Dyke (not LeConte), 1919:8 (in part); 1925:116 (in part); 1926:10 (in part).

Nebria vandykei Bänninger, 1928:5. LECTOTYPE (here designated), a male, in ETHZ, labelled: "Paradise Val. Mt. Rainier Wash. VII-18-1920"/ "Coll. by E. C. Van Dyke"/ "1. Fühl.gld. as.

1 + 2 B."/ "FG. Basig. bil. OP!"/ "Nebria trifaria LeC."/ "Type Nebria Van Dykei 10.1927" [red-trimmed label]/ "Lectotype Nebria vandykei Bänninger designated by D. H. Kavanaugh 1976" [red label]. Two paralectotypes also in ETHZ. TYPE LOCALITY.--Paradise Valley, Mount Rainier National Park, Washington.--Blackwelder and Blackwelder, 1948:2.--Csiki, 1933:630.--Darlington, 1931:24.--Erwin and Ball, 1972:87 (in part).--Hatch, 1939a:118 (in part); 1949:116.--Leng and Mutchler, 1933:11.--Lindroth, 1961a:86 (in part).--Mann, 1978:20.

Nebria trifaria vandykei Bänninger.--Hatch, 1953:56 (in part).

Notes on nomenclature and types.--In his original description of N. vandykei, Bänninger listed four specimens in the type series; but only three of these are accounted for at present (W. Sauter, personal communication).



Nebria vandykei wyeast Kavanaugh, NEW SUBSPECIES

(Figures 37, 218, 258-259, 408)

Nebria vandykei; auctorum.--Erwin and Ball, 1972:87 (in part).--Hatch, 1939a:118 (in part).--Lindroth, 1961a:86 (in part).

Nebria trifaria vandykei Bänninger.--Hatch, 1953:56 (in part).

Nebria vandykei wyeast, new subspecies. HOLOTYPE, a male, in CAS, labelled: "U.S.A., Ore., Clackamas Co., Cascade Range, s. slope Mt. Hood, headwaters Salmon R. near Timberline Lodge, 1830m-1950m, 3Aug.74 D. H. Kavanaugh"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria vandykei wyeast Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California

Academy of Sciences Type No. 12517." Allotype (same data as holotype) also in CAS. 186 paratypes (see Appendix B for locality data) are deposited in the following collections: CAS, DHKa, MCZ, OSUO, UASM, USNM, UWBM. TYPE LOCALITY.--Salmon River headwaters, Mount Hood, Clackamas County, Oregon.

Derivation of taxon name.--For this subspecies, I choose the name given to Mount Hood by local native peoples--Wy'east, which means "The Mountain."

3.43532 The schwarzi subgroup

3.435321 Nebria piperi Van Dyke

(Figures 118, 125A, 144, 153, 204, 208, 317, 350, 364, 409)

Nebria piperi Van Dyke, 1925:117. HOLOTYPE, a male, in CAS, labelled: "Nesqually Riv. below glacier"/ "Mt. Rainier Wash. IX-5-1912"/ "Coll. by Elliott"/ "Van Dyke Collection"/ "Type ♂ Nebria piperi Van Dyke" [red-tipped label]/ "California Academy of Sciences Type No. 1621." Allotype, also in CAS, from Mount Baker, Washington (California Academy of Sciences Type No. 1622). TYPE LOCALITY.--Nisqually River (below toe of Nisqually Glacier), Mount Rainier National Park, Washington.--Bänninger, 1928:5; 1931:178.--Blackwelder, 1939:12.--Blackwelder and Blackwelder, 1948:2.--Criddle, 1926:96.--Csiki, 1927:289; 1933:631.--Hatch, 1939a:119.--Leng and Mutchler, 1933:10.--Lindroth, 1961a:85.--Perrault, 1972:62.--Van Dyke, 1926:10.

Nebria metallica piperi Van Dyke.--Hatch, 1953:57.

3.435322 Nebria schwarzi Van Dyke

Nebria schwarzi schwarzi Van Dyke

(Figures 119, 161, 168, 205, 226, 409)

Nebria schwarzi Van Dyke, 1925:116. HOLOTYPE, a male, in USNM, labelled: "Banff Sp 10.6 Alb."/ "Coll Hubbard & Schwarz"/ "U.S.N.M. Type No. 28174" [red label]/ "Type Nebria schwarzi Van Dyke" [red-tipped label]. TYPE LOCALITY.--Banff, Banff National Park, Alberta.--Bänninger, 1928:5; 1931:178.--Blackwelder, 1939:12.--Blackwelder and Blackwelder, 1948:2.--Criddle, 1926:96.--Csiki, 1927:389; 1934:681.--Hatch, 1939:119.--Leng and Mutchler, 1933:10.--Lindroth, 1961a:86.--Van Dyke, 1926:10.

Nebria metallica schwarzi Van Dyke.--Hatch, 1953:57

Nebria schwarzi beverlianna Kavanaugh, NEW SUBSPECIES

(Figures 120, 227, 296, 409)

Nebria schwarzi beverlianna, new subspecies, HOLOTYPE, a male, in CAS, labelled: "U.S., Wyo., Sublette Co., Gros Ventre Mts., Hwy. 187/189, 8 mi. nw. Bondurant, Hoback R., 6900', 1-2 August 73 DHKavanaugh Family"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria schwarzi beverlianna Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12515." Allotype (same data as holotype) also in CAS. 253 paratypes (see Appendix B for locality data) have been distributed among the following collections: CAS, CNC,

DHKa, FMNH, HGou, MCZ, UASM, USNM. TYPE LOCALITY.--Hoback River (8 miles northwest of Bondurant), Sublette County, Wyoming.

Derivation of taxon name.--I take great pleasure in naming this subspecies in honor of my wife, Beverly Ann Kavanaugh.

3.43533 The trifaria subgroup

3.435331 The purpurata infragroup

3.4353311 Nebria purpurata LeConte

(Figures 42, 81 120A, 131, 187, 241, 244, 358, 49)

Nebria purpurata LeConte, 1878:477. HOLOTYPE, a male, in MCZ, labelled: "9-10,000 ft. Leavenworth Vall. ab. Georgetown, Col. July 14, 17, 1877"/ "Type 649" [red label]/ "N. purpurata LeC."/ "Holotype Nebria purpurata LeConte det. D. H. Kavanaugh 1976" [red label]. TYPE LOCALITY.--Leavenworth Valley (2740m-3050m), Clear Creek County, Colorado.--Armin, 1963:93.--Bänninger, 1925:250.--Beaulne, 1914:29 (cannot refer to this species, but otherwise uninterpretable).--Blackwelder and Blackwelder, 1948:2.--Casey, 1913:49.--Csiki, 1927:367.--Erwin and Ball, 1972:89.--Fall and Cockerell, 1907:156.--Hatch, 1939:119; 1953:58 (in part).--Haubold, 1951:704.--Henshaw, 1881:206; 1885:4.--Kavanaugh and Martinko, 1972:147.--LeConte, 1879:500.--Leng, 1920:46.--Lindroth, 1961a:86 (in part); 1975:112.--Schaupp, 1878:45.--Van Dyke, 1925:116; 1926:10 1943:20.--Wickham, 1902:231.

Nebria mobilis Casey, 1913:50. LECTOTYPE (designated by Lindroth,

1975:112), a female, in USNM, labelled: "Col."/ "Casey bequest 1925"/ "Type USNM 46850" [red label]/ "mobilis Csy."/ "Lectotype mobilis Csy. By C. H. Lindroth." TYPE LOCALITY.--Colorado.--Csiki, 1927:364.--Erwin and Ball, 1972:89.--Leng, 1920:46.--Lindroth, 1961a:86; 1975:112.

3.435332 The trifaria infragroup

3.4353321 Nebria trifaria LeConte

Nebria trifaria trifaria LeConte

(Figures 38, 77, 121, 173, 281, 337, 411)

Nebria trifaria LeConte, 1878:478. LECTOTYPE (here designated), a male, in MCZ, labelled: "9500 ft. Amer. Fork Canon Utah, Aug. 2-3, 1877"/ "Type 651" [red label]/ "N. trifaria LeC."/ "Lectotype Nebria trifaria LeConte designated by D. H. Kavanaugh 1976" [red label]. TYPE LOCALITY.--American Fork Canyon (2900m), Utah County, Utah.--Armin, 1963:94.--Bänninger, 1925:258; 1928:5.--Blackwelder and Blackwelder, 1948:2.--Blake, 1945:237.--Casey, 1913:48; 1924:21.--Csiki, 1927:367.--Hatch, 1939a:118; 1949:116.--Henshaw, 1881:206; 1885:4.--Lavigne, 1977:46.--Leng, 1920:46.--Lindroth, 1961a:86.--Schaupp, 1878:45.--Van Dyke, 1919:8 (in part); 1925:116 (in part); 1926:10 (in part).--Wickham, 1902:232 (in part).

Nebria trifaria trifaria LeConte.--Erwin and Ball, 1972:93.--Hatch, 1953:57.

Nebria trifaria coloradensis Van Dyke.--Erwin and Ball, 1972:95 (in

part).

Nebria trifaria tetonensis Erwin and Ball, 1972:95. HOLOTYPE, a male, in USNM, labelled: "Teton Natl. Park, Wyo. 22 July 60"/ "S. Fk. Cascade Cyn. --10000 ft. snow --10:30 pm"/ "Alice Edwards J. G. Edwards"/ "6267"/ "2197"/ "♂ apex drawn Erwin 1970"/ "Holotype Nebria trifaria tetonensis Erwin and Ball USNM 71975" [red label]. Allotype (same data as holotype) also in USNM. TYPE LOCALITY.--South Fork Cascade Canyon (3050m), Grand Teton National Park, Wyoming. NEW SYNONYMY.

Nebria trifaria catenata Casey

(Figures 39, 78, 198, 282, 338, 411)

Nebria trifaria; Wickham, 1902:232 (in part).

Nebria catenata Casey, 1913:49. LECTOTYPE (designated by Lindroth, 1975:112), a female, in USNM, labelled: "Col"/ "Casey bequest 1925"/ "Type USNM 46849" [red label]/ "catenata Csy."/ "Lectotype catenata Csy. By C. H. Lindroth." TYPE LOCALITY.--Colorado; restricted by Erwin and Ball (1972:97) to San Juan Mountains, and here further restricted to Wolf Creek Pass, Mineral County, Colorado.--Csiki, 1927:357.--Leng, 1920:46.--Lindroth, 1961a:84 (in part).

Nebria trifaria catenata Casey.--Erwin and Ball, 1972:97.--Lindroth, 1975:112.

Nebria trifaria utahensis Kavanaugh, NEW SUBSPECIES

(Figures 121A, 196, 283, 339, 4..)

Nebria trifaria utahensis, new subspecies. HOLOTYPE, a male, in CNC, labelled: "Lonesome Beaver, 7500', Henry Mts., Utah VII 20-22, 68 H. F. Howden"/ "Holotype Nebria trifaria utahensis Kavanaugh det. D. H. Kavanaugh 1976" [red label]. Allotype (same data as holotype) also in CNC. 13 paratypes (see Appendix B for locality data) deposited in the following collections: CAS, CNC. TYPE LOCALITY.--Lonesome Beaver, Henry Mountains, Garfield County, Utah.

Derivation of taxon name.--This subspecies is named for the State of Utah, in which its geographical range is restricted.

3.4353322 Nebria coloradensis Van Dyke

(Figures 40, 122, 184, 336, 4]0)

Nebria coloradensis Van Dyke, 1943:19. HOLOTYPE, a male, in CAS, labelled: "Twin Lakes Col. Lake Co. VI-26-35"/ "Van Dyke Collection"/ "Holotype No. 5298 Nebria coloradensis Van Dyke" [red-tipped label]/ "California Academy of Sciences Type No. 5298." TYPE LOCALITY.--Twin Lakes, Lake County, Colorado.--Blackwelder and Blackwelder, 1948:2.--Lindroth, 1961a:84.

Nebria catenata; Lindroth (not Casey), 1961a:84 (in part).

Nebria trifaria coloradensis Van Dyke.--Erwin and Ball, 1972:96 (in part).

3.4353323 Nebria piute Erwin and Ball, NEW STATUS

(Figures 41, 285, 336A, 410)

Nebria trifaria piute Erwin and Ball, 1972:95. HOLOTYPE, a male, in USNM, labelled: "Utah. Piute Co., LaBaron L., Circleville Mt., 15.9 mi. w. Junction 9700', Sept/ 17, 1967"/ "Ball, T. L. Erwin, R. E. Leech Collectors"/ "Holotype Nebria trifaria piute Erwin and Ball USNM 71976" [red label]. Allotype (same data as holotype) also in USNM). TYPE LOCALITY.--LaBaron Lake, Circleville Mountain, Beaver County, Utah. NEW STATUS.

4.0 ANALYSES OF THE NEARCTIC NEBRIA FAUNA

In this section, data from comparative morphological, chorological, and natural history studies presented above are used in phylogenetic and zoogeographic analyses of the Nearctic Nebria fauna. The classification provided in section 3.33 is based on these analyses.

4.1 Phylogeny

4.11 Introduction

I here present a phylogenetic classification of characters, a cladistic analysis of Nearctic Nebria taxa, and a cladogram which represents hypothetically, phylogenetic relationships among these taxa. As noted by Griffiths (1974a) and Kavanaugh (in press C), the primary goal of cladistic analysis is systematization (see definition and further discussion above, section 3.31) rather than classification. In my view, the relationship between systematization and classification is sequential--the latter follows from the former. The rationale behind and justification for use of cladistic techniques for recognition of systems and elucidation of relationships among their elements (i.e. systematization) has been explored in depth by Brundin (1972), Griffiths (1974a and 1974b), and Whitehead (1972). Because I agree with both presentations and conclusions of these authors, I here omit further theoretical review and simply present the procedures and assumptions used in the study of Nebria species.

Taxa as systems and as elements.--As noted in section 3.31, species are, necessarily, elements of natural systems produced by speciational processes of evolution. Correspondence between taxonomic groups (e.g. species groups) and natural systems is achieved only if a criterion of strict monophyly (sensu Hennig, 1966; ="holophyly" of Ashlock, 1974) is applied in recognition of the former. Monophyletic groups are defined as those which include a stem species (common ancestor) and only and all its descendants. Groups which include species with separate ancestry (i.e. polyphyletic groups) or from which one or more descendant species have been excluded (i.e. paraphyletic groups) are not systems at all or only incomplete ones, respectively. The objective of the cladistic analysis presented here was, therefore, recognition of strictly monophyletic groups (systems) of successively greater inclusiveness, from single species (element) pairs to an ultimate group comprising all members of the Nearctic fauna.

Degree of phylogenetic relationship is proportional to relative recency of common ancestry. For example, the phylogenetic relationship between two species, A and B (Fig. 367), is greater than between either and a third species, C, if and only if A and B have a common ancestor, D, not also shared with C. Taxa which share closest phylogenetic relationship are called "sister" taxa. As suggested by Hennig (1966), only possession of synapotypic (i.e. shared, derived) character states is evidence in support of close phylogenetic relationship, sister group status, or the monophyly of groups of any size. In the above example, evidence that species A and B are in fact closest relatives is obtained if their members demonstrate one or more synapotypic character states not also shared with members of species

C. The procedures outlined below are therefore directed toward recognition of sister taxa through a search for synapotypy.

Polarity and sequence of transformation series.--Recognition of synapotypy requires an existing classification of the states of a character as elements of a transformation series (i.e. an evolutionary sequence of homologous character states) (Hennig, 1966) arranged from most plesiotypic (i.e. primitive) to most apotypic (i.e. derived). Determination of this polarity is the critical phase of cladistic analysis; and hypotheses generated from these analyses are valid only to the extent that hypotheses on polarity and sequence of individual characters are accurate (i.e. reflect evolutionary history of the characters). If, in fact, we could know (with certainty) the polarity of series, reconstruction of phylogenetic relationships would be relatively simple. Because this certainty is unattainable, we must rely on criteria for and tests of hypotheses on polarity. Ball (1975), Ekis (1977), Platnick (1977), and Ross (1974) have recently reviewed these criteria and discussed their own methods for practical use of same. Here summarize my use of these criteria in order of their overall usefulness.

1. Ex-group comparisons. For a given character, a survey was made of the distribution of its states among members of closely and successively more distantly related groups. If a state represented among members of one or more Nebria species is also represented among members of other groups, that state was judged (in the absence of contradictory evidence) to be plesiotypic. The assumption made was that widespread occurrence results from common ancestry and not from

independent acquisition (i.e. convergence). For example, members of some Nearctic Nebria species and those of all related genera lack frontal pale spots. Therefore, presence of these spots is probably apotypic, their absence plesiotypic.

The character chosen for the above example is a two-state character; and, as such, polarity of its transformation series is determined simply by recognition of either the plesiotypic or the apotypic state. Many characters, however, are represented by many states--i.e. are multi-state characters--and determination of the pleisiotypic state is not of itself sufficient for determination of polarity and sequence of the entire transformation series. In analysing multi-state characters, an attempt was made to interpret states as elements of a "graded series" (Ball, 1975; the "morphocline" concept of Maslin, 1952), from most pleisiotypic (determined just as for two-state characters) to most apotypic (often recognized as the opposite extreme among states). Judgments on the relative apotypy of different intermediate states were aided by reference to ex-group comparisons and other criteria discussed below.

The evolution of some multi-state characters appears to have been extremely complex. Some transformation series exhibit multiple branches (and even secondary branching), reversal, and convergence, as interpreted through correlation with other transformation series (see below). For example, hypothetical reconstruction of the transformation series for shape of the preapical-shaft of the male median lobe (lateral aspect) is illustrated in Fig. 368 (character no. 116). The transformation is multiply-branched, and includes reversal steps (e.g from state

116A[1] to state 116B, reversing the step from state 116[1] to state 116A[1]). Most workers tend not to consider these complex transformations in their cladistic analyses. However, I have chosen to use these also because (1) they form a significant percentage of the total number of characters studied; (2) they do in fact contribute to the anaylsis of relationships among taxa; and (3) they provide an appropriate picture of the complexity of evolutionary change--a picture which is normally obscured when only simple characters (usually a minority) are analysed.

Results of ex-group comparisons provide, in general, the most useful criterion for determination of polarity in transformation series. This procedure requires two conditions, however, namely: (1) some previous (or at least independent) indication of relationships with and among other groups; and (2) representative material (specimens and other data) for comparative study. Fortunately, I have had access to abundant and diverse comparative material (see Appendix C for a list of taxa represented in samples studied), both at the University of Alberta and the California Academy of Sciences. Phylogenetic relationships among nebriine genera as well as those between tribe Nebriini and related "tribes" (i.e. Notiophilini and Opisthiini) had not been analysed previously. I therefore attempted to explore [illegible]ionships and thereby provide a tentative systematiza[illegible]e[illegible]riine genera and their close relatives. This systematizati[illegible]o serve as the framework for evaluation of data from ex-group comparisons. To this end, I expanded my comparative study to include representatives of most groups thought to be direct descendants of the primitive caraboid stock (see Appendix C),

including "hydradephagan" groups. Part of the systematization of these groups which resulted from cladistic analysis is presented in Fig. 369; and it was used as the basis for ex-group comparisons in this study. I reserve discussion of intergeneric and more inclusive relationships for a subsequent paper dealing expressly with this topic. I note here only that hypothetical relationships inferred represent a choice among different but almost equally plausible (and "parsimonious" (see below)) sets of relationships (see also comments on relationships of the virescens lineage, section 4.13).

2. Character correlations. According to Ekis (1977) and Hennig (1966), transformation series the polarity of which have been determined with some degree of confidence, can be used to infer polarity in transformations of other characters in which evolutionary sequence is less easily inferred. I found this criterion very useful, especially in working with complex, multi-state characters. However, its use requires further explanation than that provided by the above authors because, in and of themselves, transformations of different characters (except perhaps two or more characters of a single, integrated, adaptive complex) are not necessarily correlated. It is only through reference to a set of tentative hypotheses of relationship (as suggested by analyses of distributions of character states in transformations with established polarity) that polarity in other series can be inferred. For example, if members of species A and B share apotypic states of one or more characters for which transformation polarities are confidently established, a tentative hypothesis of relationship with species C (members of which exhibit the plesiotypic state(s) of this(these) character(s)) is as

illustrated in Fig. 370A. If the distributions of states of another character is such that A and C (but not B) share a given state, and we accept the hypothetical relationships noted above, then it follows that either (1) the shared state is plesiotypic and the apotypic state is restricted to members of species B (Fig. 370C), or (2) the shared state is apotypic and its occurrence in A and C is due to convergence (Fig. 370B). In the absence of other evidence or criteria, acceptance of the least complex (most "parsimonious"; see Platnick, 1975) explanation (i.e. (1) above) is preferred. The third option here is to reject the original hypotheses of relationship, based on evidence from this new character.

3. Group trends. Ball (1975) noted that within groups, certain characters "appear to follow the same evolutionary development [transformation] in many independent lineages". Members of Nebria species, for example, which inhabit highest montane habitats tend (without regard to their phylogenetic relationships) to have hindwings reduced, elytra shortened and with reduced humeral angles, metasterna shortened, and appendages lengthened. Members of species inhabiting extreme lowland habitats, especially in relatively arid areas, tend to have pale appendages and, in some instances, pale bodies. In general, repeated, independent transformations of characters in which such group trends appear were correlated with one another; and their respective polarities were thereby determined simultaneously.

4. Correlation with adaptive significance. Character states (of structural and other characters) evidently correlated with specialized (presumably apotypic) behavior could themselves, on this basis, be

interpreted as apotypic. For example, unique structural characteristics of the tarsi of N. ingens adults can be correlated with their observed ability to walk over exposed stone surfaces underwater. This behavior and its structural correlates were both judged to be apotypic. Such clear relationships between structure and function were infrequently recognized among Nearctic Nebria; and this criterion was, therefore, used in few instances only. Mouthparts and genitalia collectively form functional/adaptive complexes, characters of which are numerous and, presumably, not fully independent of each other. It should therefore be possible to determine polarity of transformations in several of these characters simultaneously if one or only a few can be correlated with apotypic function (e.g. feeding or mating behavior).

5. In-group comparisons. In some instances, the evolution of characters (and resultant diversity of character states) among members of a single group is so great that ex-group comparisons and other criteria are of little or no use in determination of sequence and/or polarity in transformations. In analyses of such characters, I resorted to so-called "in-group" comparisons (Ball, 1975; Ross, 1974). Procedure was as follows: (1) determine the character state exhibited by members of species judged to be (on other grounds) the most plesiotypic ("primitive"); (2) accept this character state as plesiotypic; and (3) determine transformation sequence for the other states by correlation with other transformations (see above). This criterion is, admittedly, weak and fraught with opportunities for misinterpretation. Nonetheless, used as a last resort, and then only with due caution, it can help resolve some questions. For example,

transformation series of several characters of the male median lobe were determined using this criterion. A major difficulty was encountered, however. In males of N virescens, the species judged to be most "primitive", the median lobe exhibits several character states judged to be apotypic (based on ex-group comparisons). I then considered as plesiotypic states represented in members of the species judged to be next most "primitive", namely members of the gyllenhali lineage; and transformation series which correlated well with other series were obtained. The major problem with this criterion is evident from the above, namely, that members of taxa judged to be "primitive" based on some or even most characters, may be expected to exhibit both plesiotypic and apotypic states for different characters (including the character of interest).

I did not find Hennig's (1966) criterion of "chorological progression" useful in analysis of characters for Nebria species and, therefore, will not consider it here.

The transformations of some characters studied could not be determined using any of the above criteria. In such instances, distributions of character states among Nearctic taxa were either without apparent pattern or otherwise too complex to interpret. These characters could not be used in the cladistic analysis of taxa. Analysis of many other characters required use of several criteria, in combinations, in order to recognize transformation patterns.

Procedure for cladistic analysis.--After transformation series of characters had been determined, distributions of their apotypic states among members of Nearctic species were studied. I consider the

biological species (Mayr, 1969) to be the basic phylogenetic unit [the term 'phylogenetic relationship', by definition, cannot be applied logically to infraspecific entities]. Consequently, a single state for each character was chosen to represent members of all populations (including those of different subspecies). Except when evidently inappropriate, the state of choice was, in each instance, the most plesiotypic state represented among species members. The effect, if any, of this choice was to reduce the number of synapotypies recognized for any two species, specifically by eliminating those synapotypies which are not universal among members of both species. I suggest that, consequently, the significance of those synapotypies finally recognized was increased.

The next step was recognition of species pairs (sister species) based on the criterion of synapotypy. By applying this criterion repeatedly, successively more inclusive groups were recognized. Unfortunately, this procedure was greatly complicated by a high level of discordance (incongruence) in patterns of synapotypy for different characters among species and groups. In such instances, I resorted to three additional steps in an attempt to reduce discordance (or at least recognize and evaluate its source). First I reassessed judgments on polarities of particular transformation series involved in discordant patterns. In some instances, I was able to resequence series or reverse their polarities through correlations with other transformations (criterion "2" above) as suggested by new tentative hypotheses on relationship. Residual discordance was then examined by plotting the distributions of character states of all characters studied on different cladograms, each reflecting a specific set of

relationships suggested by one of the discordant patterns of synapotypy. For each cladogram, I calculated the total number of 'extra evolutionary steps' (i.e. instances of convergence and reversal) required to account for the distributions of character states for all characters over the set of relationships proposed. Cladograms were then compared directly. Based on the assumption that divergence is more common than convergence or reversal in the evolution of characters, and on the contention that least complex explanations for observed phenomena are to be preferred in general, cladograms requiring the fewest extra evolutionary steps were selected as preferred hypotheses of phylogenetic relationship.

In few instances (for example, in reconstruction of relationships among members of the ovipennis species group), two or more cladograms were found to be almost equally parsimonious. At this point, I again focused attention on the discordant characters and reinterpreted these according to the character weighting scheme proposed by Hecht (1976) and Hecht and Edwards (1977). By ignoring discordance in "low weight" characters and giving emphasis to that in "high weight" characters (i.e. those referable to Hecht's weighting groups "IV" and "V"), I was able to evaluate the relative significance of discordance in each cladogram and, ultimately, choose the one with least significant discordance.

4.12 Cladistic analysis

A total of 318 structural and natural history characters were analysed (through procedures outlined above), 171 of which were then used in a cladistic analysis of Nearctic species and their relatives.

Remaining characters include (1) those in which transformations could not be interpreted (see above), (2) those that are represented among Nebria members by single states judged to be plesiotypic (i.e. symplesiotypic for genus Nebria), and (3) those that are represented by single apotypic states in members of single species (i.e. autapotypic). As noted in section 3.33, all Palaearctic taxa presumed to be closely related to Nearctic taxa were also analyzed. Results of studies to determine transformation series of characters are presented in Tables 14 and 15. The former lists character states judged to be symplesiotypic among all Nebria members. The latter lists all other characters and presents for each the sequence and relative apotypy of character states and the criterion(-a) used for determination of polarity and sequence.

The distributions of character states among Nearctic Nebria and their Palaearctic relatives are summarized and illustrated in Fig. 372. Refer to the figure legend for an explanation of notation, symbols, and format used (modified from Griffiths, 1972).

Table 14. Character states plesiotypic[1] for Nearctic *Nebria* species.

Character	Character state
Supraorbital setae	one pair (posterior pair)
Vertex macrosculpture	smooth
Occiput shape	evenly broad, not abruptly constricted (i.e. "necked")
Setae on antennal scape	one
Setae on clypeus	one pair (mediolaterally)
Setae on labrum	three pair, across apical margin
Apex right mandible	not hooked
Mandibular scrobe	well-developed
Setae in mandibular scrobe	one present
Form maxilla	ventrolaterally flat, without spiniform processes
Form ligula	longitudinally carinate in midline
Setae on ligula	one pair (apicomedially)
Labial palpus	penultimate and terminal palpomeres approximately equal in length
Mentum M_1 setae	one pair, at base o ntum tooth
Mentum M_4 setae	absent
Form gula	thout spiniform processes or ridge
Base of pronotum	without margination
Setae on prosternal intercoxal process	none

Table 14. (continued)

Closure anterior coxal cavity	open posteriorly
Perforation anterior coxal cavity	uniperforate
Separation anterior coxal cavities	confluent
Elytral vestiture	without pubescence
Elytral internal plica	simple, keel-like, extended to but not across epipleuron
Scutellar striole	short, medial to first complete stria, not joined with same basally
No. of complete striae	eight
Macrosculpture elytral intervals	smooth (excluding catenations)
Hindwing: marginal cell between $P+Cu_2$ and E_1 veins	without sclerotized microtrichial field
Metepimeron	apparently absent
Closure middle coxal cavity	disjunct
Separation middle coxal cavities	confluent
Closure hind coxal cavity	conjunct
Separation hind coxal cavities	confluent
Setae on front coxa	none

Table 14. (continued)

Setae on front trochanter	one (ventroapically)
Setae on middle trochanter	one (ventroapically)
Setae on hind trochanter	none
Front tibial antenna cleaner	simple, sulcate
Front tibial spur	obliquely isochaetous
Male hind tarsomeres	without ventral pads of setae
Abdominal sterna	dorsolaterally carinate, but not otherwise modified for elytra lock function
Basal piece (male genitalia)	fused with base of median lobe
Internal sac median lobe	present, eversible
Setae on parameres	both asetose
Form eighth sternum	split medially, in form of two hemisterna
Vestiture eighth sternum	without pubsecence
Setae on middle one-third of apical margin each eighth hemisternum	none
Setae on lateral one-third of apical margin each eighth hemisternum	none
Setae on medial margin of each hemisternum	none
Length apodeme each eighth hemisternum	medium

Table 14. (continued)

Reinforcement rod on each eighth hemisternum	absent
Proctiger integrity	moderately sclerotized
Vestiture of proctiger	glabrous, asetose
Paraprocts integrity	moderately sclerotized
Vestiture of paraprocts	glabrous, asetose
Position apodeme of valvifer	dorsal on basal margin
Form coxostylus	unilobate, unsegmented, without attached "teeth"
Vestiture coxite region (ventral surface)	asetose, glabrous
Symmetry vestibular chamber bursa copulatrix	symmetrical
Separate dorsal or ventral bursal chambers	none
Spermathecal gland form	none
Reinforcement rod in oviduct	present

[1] Character states which are judged to be synapotypic for Nebria membe- and those of other related taxa are considered (relatively) symplesiotypic for Nebria alone and are, therefore, listed here.

Table 15. Phylogenetic classification of states of characters used in cladistic analysis of Nearctic *Nebria* species.

No.	Character	Character state[1] Plesiotypic (open squares)	Apotypic (solid squares)[2]	Criterion[3]
	Habitus:			
1	Overall size	small	very small=1^1	a,b,c
			medium=1^2	
			large=$1A^1$ (1^2)	
			very large=$1B^1$ ($1A^1$)	
			small=$1A^2$ (1^2)	
			very small=$1B^2$ ($1A^2$)	
			medium=$1B^3$ ($1A^2$)	
2	Relative size, by sex	medium	males larger than females=2	a
3	Relative head size	medium	slightly large=3	a,e

Table 15. (continued)

			moderately large=3A (3)	
			markedly large=3B (3A)	
4	Relative head size	equal in males	larger in females=4^1	a,e
			larger in males=4^2	
5	Relative head width	medium	slightly wide=5	a,e
			markedly wide=5A (5)	
			extremely wide=5B (5A)	
6	Relative pronotum size	large	medium=6	a,b,e
			slightly large=$6A^1$ (6)	
			moderately large=$6B^1$ ($6A^1$)	
			markedly large=6C ($6B^1$)	
			small=$6B^3$ ($6A^1$)	
			slightly small=$6A^2$ (6)	
			small=$6B^2$ ($6A^2$)	
7	Relative pronotum width	moderately wide	medium=7	a,b,e
			slightly wide=$7A^1$ (7)	

Table 15. (continued)

			moderately wide=7B[1] (7A[1])	
			markedly wide=7C (7B[1])	
			extremely wide=7D (7C)	
			slightly narrow=7B[3] (7A[1])	
			slightly narrow=7A[2] (7)	
			moderately narrow=7B[2] (7A[2])	
8	Relative elytra length	short	medium=8	a,c,e
			slightly long=8A[1] (8)	
			markedly long=8B[1] (8A[1])	
			slightly short=8A[2] (8)	
			moderatel short=8B[2] (8A[2])	
			markedly short=8C (8B[2])	
9	Relative elytra length, by sex	distinctly longer in females	not or slightly longer in females=9	a,e
10	Relative elytra width	medium	slightly wide=10[1]	b,e
			moderately wide=10A[1] (10[1])	

Table 15. (continued)

			markedly wide=10B (10A[1])	
			medium=10C (10B)	
			slightly narrow=10A[3] (10[1])	
			slightly narrow=10[2]	
			moderately narrow=10A[2] (10[2])	
	Color:			
11	Head color	piceous or black	brown=11	a,b,e
			rufous=11A (11)	
			orange-tan or yellow=11B (11A)	
12	Frontal pale spots	absent	present=12	a,b
13	Pronotum color	piceous or black	brown=13	a,c,e
			rufous=13A (13)	
			orange-tan or yellow=13B (13A)	
14	Elytra color	piceous or black	brown=14	a,c,e
			orange-tan=14A (14)	
			yellow=14B (14A)	

Table 15. (continued)

15	Leg color	piceous or black	brown=15	a,c,e
			rufous=15A (15)	
			orange-tan or yellow=15B (15A)	
	Reflection:			
16	Metallic reflection on head	faint	moderate=16[1]	a,b,e
			distinct=16A[1] (16[1])	
			absent=16[2]	
			faint=16A[2] (16[2])	
			moderate=16B (16A[2])	
17	Metallic reflection on pronotum	faint	moderate=17[1]	a,b,e
			distinct=17A[1] (17[1])	
			faint=17A[3] (17[1])	
			absent=17B[1] (17A[3])	
			absent=17[2]	
			faint=17A[2] (17[2])	
			moderate=17B[2] (17A[2])	

Table 15. (continued)

18	Metallic reflection elytra	faint	moderate=18[1] distinct=18A[1] (18[1]) faint=18B[1] (18A[1]) absent=18C (18B[1]) absent=18[2] faint=18A[2] (18[1]) moderate=18B[2] (18A[2])	a,b,e
19	Metallic reflection on thoracic venter	absent	faint=19 moderate=19A[1] (19) absent=19A[2] (19)	a,e
20	Metallic reflection on abdominal venter	absent	faint=20 moderate=20A (20)	a,e
	Luster:			
21	Head luster	moderately dull	faintly shiny=21 markedly shiny=21A (21)	b,c,e

Table 15. (continued)

			very shiny=21B (21A)	
22	Pronotum luster	moderately dull	faintly shiny=22^1	b,c,e
			markedly shiny=22A (22^1)	
			very shiny=22B (22A)	
			very dull=22^2	
23	Elytra luster	moderately dull	faintly shiny=23^1	b,c,e
			markedly shiny=23A (23^1)	
			very shiny=23B (23A)	
			very dull=23^2	
	Microsculpture:			
24	Frons microsculpture: impression	moderate	faint=24	a,b,c,e
			more or less effaced=24A (24)	

Table 15. (continued)

25	Pronotum microsculpture: impression	deep	moderate=25[1] faint=25A[1] (25[1]) more or less effaced=25B (25A[1]) absent=25C (25B) very deep=25A[2] (25[1]) very deep=25[2]	a,b,c,e
26	Pronotum microsculpture: alveolar shape	isodiametric	slightly transverse=26[1] absent=26[2]	a,b,c,e
27	Elytra microsculpture: impression	deep	moderate=27 faint=27A[1] (27) deep=27A[2] (27) very deep=27B (27A[2])	a,b,c,e
28	Elytra microsculpture: alveolar shape	isodiametric	irregular (mixed shapes, mainly isodiametric and slightly transverse)=28 slightly transverse=28A (28)	a,b,c,e

Table 15. (continued)

			moderately transverse=28B (28A)	
			markedly transverse=28C (28B)	
			stretched lines with no or few meshes=28D (28C)	
	Head:			
29	Shape of genae	not inflated	slightly inflated=29	a,e
			moderately inflated=29A (29)	
			markedly inflated=29B (29A)	
30	Shape of genae, by sex	same in both sexes	more inflated in males=30[1]	a,e
			more inflated in females=30[2]	
31	Shape of occiput	not inflated	slightly inflated=31	a,e
			moderately inflated=31A (31)	
			markedly inflated=31B (31A)	
32	Shape of occiput, by sex	same in both sexes	more inflated in males=32[1]	a,e
			more inflated in females=32[2]	
33	Eye size	moderate	slightly reduced=33	a
			moderately reduced=33A (33)	

Table 15. (continued)

34	Eye shape	moderately convex	markedly convex=34[1]	a
			slightly flat=34[2]	
			moderately flat=34A (34[2])	
35	Relative length antenna	medium	moderately long=35	a,c,e
			markedly long=35A[1] (35)	
			extremely long=35B[1] (35A[1])	
			slightly long=35B[2] (35A[1])	
			slightly long=35A[2] (35)	
			markedly long=35B[3] (35A[2])	
36	Pubescence of fourth antennomere	glabrous throughout	apical one-third sparsely pubescent=36	a,b
37	Relative length antennal scape	medium	slightly short=37[1]	a,b,c,e
			markedly short=37A (37[1])	
			long=37[2]	

Table 15. (continued)

38	Axis of antennal scape	straight	very slightly arcuate=38	a,b,e
			moderately arcuate=38A (38)	
			markedly arcuate=38B (38A)	
			bisinuate=38C (38B)	
39	Shape antennal scape	cylindrical	slightly narrowed basally=39[1]	a,b,e
			moderately narrowed basally=39A (39[1])	
			markedly narrowed basally=39B (39A)	
			convex anteriorly at middle=39[2]	
40	No. setae on pedicel	one	two or three=40	a
			three only=40A (40)	
41	Shape flagellar antennomeres	medium length and width	slightly elongate, more slender=41	a,b,c,e
			markedly elongate, very slender=41A[1] (41)	
			slightly elongate, moderately slender=41B[1] (41A[1])	
			medium length and width=41C (41B[1])	
			slightly short, slightly broad=41D (41C)	

Table 15. (continued)

			medium length and width=41A^2 (41)	
			slightly short, slightly broad=41B^2 (41A^2)	
42	Shape mandibles	moderately explanate basolaterally	broadly explanate basolaterally=42	a,e
43	Shape tooth of ligular margin	blunt and/or medium length	sharp, long=43^1	a,e
			absent, margin truncate=43^2	
44	Paraglossae	separate, lobate	separate, but minute, dentiform=44	a
			adnate, completely fused with ligula=44A (44)	
45	No. setae on penultimate labial palpomere	two	three=45	a,b
			two=45A (45)	
46	Shape tooth of mentum	moderately or deeply bifid	slightly emarginate medially=46	a,e
			truncate apically=46A	
47	Position of M_2 setae on mentum	moderately distant from basal margin	near basal margin=47^1	a,e
			very remote from apical margin=47^2	

Table 15. (continued)

48	M_3 setae on mentum	present	absent=48	a,e
49	Tooth of epilobe of mentum	moderate length	minute=49[1] long=49[2]	a,e
	Pronotum:			
50	Overall shape	semiovoid	moderately cordate=50[1] markedly cordate=50A[1] (50[1]) extremely cordate=50B[1] (50A[1]) moderately cordate=50B[2] (50A[1]) slightly cordate=50A[2] (50[1]) slightly cordate=50[2]	a,b,e
51	Overall convexity	markedly convex	moderately convex=51 markedly convex=51A (51)	a,e
52	Shape lateral margin	moderately arcuate	markedly arcuate=52[1] moderately arcuate=52A[1] (51[1]) slightly arcuate=52[2]	a,b,e

Table 15. (continued)

			slightly arcuate and faintly sinuate anteriorly =52A^2 (52^2)	
53	Depth basal sinuation of lateral margin	absent	faintly sinuate=53	a,b,e
			moderately sinuate=53A (53)	
			markedly sinuate=53B^1 (53A)	
			very deeply sinuate=53C (53B^1)	
			faintly sinuate=53B^2 (53A)	
			slightly sinuate=53B^3 (53A)	
54	Length basal sinuation of lateral margin	absent	short=54	a,e
			moderate=54A (54)	
			long=54B^1 (54A)	
			very long=54C^1 (54B^1)	
			short=54B^2 (54A)	
			moderate=54C^2 (54B^2)	
			slightly short=54B^3 (54A)	

Table 15. (continued)

55	Width lateral explanation	medium	broad=55[1] moderate=55A (55[1]) narrow=55[2]	a,c,e
56	Relative width of base	medium	slightly narrow=56[1] markedly narrow=56A[1] (56[1]) slightly broad=56[2] moderately broad=56A[2] (56[2]) very broad=56B (56A[2])	a,b,e
57	Shape basal margin	truncate	slightly bisinuate=57[1] markedly bisinuate=57A[1] (57[1]) slightly sinuate laterally=57A[2] (57[1]) slightly bisinuate and convex medially=57[2] slightly sinuate laterally=57[3] markedly sinuate laterally=57A[3] (57[3]) convex medially=57[4]	a,b,e

Table 15. (continued)

58	Length (projection) of apical angles	medium	moderately long=58[1]	b,e
			very long, projected=58A (58[1])	
			moderately short=58[2]	
59	Width of apical angles	medium	slightly broad=59[1]	b,e
			very broad=59A[1] (59[1])	
			medium=59A[3] (59[1])	
			slightly narrow=59[2]	
			markedly narrow=59A[2] (59[2])	
60	Shape apex of apical angles	moderately rounded	pointed=60[1]	a,e
			broadly rounded=60[2]	
			moderately rounded=60A (60[2])	
61	Shape basal angles	rectangular	rectangular, projected posteriorly=61[1]	a,b,c,e
			obtuse=61[2]	
			rectangular=61A (61[2])	
			acute=61[3]	

Table 15. (continued)

62	Impression lateral margination	medium	slightly shallow=62	a,b,e
			faint=62A (62)	
			very faint=62B (62A)	
63	Width lateral margination	medium	slightly wide=63[1]	b,e
			slightly narrow=63[2]	
			markedly narrow=63A (63[2])	
64	Posterior transverse impression	deep, narrow	slightly shallow=64[1]	b,e
			moderately shallow=64A (64[1])	
			very deep, narrow=64[2]	
			deep, but broad=64[3]	
65	Depth basal foveae	deep	slightly shallow=65	a,b,e
			moderately shallow=65A (65)	
			markedly shallow=65B (65A)	
66	Width basal foveae	extremely broad	markedly broad=66	a,b,e
			moderately broad=66A (66)	
			slightly broad=66B[1] (66A)	

Table 15. (continued)

			medium=66C (66B[1])	
			slightly narrow=66D[1] (66C)	
			moderately narrow=66E[1] (66D[1])	
			markedly narrow=66F (66E[1])	
			extremely narrow=66G (66f)	
			moderately broad=66D[2] (66C)	
			markedly broad=66E[2] (66D[2])	
			markedly broad=66B[2] (66A)	
67	Orientation of basal foveae	parallel	slightly divergent basally=67	a,b,e
			moderately divergent basally=67A (67)	
			markedly divergent basally=67B (67A)	
68	Midlateral seta	present	absent=68	a
69	Tubercle medial to midlateral seta	absent	present=69	a,e
70	Basolateral seta	present	absent=70	a

Table 15. (continued)

	Prosternum:			
71	Intercoxal process	sublanceolate	moderately lanceolate=71[1]	a,b,e
			markedly lanceolate=71A[1] (71[1])	
			lanceolate, narrow=71A[2] (71[1])	
			sublanceolate=71A[3] (71[1])	
			spatulate=71[2]	
72	Macrosculpture intercoxal process	smooth	rugose=72	a,e
73	Margination intercoxal process	complete	complete, except at apex=73	a,e
			present laterally in basal half only=73A[1] (73)	
			present only anteromedial to coxa=73B[1] (73A[1])	
			present laterally in basal half, but interrupted at base=73B[2] (73A[1])	
			complete (or nearly so across apex)=73A[2] (73)	

Table 15. (continued)

	Elytra:			
74	Overall silhouette	rectangular	subrectangular=74 subovoid=74A[1] (74) ovoid=74B (74A[1]) subovoid, but sides straight in basal half=74A[2] (74)	a,c
75	Overall convexity	medium	slightly flattened=75[1] moderately flattened=75A[1] (75[1]) very convex=75A[3] (75[1]) markedly convex=75[2] very convex=75A[2] (75[2])	a,b,e
76	Length basal margination	very long	moderately long=76 slightly long=76A (76) medium=76B (76A)	a,b,c,e

Table 15. (continued)

			slightly short=76C (76B)	
			moderately short=76D (76C)	
			markedly short=76E (76D)	
			extremely short=76F (76E)	
77	Shape humerus	rectangular	distinctly angulate, but slightly rounded=77	a,c
			moderately rounded=77A (77)	
			markedly rounded=77B (77A)	
			extremely rounded=77C (77B)	
			slightly flattened=77D (77C)	
			obliterated=77E (77D)	
78	Humeral carina	absent	faint, vaguely linear=78[1]	a,c,e,
			distinct, moderately sharp, not projected =78A[1] (78[1])	
			distinct, sharp, slightly projected=78B (78A[1])	

Table 15. (continued)

			markedly sharp, moderately projected=78C ($78B^1$)	
			extremely sharp, markedly projected=78D (78C)	
			present as minute marginal tooth=78^2	
			present as distinct marginal tooth=$78A^2$ (78^2)	
79	Subhumeral sinuation	very faint, very shallow	distinct but shallow=79^1	a,e
			moderately deep=$79A^1$ (79^1)	
			markedly deep=79B ($79A^1$)	
			absent=79^2	
			faint, shallow, slightly displaced anteriorly=79^3	
			distinct, shallow, displaced anteriorly=$79A^2$ (79^3)	
80	Shape apex	bluntly pointed, at midline, sutural margin straight	rounded, slightly lateral from midline; sutural margin straight=80	a,b,e
			broadly pointed, displaced laterally; sutural margin arcuate to apex=$80A^1$ (80)	

Table 15. (continued)

		narrowly pointed, displaced laterally; sutural margin sinuate=80B ($80A^1$)	
		narrow, obliquely truncate, displaced laterally; sutural margin straight=$80A^2$ (80)	
		broad, rounded, but apically truncate, slightly displaced laterally; sutural margin straight=$80A^3$ (80)	
81	Depth of striae	medium	a,b,c,e
		moderately shallow=81^1	
		markedly shallow=$81A^1$ (81^1)	
		moderately deep=81^2	
		markedly deep=$81A^2$ (81^2)	
		extremely deep=81B ($81A^2$)	
		medium=$81A^4$ (81^2)	
		medial striae medium, lateral striae very shallow =81^3	

Table 15. (continued)

			medial striae slightly shallow, lateral striae almost obliterated=81A^3 (81^3)	
82	Convexity of intervals	moderately flat	very faintly convex=82	a,b,e
			slightly convex=82A (82)	
			moderately convex=82B (82A)	
			markedly convex=82C^1 (82B)	
			extremely convex=82D (82C^1)	
			slightly convex=82C^2 (82B)	
83	Continuity of intervals	uniform, uninterrupted	faintly catenate=83	a,b,e
			moderately catenate=83A (83)	
			markedly catenate, but not tuberculate=83B^1 (83A)	
			markedly catenate, tuberculate=83C^1 (83B^1)	
			moderately catenate=83C^2 (83B1)	
			faintly catenate=83B^2 (83A)	

Table 15. (continued)

84	Pores for discal setae	slightly foveate	moderately foveate=84[1]	a,b,e
			broadly foveate=84A (84[1])	
			deeply and broadly foveate=84B (84A)	
			weakly foveate=84C (84B)	
			minute, barely evident=84[2]	
85	Basal pore	present	absent=85	a,e
86	Setae on fifth interval	none	few=86	a,b,e
			none=86A[1] (86)	
			many=86A[2] (86)	
			few or none=86B (86A[2])	
87	Setae on seventh interval	none	few=87	a,b,e
			many=87A[1] (87)	
			few or none=87B (87A[1])	
			none=87A[2] (87)	

Table 15. (continued)

	Wings:			
88	Size	full-sized	truncate at stigma, broad=88[1]	a,c
			truncate and narrow=88A[1] (88[1])	
			short and narrow, stigma barely evident=88B[1] (88A[1])	
			short, lobate, some venation present=88C (88B[1])	
			strap-like, very thin, elongate=88D (88C)	
			scale-like, short=88E (88D)	
			full-length, but narrowed=88[2]	
			slightly short, narrowed=88A[2] (88[2])	
89	Shape oblongum cell	almost quadrate, stalk minute	slightly narrowed posteriorly, stalk short=89[1]	a,b,e
			slightly narrowed posteriorly, stalk long=89A[1] (89[1])	
			faintly triangular, markedly narrowed, stalk medium=89A[2] (89[1])	

Table 15. (continued)

			distinctly triangular, stalk long=89B (89A[2])	
			broad, rounded posteriorly, stalk minute=89[2]	
	Pterothoracic venter:			
90	Mesosternum macrosculpture	moderately punctate	sparsely, faintly punctate=90	a,e
			smooth, impunctate=90A (90)	
			sparsely, faintly punctate=90B (90A)	
91	Mesepisternum macrosculpture	moderately punctate	sparsely, faintly punctate=91	a,e
			faintly punctulate=91A (91)	
			smooth, impunctate=91B (91A)	
92	Metasternum macrosculpture	moderately punctate	sparsely, faintly punctate=92	a,e
			faintly punctulate=92A (92)	
			smooth, impunctate=92B (92A)	
93	Metepisternum macrosculpture	punctate	faintly punctulate=93	a,e
			smooth, impunctate=93A (93)	

Table 15. (continued)

94	Relative length metasternum	moderately long	very slightly short=94[1] slightly short=94A (94[1]) moderately short=94B (94A) markedly short=94C (94B) very short=94D (94C) extremely short=94E (94D) very long=94[2]	a,e
95	Margination metasternum anterior intercoxal process	complete, deep throughout	complete, moderate throughout=95 complete, faint at middle=95A (95) incomplete, only vague depression medially=95B (95A) incomplete, absent medially=95C (95B)	a,b,e
	Legs:			
96	Relative leg length	medium	slightly long=96[1] moderately long=96A[1] (96[1]) markedly long=96B (96A[1])	a,b,e

Table 15. (continued)

			extremely long=96C[1] (96B)	
			slightly long=96C[2] (96B)	
			slightly short=96[2]	
			moderately short=96A[2] (96[2])	
			slightly long=96A[3] (96[2])	
97	No. setae at base of hind coxa	one	few=97	a,b,e
			many=97A (97)	
			few=97B (97A)	
			one=97C (97B)	
98	Dorsal groove on middle tibia	distinct, present except at apex	distinct even near apex=98[1]	a,b,e
			distinct only on middle one-third=98[2]	
			absent; dorsum flat or convex=98B (98[2])	
99	Brush of setae on dorsum middle tibia	moderately dense	sparse=99	a,e

Table 15. (continued)

100	Ventral pads of setae on mesothoracic tarsomeres	present	absent=100	a
101	Shape ventroapical margin fourth tarsomere hind tarsus	truncate	slightly lobate laterally=101 moderately lobate laterally=101A^1 (101) markedly lobate laterally=101B^1 (101A^1) extremely lobate laterally=101C (101B) slightly lobate laterally=101A^2 (101) faintly lobate laterally=101B^2 (101A^2)	a,b,e
102	Dorsal pubescence tarsomeres	present	absent=102 present=102A (102)	a,e
	Abdomen:			
103	Setae on second visible sternum	none	patch of setae medially=103^1 none=103A^1 (103^1) one pair of paramedial setae present=103^2	a,b,e

Table 15. (continued)

			patch of setae medially=103A^2 (103^2)	
104	No. posterior paramedial setae on third to fifth visible sterna	one pair	few pairs=104	a,b,e
			many pairs=104A^1 (104)	
			few pairs=104B (104A^1)	
			one pair=104A^2 (104)	
105	No. anterior paralateral setae on third to fifth visible sterna	none	few pairs=105	a,b,e
			many pairs=105A^1 (105)	
			few pairs=105B (105A^1)	
			none=105A^2 (105)	
106	No. paramedial setae male sixth visible sternum	one pair	two or more pairs=106	a,b,e
107	No. paramedial setae female sixth visible sternum	two or more pairs	one pair=107	a,b,e

Table 15. (continued)

108	Macrosculpture first visible sternum	moderately punctate	faintly, sparsely punctate=108[1] faintly punctulate=108A (108[1]) smooth, impunctate=108B (108A) coarsely, densely punctate=108[2]	a,e
	Male genitalia:			
	Median lobe:			
109	Shape basal bulb	quadrate, broadly open basally	rounded, partially closed basally=109	a,b
110	Dorsobasal piece	present as collar on basal bulb	present as dorsal midline crest=110	a,b
111	Thickness mid-shaft	medium	thick=111[1] very thick=111A (111[1]) slender=111[2]	a,b,e
112	Taper mid-shaft	moderately narrowed apically	cylindrical, diameter roughly equal throughout=112[1] moderately narrowed basally=112A (112[1])	a,b,e

Table 15. (continued)

			markedly narrowed basally=112B (112A)	
			markedly narrowed apically=112[2]	
113	Bend in axis of mid-shaft	less than 90°	90° or more, but less than 135°=113	a,b,e
			135° or more=113A[1] (113)	
			less than 90°=113A[2] (113)	
114	Cross-section shape mid-shaft	slightly compressed	moderately compressed=114[1]	a,b,e
			markedly compressed=114A (114[1])	
			circular=114[2]	
115	Right dorsal face mid-shaft	unmodified	faint indentation=115[1]	a,b
			moderately deep pouch, directed basally=115A (115[1])	
			very deep pouch=115B (115A)	
			longitudinal groove lateral to dorsal ridge=115[2]	
116	Shape preapical-shaft (lateral aspect)	narrow, margins almost parallel	moderately broad, moderately tapered apically=116[1]	a,b,e
			markedly broad, sharply tapered apically=116A[1] (116[1])	

Table 15. (continued)

			moderately broad, moderately tapered apically=116B ($116A^1$)	
			extremely broad, truncate apically=116^2	
			very broad, subtruncate apically=$116A^2$ (116^2)	
			very narrow, margins almost parallel=116^3	
			narrow, narrowest at base of apex=116^4	
117	Symmetry preapical-shaft (apical aspect)	symmetrical	asymmetrical, apical orifice deflected slightly right=117	a,b,e
			asymmetrical, orifice moderately deflected right=117A (117)	
			asymmetrical, orifice markedly deflected right=117B (117A)	
			asymmetrical, orifice extremely deflected right=117C (117B)	
118	Symmetry preapical-shaft (dorsal aspect)	symmetrical	faintly deflected right=118	a,b,e
			slightly deflected right=118A (118)	

Table 15. (continued)

			moderately deflected right=118B[1] (118A)	
			markedly deflected right=118C[1] (118B[1])	
			symmetrical=118B[2] (118A)	
			slightly deflected right=118C[2] (118B[2])	
119	Shape preapical-shaft (dorsal aspect)	broadly tapered apically	narrowly tapered apically=119[1]	a,b,e
			faintly tapered apically=119[2]	
			slightly tapered basally=119A (119[2])	
120	Shape ventral margin preapical-shaft (lateral aspect)	straight or smoothly concave	faintly recurved subapically=120[1]	a,b,e
			moderately recurved=120A (120[1])	
			markedly recurved=120B (120A)	
			abruptly deflected ventrally=120[2]	
			slightly recurved apically=120[3]	
121	Shape apex (ventral aspect)	broadly pointed	bluntly pointed=121[1]	a,b,e
			shovel-shaped=121A[1] (121[1])	
			shovel-shaped, with minute lobe near middle=121B[1] (121A[1])	

Table 15. (continued)

122	Symmetry apex (ventral aspect)	symmetrical (centered on shaft)	shovel-shaped, with moderate lobe near middle=121C ($121B^1$) broadly pointed=$121A^2$ (121^1) narrowly pointed=$121B^2$ ($121A^2$) narrowly pointed=121^2 asymmetrical, slightly deflected right=122 asymmetrical, moderately deflected right=$122A^1$ (122) asymmetrical, markedly deflected right=122B ($122A^1$) asymmetrical, slightly or moderately deflected left=122C (122B) symmetrical, centered on shaft=$122A^2$ (122)	a,b,e
123	Plane of apex face (apical aspect)	vertical	horizontal=123^1 twisted slightly left=123^2 markedly twisted left=$123A^1$ (123^2)	a,b,e

Table 15. (continued)

			vertical=123A^2 (123^2)	
124	Length apex (lateral aspect)	medium	long=124^1	a,b,e
			short=124^2	
			very short=124A (124^2)	
125	Shape apex (lateral aspect)	bluntly pointed	blunt=125^1	a,b,e
			broadly blunt=125A^1 (125^1)	
			rounded=125B^1 (125A^1)	
			hooked=125B^2 (125A^1)	
			roundly hooked=125C (125B^2)	
			moderately pointed=125^2	
			narrow, sharply pointed=125A^2 (125^2)	
126	Axis of apex (lateral aspect)	straight	slightly deflected ventrally=126^1	a,b,e
			slightly recurved=126^2	
	Parameres:			
127	Symmetry parameres	asymmetric, right longer than left	symmetric, equal length=127^1	a,b,e
			asymmetric,right slightly longer than left=127^2	

Table 15. (continued)

128	Shape left paramere	broad, short	broad, slightly long, pointed apically=128[1] slightly narrow, slightly long=128[2] broad, moderately long=128[3]	a,b,e
129	Shape right paramere	slender, long, arcuate	slender, very long=129[1] broad, moderately short=129[2]	a,b,e
130	Right medial parameric sclerite	absent	present=130 absent=130A (130)	a,b,e
	Female genitalia:			
	Eighth sternum:			
131	Length setae on medial end apical margin	medium and long	medium only=131 long only=131A[1] (131) short only=131A[2] (131)	a,b,e
132	Density setae on medial end apical margin	medium	dense=132[1] sparse=132[2]	a,b,e

Table 15. (continued)

133	Setae at middle of apical margin	present	absent=133	a
134	Width basal apodeme	medium	narrow=134	a,b,e
135	Shape basal apodeme	moderately emarginate, arms equal length	deeply emarginate, arms equal length=135 lateral arm slightly shortened=135A (135) lateral arm moderately shortened=135B (135A) lateral arm markedly shortened=135C (135B) lateral arm reduced to faint lobe=135D (135C) lateral arm obliterated=135E (135D)	a,b,e
	Proctiger:			
136	Shape	hemispheric, well sclerotized throughout	hemispheric, narrowly membranous apically=136 short, broad, extensive apical area membranous 136A (136)	a,b,e
	Paraprocts:			
137	Vestiture	sparsely pubescent	glabrous=137	a

Table 15. (continued)

138	Continuity with valvifer	very broadly continuous basally	broadly continuous basally=138 moderately continuous basally=138A (138) narrowly continuous basally=138B[1] broadly continuous basally=138B[2]	a,b.e
	Valvifers:			
139	Integrity	divided into lateral and medial areas, by intervening membranous area	medial area very lightly sclerotized=139 medial area membranous=139A (139)	a,b,e
140	Vestiture	setae on medial area and adjacent membrane	setae sparse, on medial sclerotized area only=140 asetose=140A (140)	a,b,e
141	Length setae	short	absent=141[1] medium only=141[2]	a,b,e

Table 15. (continued)

			medium and long=141A (141^2)	
142	Density setae	medium	sparse=142	a,b,e
			absent=$142A^1$ (141)	
			medium=$142A^2$ (141)	
143	Shape basal apodeme	medium length, broad	short, very broad=143^1	a,b,e
			medium length, slightly narrow=143^2	
	Coxostylus:			
144	Vestige of tenth sternum	fused basally with base of coxostylus	separate, not fused basally with coxostylus=144	a,b,e
145	Fusion of coxite with stylus	fused medially and ventromedially	fused ventromedially but not medially=145	a,e
146	Shape stylus (ventral aspect)	slender, slightly arcuate, rounded apically	broad, moderately arcuate, pointed apically=146^1	a,b,e
			broad, slightly arcuate, spatulate apically=146^2	

Table 15. (continued)

147	Shape stylus (lateral aspect)	medium width, apex bluntly rounded, deflected dorsally	broad, apex narrowly rounded, straight=147[1]	a,b,e
			very broad, apex broadly rounded, straight=147[2]	
148	Length stylus	medium	slightly short=148[1]	a,b,e
			moderately short=148A (148[1])	
			moderately long=148[2]	
149	Ventral diagonal row of setae (on coxite)	three to six medium length, setiform setae	one to four medium length, setiform setae=149[1]	a,b,e
			three to six medium length, spiniform setae=149[2]	
			five or six long, spiniform setae=149A (149[2])	
			two to four short, setiform setae=149[3]	
150	Mediodorsal row of setae (on stylus)	three [illegible]e medium length, setiform setae, row longitudinal	one to three medium length, setiform setae, row longitudinal=150[1]	a,b,e
			three to five medium length, spiniform setae, row diagonal=150[2]	

Table 15. (continued)

			two or three long, spiniform setae, row diagonal=150A (150^2)	
			three or four medium length, setiform setae, row diagonal=150^3	
			three moderately long, setiform setae, row longitudinal=150^4	
151	Vestiture ventral surface	sparsely setose	asetose=151	a,b,e
152	Vestiture medial surface	densely setose subapically and and at middle	densely setose at middle only=152^1	a,b,e
			moderately setose subapically and at middle=152^2	
			densely to sparsely pubescent (very fine setae) subapically only=$152A^1$ (152^2)	
			glabrous=152B ($152A^1$)	
			sparsely setose subapically and at middle=$152A^2$ (152^2)	
			sparsely setose at middle only=$152A^3$ (152^2)	

Table 15. (continued)

	Bursa copulatrix:			
153	Longitudinal axis (lateral aspect)	simple, slightly deflected dorsally	faintly sigmoid=153	a,b,e
			moderately or markedly sigmoid=153A^1 (153)	
			sigmoid, but anterior end reduced=153B^2 (153A^1)	
			slightly deflected dorsally=153A^2 (153)	
			markedly deflected dorsally=153A^3 (153)	
			recurved posterodorsally=153B^1 (153A^3)	
154	Shape vestibular chamber (dorsal aspect)	gradually widened anteriorly	bell-shaped, simple=154	a,b,e
			bell-shaped, recurved posteriorly at sides= 154A^1	
			bell-shaped, slightly constricted anteriorly= 154A^2 (154)	
			bell-shaped, slightly constricted anteriorly, recurved posteriorly at sides=154B (154A^2)	

Table 15. (continued)

155	Shape spermathecal chamber (lateral aspect)	flat, thin	flat, thick=155	a,b,e
			thinly fusiform=155A	
			thick, apex moderately recurved dorsally=155B[1] (155A)	
			thick, apex markedly recurved dorsally=155C (155B[1])	
			thick, apex recurved ventrally=155B[2] (155A)	
			thickly fusiform=155B[3] (155A)	
			fusiform, markedly inflated basally=155B[4] (155A)	
156	Length spermathecal chamber (lateral aspect)	slightly short	medium length=156[1]	a,b,e
			slightly long=156A[1] (156[1])	
			markedly long=156B (156A[1])	
			short=156A[2] (156[1])	
			short=156[2]	
			very short=156A[3] (156[2])	

Table 15. (continued)

157	Shape spermathecal chamber (dorsal aspect)	broadly cordate, elongate	moderately broad, cordate=157^1	a,b,e
			broad, anteriorly truncate=157^2	
			subquadrate=$157A^1$ (157^2)	
			trapezoidal, slightly narrowed anteriorly=157B ($157A^1$)	
			ovoid, slightly elongate=$157A^2$ (157^2)	
			spatulate=157^3	
			broadly cordate=$157A^3$ (157^3)	
			ovoid, slightly elongate=$157A^4$ (157^3)	
			round=$157A^5$ (157^3)	
			cordate, posterior margin emarginate=$157A^6$ (157^3)	
158	Symmetry of spermathecal chamber (dorsal aspect)	symmetrical	slightly deflected left=158^1	a,b,e
			moderately deflected left=$158A^1$ (158^1)	
			markedly deflected left=158B ($158A^1$)	
			slightly deflected right=$158A^2$ (158^1)	

Table 15. (continued)

159	Accessory lobes on dorsum of spermathecal chamber	none	
		moderately deflected right=158[2]	
		paired, elongate, thick, paramedial lobes, not associated with spermathecal duct insertion 159[1]	a,b,e
		single, short, slender lobe in midline underlying spermathecal duct insertion=159[2]	
		single, elongate, slender lobe in midline underlying spermathecal duct insertion=159A 159[2])	
		single, markedly elongate, slender lobe in midline underlying spermathecal duct insertion= 159B (159A)	
		none=159C (159B)	
		single, elongate, slender lobe in midline overlying spermathecal duct insertion=159[3]	

Table 15. (continued)

160	Sclerite on dorsum of spermathecal chamber	none	
		small or large, flat plate anterior to spermathecal duct insertion (s.d.i.)=160^1	a,b,e
		medium-sized, flat plate, involuted medially, lateral margins recurved, anterior to s.d.i.= $160A^1$ (160^1)	
		small, domed plate, not involuted medially, shape varied, anterior to or surrounding s.d.i.= $160B^1$ ($160A^1$)	
		oval plate, depressed medially, recurved laterally, anterior to s.d.i.=$160B^2$ ($160A^1$)	
		raised, horseshoe-shaped plate, depressed medially, s.d.i. centered in posterior half of plate=$160C^3$ ($160B^2$)	
		raised, horseshoe-shaped plate, depressed medially, s.d.i. centered in anterior half of plate=$160D^2$ ($160C^3$)	

Table 15. (continued)

small or large plate, shallowly or deeply invaginated medially (shape varied), anterior to s.d.i.=160A^{2} (160^{1})

large, quadrate, flat plate, surface crenulated, anterior to s.d.i.=160A^{3} (160^{1})

medium-sized oval plate, surface crenulated, anterior to s.d.i.=160B^{3} (160A^{3})

small oval plate, surface crenulated, at anterior end of chamber=160C^{1} (160B^{3})

very small plate, surface crenulated, at anterior end of chamber=160D^{1} (160C^{1})

small oval plate, faintly sclerotized, surface convoluted, at anterior end of chamber=160C^{2} (160B^{3})

elongate, slender, on dorsal accessory lobe=160^{2}

Table 15. (continued)

			small, quadrate plate, surface longitudinally convoluted, anterior to s.d.i.=160^3	
161	Sclerite in venter of spermathecal chamber	only an opaque reinforcement rod in midline, not sclerotized	opaque rod short, barely extended to chamber=161^1	a,b,e
			opaque rod double-wide in midline=161^2	
			broad plate deeply infolded longitudinally in midline, s.d.i. between rod and plate=$161A^1$ (161^2)	
			as $161A^1$, but midline area everted=$161B^1$ ($161A^1$)	
			as $161B^1$, but plate smaller, narrower laterally=$161C^1$ ($161B^1$)	
			as $161B^1$, but plate simply convoluted longitudinally=$161C^2$ ($161B^1$)	
			as $161B^1$, but plate doubly convoluted longitudinally=$161C^4$ ($161B^1$)	

Table 15. (continued)

			opaque rod broad, flat, extended anterodorsally in chamber, no sclerite=161C^3 (161B^1)	
			opaque rod broad, flat, extended anterodorsally in chamber, no sclerite=161B^2 (161A^1)	
			opaque rod double-wide, but shorter than in 161^2, not expanded in chamber=161C^5 (161B^2)	
			very large, broad plate, extended around margins to fringes of dorsum=161A^2 (161^2)	
			opaque rod short, barely extended in chamber=161A^3 (161^2)	
162	Location of spermathecal duct insertion on spermathecal chamber	posterior/dorsal	anterior/dorsal=162^1	a,b,e
			anterior/middle=162A^1 (162^1)	
			anterior/ventral=162B (162A^1)	
			posterior/ventral=162^2	
			posterior/middle=162A^2 (162^2)	
			posterior/dorsal=162A^3 (162^2)	

Table 15. (continued)

			dorsal/posterior=162A^4 (162^2)	
163	Symmetry insertion of spermathecal duct	medial	slightly right of midline=163	a,b,e
			markedly right of midline=163A^1 (163)	
			slightly left of midline=163A^2 (163)	
164	Shape spermathecal duct	loosely, unevenly convoluted	sinusoidal, regularly wavy=164^1	a,b,e
			more or less straight=164^2	
			tightly, unevenly convoluted=164^3	
			loosely, unevenly convoluted=164A (163^3)	
165	Length spermathecal duct	medium	slightly short=165^1	a,b,e
			markedly short=165A^1 (165^1)	
			slightly long=165^2	
			markedly long=165A^2 (165^2)	
166	Diameter proximal portion of spermathecal duct	same as distal portion	dilated, markedly greater diameter than in distal portion=166	a,b,e

Table 3. (continued)

167	...ter distal ...tion of sper... duct	narrow	slightly thick=167 moderately thick=167A (167) markedly thick=167B (167A) extremely thick=167C (167B)	a,b,e
168	Shape spermatheca	lanceolate, narrow, markedly arcuate	lanceolate, slightly arcuate, narrow=168[1] lanceolate, thickened near apex, otherwise narrow=168A (168[1]) vaguely lanceolate, somewhat convoluted, thickest subapically=168B (168A) lanceolate, straight, narrow=168[2]	a,b,e
	Natural history:			
169	Center of life zone range	Canadian	between Canadian and Hudsonian=169[1] Hudsonian=169A[1] (169[1]) between Hudsonian and Arctic/Alpine=169B[1] (169A[1]) Arctic/Alpine=169C[1] (169B[1]) between Canadian and Transition=169[2]	a,e

Table 15. (continued)

			Transition=169A[2] (169[2])	
			between Transition and Upper Sonoran ...B[2] (169A[2])	
			Upper Sonoran=169C[2] (169B[2])	
170	Predominant microhabitat type	mesic forest floor	streamside=170[1]	a,e
			lakeside=170A[1] (170[1])	
			perinival areas=170A[2] (170[1])	
			talus=170A[3] (170[1])	
			tundra=170A[4] (170	
			open seabeach=170A[5] (170[1])	
			tundra=170[2]	
171	Life cycle timing	overwinter only or almost exclusively as larvae	overwinter as adults, in part only=171[1]	a,b,e,
			overwinter only or almost exclusively as adults 171[2] .	
			overwinter as larvae, in part only=171A (171[2])	

Table 15. (continued)

---

[1] Each apotypic (derived) character state is given a unique code name in this table. For characters represented by only one apotypic state, the character number alone stands as code name for that apotypic state (e.g. character no. 2). Where two or more apotypic states have evolved from a single plesiotypic (primitive) state, the former are differentiated by different superscript numbers appended to the character number (e.g. character no. 4). For characters in which apotypic states have evolved sequentially from other apotypic (i.e. relatively plesiotypic) states, relatively apotypic states are coded by a combination of the character number and a capital letter (e.g. character no. 13). Note that capital letters used in the code here refer also to successive rows following the first row for a character listed in Fig. 372. Apotypic character states of characters with multiply-branched transformations have been coded with a combinations of character numbers, capital letters, and superscript numbers (e.g. character no. 1). Immediately following the code name for each subsequent apotypic state, code name of the derived state from which I judge it has evolved is noted in parentheses. My hypothesis on the transformation of each character can therefore be reconstructed directly from data presented in the table.

[2] Distributions of character states among members of Nearctic species and their Palaearctic relatives are presented in Fig. 372. In that figure, possession of an apotypic state is denoted by a solid square.

Table 15. (continued)

Open squares denote plesiotypic states. Notation here is just to facilitate cross-reference.

[3] Criteria used in evaluating the apotypy or plesiotypy of character states are discussed in the text. Code used here is as follows: a=ex-group comparisons; b=character correlations; c=group trends; d=correlation with adaptive significance; and e=in-group comparisons.

4.13 Phylogeny of Nearctic Nebria

Results of the cladistic analysis of Nearctic Nebria are presented in Fig. 373. This cladogram was chosen from among several through the procedure and according to criteria described above. It represents the simplest explanation (i.e. requires the fewest possible extra evolutionary steps--instances of parallelism, convergence or reversal) to account for the observed distribution of apotypic character states as presented in Table 15 and Fig. 372. I suggest that reference to these two data sources will permit rapid and accurate interpretation of the cladogram; and I will therefore confine discussion here to a few brief supplementary comments.

It has become customary to list, directly on a cladogram, the character states (or coded symbols for them) which demonstrate synapotypy for each lineage. I have found this impractical here, however, because of the large number of synapotypies involved. I have therefore chosen to list only the number of synapotypies found for each lineage (i.e. between any two nodes on the cladogram) without identifying the characters involved. Reference to Fig. 372 and Table 15 will permit recognition of synapotypies for any segment of the cladogram. Each hypothesis of relationship suggested by the cladogram is supported by at least five synapotypies (up to a maximum of 32). I therefore have considerable confidence in the accuracy of this reconstruction and look forward to the opportunity to test these hypotheses with data from new and independent character systems (e.g. external structure of larvae, pupae, and eggs; structure of various internal organ systems).

Monophyletic groups and inter-group relationships.--Based on the cladistic analysis of Nearctic species, I recognize four main groups of species. Synapotypic character states for each of these groups are listed under their respective descriptions (section 3.43).

As noted in the cladogram, the group comprising N. virescens and its Palaearctic relatives, the virescens lineage, is evidently the sister group of all other Nebria (including all Palaearctic species and groups not treated in this study [i.e. the so-called "endemic Palaearctic lineages" in Fig. 373]). This group is highly distinctive, its members easily distinguished from those of all other Nebria groups on the basis of numerous characters of male or female genitalia, mouthparts, pronotum, elytra, and legs. It would, perhaps, be appropriate here to recognize this group as a separate genus on the basis of 32 synapotypic features shared among members species. However, I prefer to make such a taxonomic decision only after a thorough review of inter-group relationships within Nebriini and between Nebriini and related tribes (e.g. Notiophilini, Opisthiini) has been completed.

Although the most parsimonious hypothesis of relationship (i.e. that requiring fewest extra evolutionary steps) between the virescens lineage and other nebriine groups is as suggested here, several discordant patterns of character state distribution are required by this arrangement of taxa. Most disturbing among these are patterns in several characters of male and female genitalia. For example, males of N virescens, N. pusilla Ueno, and N. chalceola Bates are unique among males of Nebria species considered here in shape of the basal bulb of the median lobe and of the dorsobasal piece and in the spatial

relationships between these two structures. Based on broad ex-group and in-group comparisons, I interpret each of the character states involved as apotypic. However, these states are also represented among males of Leistus and Notiophilus species (but not among those of Pelophila and opisthiine species). The same pattern is apparent among females for several characters of the coxostyli. There is, therefore, some evidence for closer phylogenetic relationship between the virescens lineage and Leistus and Notiophilus than between the former and all other Nebria species; but realignment of groups (i.e. rearrangement of taxa included in Fig. 369) based on this pattern of synapotypy creates discordance (and requires 20 extra evolutionary steps) in other characters. Also, six synapotypies (see Fig. 372) support the monophyly of a group including the virescens lineage and all other Nebria species and excluding Leistus and Notiophilus; and I therefore suggest that the preferred hypothesis comprises that set of relationships suggested by cladograms presented here (i.e. Figs. 369 and 373).

Sister group of the virescens lineage comprises all other species included in genus Nebria. Numerous subgenera have been proposed for groups of Palaearctic species; and, no doubt, some of these constitute monophyletic groups at some level of inclusiveness. I have studied representatives of each of these groups and conclude that they represent one or more independent lineages that diverged from the ancestral stock of the remaining Nearctic lineages and evolved independently in Eurasia. Relationships among these 'endemic Palaearctic lineages' are not yet clear, nor are they considered here further. Monophyly of the group comprising these lineages and the

Nearctic lineages (excluding the virescens lineage) is supported by five synapotypies, namely: (1) elytral microsculpture moderately impressed; (2) paraglossae completely fused (i.e. adnate) with ligula; (3) ventroapical margin of fourth hind tarsomere lobate laterally; (4) ventral surface of coxostylus asetose; and (5) opaque reinforcement rod in ventral wall of spermathecal chamber (bursa copulatrix) double-wide in midline.

The monophyly of the group including the remaining Nearctic species and their Palaearctic relatives in supported by 24 synapotypies (see Fig. 372). Three main groups included are the gyllenhali, gregaria, and metallica lineages. The gyllenhali lineage is judged to be the sister group of the other two together, a relationship supported by six synapotypies. This figure would be substantially greater if N. paradisi were excluded from the group. Members of this species exhibit a confounding mosaic of apotypic character states shared with both the remaining gyllenhali lineage species and those of the metallica and gregaria lineages. For example, all members of N. paradisi have frontal pale spots, an apotypic condition shared with all members of the metallica and gregaria lineages. In addition, N. paradisi females share with members of these lineages bursae copulatrices the longitudinal axes of which (in lateral aspect) are sigmoid, as opposed to the dorsally deflected condition exhibited by other females of the gyllenhali lineage. N paradisi females are the only ones among gyllenhali lineage species which have a dorsal sclerite on the spermathecal chamber, a condition shared with females of some but not all species of the other lineages. In contrast, apotypic states of characters of

male genitalia all support close phylogenetic relationship between N. paradisi and N. sakagutii and its relatives. Close phylogenetic relationship between the latter and the other species of the gyllenhali lineage is supported by numerous synapotypies. I choose to accept evidence from male rather than female genitalia in this instance. Apotypic states of ventral characters shared between N. paradisi females and those of the other lineages are, in fact, very slightly derived relative to the proposed plesiotypic states. It is therefore less difficult to accept their independent evolution than that of more unique and highly derived apotypic states shared by males of N. paradisi and other gyllenhali lineage species. Also, few N. shibanaii Ueno and N. shiretokoana Nakane adults have faint frontal pale spots. This suggests that tendency for development of frontal spots is not restricted to N. paradisi members among gyllenhali lineage species; and I therefore place little importance on this character as evidence against the relationship suggested here.

Seventeen synapotypies (see Fig. 372) support the monophyly of a group including the gregaria and metallica lineages. These two lineages are also highly distinctive as sister groups--11 synapotypies characterize gregaria lineage members and 17 distinguish those of the metallica lineage. Reconstruction of phylogenetic relationships of species within these lineages was relatively uncomplicated, except for specific instances. I found characters of female genitalia very useful in demonstrating relationships among gregaria lineage species. Unfortunately, I have not studied females of N. angustula Motschulsky, N. charlottae Lindroth, or N. navajo new species (females of the latter two species have not yet been collected); and placement

of these three species is therefore more tentative than that of other species in the lineage.

Relationships among members of the ovipennis species group (metallica lineage) were especially difficult to interpret. Males of all included species, except those of N. gebleri and N. mellyi Gebler,are characterized by a deep, basally-directed pouch on the right dorsolateral surface of the median lobe mid-shaft. Males of the two exceptional species have only a faint indentation of the mid-shaft surface at a corresponding point. Several apotypic character states are shared by N. mellyi, N. ovipennis, and N. spatulata members (e.g. loss of metallic reflection from elyta; reduced pigmentation (e.g. body color brown rather than black); elytral microsculpture very deeply impressed; elytral intervals faintly catenate). However, group trends are apparent in each of these characters, and these same apotypic states have evidently evolved repeatedly and independently in different groups. Close phylogenetic relationship among these three species is therefore unlikely (especially if distributional data are considered (see below)). Evidence suggests that, in fact, N. gebleri is the sister group of all the other ovipennis group species. Seventeen synapotypies characterize the group exclusive of N. gebleri (whereas, if N. mellyi is excluded and N. gebleri included, only two synapotypies distinguish the resulting group). The difference between these alternative sets of relationship is, however, not as great as is apparent . Several synapotypies for the group exclusive of N. gebleri involve characters transformations of which are involved in group trends associated with wing reduction (e.g. changes in shape of elytra, length of legs, length of metasterna, etc.). In spite of the

reduced significance of differences in number of synapotypies and the more complex hypothesis required to account for the geographical distributions of group members (see discussion in section 4.2), I suggest that intra-group relationships are best interpreted as presented in the cladogram.

In general, relationships suggested from the cladistic analysis were similar to those I expected intuitively, based on observations over the course of my study. Differences were, in each instance, due to my recognition of similarities which now appear (from the analysis) to represent symplesiotypies. Two sets of relationships, however, were particularly unexpected; and I am not yet satisfied that these reflect evolutionary histories of the species involved. The first of these is the group which comprises N. arkansana, N. fragilis, and N. zioni. I anticipated that closest phylogenetic relationship would be demonstrated between N. arkansana and N. fragilis. Cladistic analysis suggests that N. fragilis and N. zioni are more closely related to each other than either is to N. arkansana. Similarly, I expected to confirm closer relationship between N. eschscholtzii, N. desolata, and N. navajo new species than between N. diversa and any one or more of these. However, analysis suggests that N. diversa and N. eschscholtzii are sister species and together serve as the sister group of N. desolata and N. navajo. My reasons for doubting these sets of relationships were mainly based on distributional patterns and tentative scenarios formulated (intuitively) for the distributional histories of these taxa. Although alternative scenarios consistent with those sets of phylogenetic relationships suggested from cladistic analysis actually require less complex explanations for observed

distribution patterns than those I constructed originally, I am not yet convinced that cladistic analysis of structural characters, alone, is capable of recognizing a particular set of conditions and sequence of evolutionary events which may have pertained in these instances.

A hypothetical example may demonstrate this point. Consider a species, A, in which geographical variation in one or more characters is clinal (Fig. 371A), ranging from a plesiotypic character state at one geographical extreme to an apotypic state at the other. At some point in time, the range of this species is split by some barrier (as in Fig. 371B) so that members of populations on both sides of the barrier exhibit the apotypic state(s). Speciation follows, producing species A_1 and A_2 (Fig. 371C). The range of species A_1 is subsequently split (in Fig. 371D), resulting in isolates which do not share the derived state(s). If and when speciation occurs (Fig. 371E) producing species B_1 and B_2, a curious situation arises. Species B_1 and B_2, which are in fact closest phylogenetic relatives (i.e.sister species), do not share the apotypic state(s) of this(these) character(s), but species A_2 and B_2 do so. Cladistic analysis would therefore suggest closest relationship between A_2 and B_2 in the absence of contradictory data--a misinterpretation of the evolutionary history.

If populations of N. eschscholtzii, N. desolata, and N. navajo were considered presently conspecific, cumulative patterns of geographical variation in several characters (e.g. body and appendage color, shape and depth of impression of elytral and pronotal microsculpture) would be apparent which closely approximate the pattern presented in the above example (Fig. 371A). Similarly, if

populations of N. arkansana, N. fragilis, and N. zioni were considered presently conspecific, cumulative variation patterns, although less obvious, would also approximate that of the example. The sequence of events suggested in the example could therefore have followed, given operation of some factors (such as changes in climate) which could promote successive divisions of the cumulative ranges of each of these groups, resulting in the present geographical distributions and diversity of species. I can at present suggest no tests of these hypotheses other than a search for synapotypies among species presumed to be most closely related. Results of the cladistic analysis have already shown, however, that on this basis, other hypotheses of relationship are preferred. Perhaps data from additional character systems will eventually support one of these alternative hypotheses.

Twenty Palaearctic species are judged to be closely related to Nearctic species; and these are distributed among eight different groups. Zoogeographic implications of proposed relationships are discussed in section 4.3 below.

Hypothetical common ancestor of Nearctic Nebria.--Together, character states listed in Table 14 and the plesiotypic states listed in Table 15 describe a hypothetical common ancestor for Nearctic Nebria species, based on both the evolutionary classification of characters and the cladistic analysis of taxa. There is no reason to believe nor need to suggest that any organism (or group of same) so characterized ever existed. Such hypothetical ancestors function only for defining evolutionary baselines, thereby providing perspective on evolutionary change within and between groups. They are especially useful as aids in recognizing sister groups, a task otherwise made difficult by the

great divergence between living representatives of even close phylogenetic relatives.

Convergence and reversal.--An important assumption made in cladistic analysis and in subsequent reconstruction of phylogenetic relationships is that, in the evolution of organisms and of characters, divergence is more common than convergence (including parallelism) or reversal. Synapotypy is therefore more likely to arise as a result of common ancestry than from convergence or reversal; and it can then be used to recognize groups descendant from a common ancestor. I therefore agree with Ball (1975) that "it is important to note similarities apparently not the result of descent from a common ancestor", not only because "such similarities give clues to the major selective forces at work on members of the genus and might give clues to other interpretations of relationship", but also because they serve as tests of the basic assumption. Once characters have been analysed, their transformation series have been established, and a set of hypotheses on phylogenetic relationships of taxa have been selected (based on criteria outlined above), characters themselves may then be re-examined in light of these relationships for instances of convergence or reversal.

Using the set of phylogenetic relationships presented in the cladogram (Fig. 373) and the classification of characters presented in Table 15, I re-analyzed data on distributions of character states and transformations of characters to identify and quantify instances and sources of similarity not due to common ancestry. I use the term extra evolutionary step for any instance of convergence (independent acquisition of a relatively apotypic character state) or reversal

(acquisition of a relatively plesiotypic character state). I make no distinction here between parallelism and convergence. Extra evolutionary steps arise from two sources. First, they may be intrinsic to the transformation series of a character. For example, in the transformation of character no. 96 (Table 15), relative leg length, states 96^1 and $96C^2$ are convergent--i.e. have apparently evolved from two different relatively plesiotypic states, namely the plesiotypic state and state 96B, respectively. Reversals may also be intrinsic to transformations (e.g. character no. 83, continuity of elytral intervals, in which two reversal steps are apparent). Intrinsic extra evolutionary steps can be likened to alternative pathways to the same (evolutionary) destination (i.e. similarity).

The second source of extra evolutionary steps is simply independent acquisition of a particular character state (i.e. extending the analogy used above, use of the same pathway two or more times); and most extra evolutionary steps arise in this manner. I term these extrinsic extra steps because they do not require changes in the number or sequence of states in transformation series.

The 171 characters analysed comprise a total of 670 apotypic character states. If hypotheses on character transformations and phylogenetic relationships among species are correct, a total of 1468 extra evolutionary steps are required to account for the distribution of character states among Nearctic Nebria. This figure represents the sum of all intrinsic and extrinsic extra steps for all characters and character states, including a number of logical extra steps, which include those instances in which convergence is implied by reference to transformation sequence although not evident as similarity. For

example, in members of N. pusilla (species no. 3, Fig. 372), elytral humeri (character no. 77, state 77E, Table 15) are completely obliterated. Although this character state is autapotypic for members of this species, evolution must have followed a sequence similar to that proposed for the transformation of the character (Table 15). Because members of N. chalceola, the sister species of N. pusilla, exhibit rectangular humeri (the primitive condition), it is logical to record an instance of convergence here with similar transformations in other lineages.

I find the number of extra evolutionary steps noted above to be unexpectedly high, although no baseline for comparison has been provided by previous studies on convergence or reversal in carabid beetles. Data presented by Ball (1975), Erwin (1970), and others were not generated from equally comprehensive analyses of either characters or character states. My findings are, therefore, incommensurable. I must also mention that alternative sets of hypotheses on phylogenetic relationship and on transformations of characters were evaluated; but in each instance, many additional steps were required to account for character state distributions.

In order to facilitate interpretation of and future comparisons with my findings, I examined sources of these extra evolutionary steps in greater detail. For example, by calculating the frequency distributions of characters in which a given total number of intrinsic and extrinsic extra evolutionary steps are required, results represented in Fig. 374 were obtained. The mean number of extra steps required per character is 8.7018; and only 28 (16% of) characters analysed exhibit character state distributions which do not require

extra steps. The mean number of intrinsic extra steps alone per character, however, is only 0.538; and 114 (66.7% of) characters have no extra steps in their transformations (Fig. 375). A comparison of intrinsic extra steps due to convergences (Fig. 376) with those due to reversals (Fig. 377) indicates that reversal steps are more common (mean equal to 0.380 reversal steps per character) in transformation series than convergent steps (mean equal to 0.164 convergent steps per character). Also, the percentage of characters with one or more (range one to three) reversals in their transformation series is greater than that for characters with one or more intrinsic convergent steps (range one to two) (29.9% and 13.45%, respectively).

Because characters differ significantly in number of apotypic states in their respective transformation series (range from one to 14 states), a more appropriate level of comparison may be the character state. I therefore calculated frequency distributions for character states independently. Without a context of respective transformation series, however, I could not relate intrinsic extra steps to particular states in every instance. I therefore analysed character state frequency distributions only for extrinsic extra steps and compared those due to convergence with those due to reversal. Apparently, 337 character states (50.3%) have been acquired more than once (range in single character states from one to 20 instances) (Fig. 378), and the mean number of times each state has been acquired is 1.960. [Extra steps considered convergences do not include repeated acquisition of states considered reversals (the latter are counted as reversal steps)]. In contrast, only 64 character states (9.6%)

represent reversal steps which have been acquired one or more times (range in single states from one to 8 instances) (Fig. 379); and, on average, only about one state in five represents a single reversal step (i.e. mean number of reversals per character state equals 0.215). This relationship is in marked contrast to that noted above for intrinsic steps. It appears that, although reversal steps are more common than convergence steps in transformation series, the frequency with which Nebria members have evolved along reversed pathways is much lower than that along convergent pathways. The extent to which this generalization may reflect the effects of genetic factors and selective forces limiting reversals and/or divergence (thereby promoting convergence) is unknown.

Range in total number of intrinsic and extrinsic extra evolutionary steps per character is quite large (from zero to 36 steps); and the frequency distribution of extra steps per character is presented in Fig. 374. Most, but not all, characters for which numerous extra steps are required are the same as those in which group trends have been recognized (see section 4.11). Characters correlated with hindwing size and color and microsculpture characters comprise a majority of these. Strong selective forces appear to favor these evolutionary trends. However, a few characters in which many extra steps are required do not belong in this category. Shape of antennal scape (character no. 39, Table 15 and Fig. 372) is represented by only four apotypic character states; yet at least 36 instances of convergence have occurred among them (e.g. state no. 39^1, scape slightly narrowed basally, has been independently acquired at least 21

times). Again, strong selective forces must be at work on the expression of this character; but the pattern of distribution of its states among Nebria species is almost random. Oddly, this character is often extremely useful in distinguishing members of closely related species, of different subspecies, or of other allopatric populations of a species. Intraspecific and/or intrapopulational variation is, in most instances, very low or essentally absent. It is difficult to reconcile this paradoxical pattern (i.e. high degree of convergence and plasticity evident interspecifically and very low variation within species, subspecies, or populations); but I suggest that this character may be important for species recognition among members, an hypothesis I hope to test with observations later.

The above example is a good one to illustrate a final point; namely, that characters which exhibit frequent convergence or reversal in their evolution may still be useful as descriptors if intra-taxon variation is low. Such characters may also be useful in cladistic analysis, if only as an aid in recognizing relationships between two or a few species. Each character may have some limited use and should not, therefore, be rejected a priori on the basis of its complexity alone.

The large number of extra evolutionary steps noted here may cast some doubt on the correctness of the basic assumption made above on the origins of similarity. I have at present no way to evaluate this test of the assumption. However, if we assume for a moment that associations of character states exhibited by members of different species are acquired at random rather than by descent, the number of possible unique distributions of 670 character states representing

171 characters among 62 species is too large to comprehend. In comparison, the 1468 extra evolutionary steps required by sets of hypotheses proposed here on the evolution of characters and the phylogenetic relationships of species are insignificant and, I suggest, indicative of a very high degree of non-randomness. I therefore continue to accept the assumption as a working hypothesis until a better general hypothesis is proposed.

TABLE OF CONTENTS

VOLUME 2

4.2 Zoogeography 522

4.21 Introduction 522

4.22 Contemporary zoogeography: present patterns of distribution 523

4.221 Generic, lineage, and species group patterns 523

4.222 Present distributions of Nearctic species and their relatives 526

4.223 *Nebria* fossils and past distributions 595

4.224 Habitat distributions; altitudinal zonation patterns 597

4.225 Range size, disjunction, and dispersal 602

4.226 Relationship between life cycle timing and distribution 605

4.23 Historical zoogeography 608

4.3 Compatibility between proposed phylogeny and historical zoogeography 610

4.4 Evolutionary trends 611

5.0 PROSPECTUS 612

5.1 Geographical distributions and undescribed taxa 612

5.2 Future directions in *Nebria* research 614

LITERATURE CITED 618

APPENDIX A. DISPOSITION OF PRIMARY TYPES OF NEARCTIC *NEBRIA* . . 661

APPENDIX B. MATERIAL EXAMINED 668

APPENDIX C. MATERIAL STUDIED FOR EX-GROUP COMPARISONS 838

AUTOBIOGRAPHY 842

FIGURES 844

LIST OF TABLES

VOLUME 2

Table 16. Total number of species and subspecies, "approximate landmass units" (LU), "average landmass 5° interval values" (ALIV), and "total interval values" (TIV) derived from Fig. 422 528

Table 17. Frequency distribution of maximum linear extent of geographical range in kilometers for Nearctic Nebria species and subspecies (based on data from Table 12 535

Table 18. Measure of Nebria faunal similarities among montane regions (as classified in Table 1): data matrix, Simpson coefficients 541

Table 19. Measure of Nebria faunal similarities among montane regions (as classified in Table 1): data matrix, Jaccard coefficients 544

Table 20. Measure of Nebria faunal similarities among mountain ranges of the central and southern Pacific Coast region: data matrix, Simpson coefficients 548

Table 21. Measure of Nebria faunal similarities among mountain ranges of the central and southern Pacific Coast region: data matrix, Jaccard coefficients 550

Table 22. Measure of Nebria faunal similarities among mountain ranges of the central and southern Rocky Mountain regions: data matrix, Simpson coefficients 554

Table 23. Measure of Nebria faunal similarities among mountain ranges of the central and southern Rocky Mountain regions: data matrix, Jaccard coefficients 555

Table 24. Nebria species and subspecies shared between different Nearctic faunas and between Nearctic and Palaearctic faunas 574

Table 25. Data on vicariance relationships among Nearctic Nebria subspecies 579

Table 26. Data on vicariance relationships among Nearctic Nebria sister species 587

LIST OF FIGURES

VOLUME 2

Fig. 1. Components of "standardized body length" 846

Fig. 2. Habitus: general body form, type aile 846

Fig. 3. Habitus: general body form, type aptere 846

Fig. 4. Generalized head, with paired frontal red spots . . . 846

Fig. 5. Generalized head, with fused frontal red spots 846

Fig. 6. Generalized head, with fused frontal red spots, M-shaped 846

Fig. 7. Elytral microsculpture, Nebria darlingtoni new species 848

Fig. 8. Elytral microsculpture, Nebria diversa LeConte 848

Fig. 9. Elytral microsculpture, Nebria appalachia Darlington . 848

Fig. 10. Elytral microsculpture, Nebria hudsonica LeConte . . . 848

Fig. 11. Elytral microsculpture, Nebria gregaria Fischer von Waldheim 848

Fig. 12. Elytral microsculpture, Nebria lacustris lacustris . . 848

Fig. 13. Head, Nebria crassicornis crassicornis Van Dyke . . . 850

Fig. 14. Head, Nebria crassicornis intermedia Van Dyke 850

Fig. 14A. Head, Nebria gyllenhali castanipes (Kirby) 850

Fig. 15. Head, Nebria gregaria Fischer von Waldheim 850

Fig. 16. Head, Nebria charlottae Lindroth 850

Fig. 17. Head, Nebria appalachia Darlington 850

Fig. 18. Head, Nebria gebleri gebleri Dejean 850

Fig. 19. Head, Nebria ovipennis LeConte 850

Fig. 20. Head, Nebria spatulata spatulata Van Dyke 850

Fig. 21. Head, Nebria metallica Fischer von Waldheim 850

Fig. 22. Head, Nebria ingens ingens Horn 852
Fig. 23. Relative measure of antenna length 852
Fig. 24. Antennal scape, Nebria gouleti new species 852
Fig. 25. Antennal scape, Nebria hudsonica LeConte 852
Fig. 26. Antennal scape, Nebria gyllenhali castanipes (Kirby) . 852
Fig. 27. Antennal scape, Nebria gyllenhali lassenensis new subspecies 852
Fig. 28. Antennal scape, Nebria gyllenhali lindrothi new subspecies 852
Fig. 29. Antennal scape, Nebria lyelli Van Dyke 852
Fig. 30. Antennal scape, Nebria arkansana uinta new subspecies 852
Fig. 31. Antennal scape, Nebria zioni zioni Van Dyke 852
Fig. 32. Antennal scape, Nebria zioni oasis new subspecies . . 852
Fig. 33. Antennal scape, Nebria ovipennis LeConte 852
Fig. 34. Antennal scape, Nebria spatulata spatulata Van Dyke . 852
Fig. 35. Antennal scape, Nebria spatulata sierrae new subspecies 852
Fig. 36. Antennal scape, Nebria vandykei vandykei Banninger . . 852
Fig. 37. Antennal scape, Nebria vandykei wyeast new subspecies 852
Fig. 38. Antennal scape, Nebria trifaria trifaria LeConte . . . 852
Fig. 39. Antennal scape, Nebria trifaria catenata Casey 854
Fig. 40. Antennal scape, Nebria coloradensis Van Dyke 854
Fig. 41. Antennal scape, Nebria piute Erwin and Ball 854
Fig. 42. Basal antennomeres, Nebria purpurata LeConte 854
Fig. 43. Basal antennomeres, Nebria ingens ingens Horn 854

Fig. 44. Basal antennomeres, Nebria virescens Horn 854
Fig. 45. Antennal pedicel, Nebria virescens Horn 854
Fig. 46. Antennal pedicel, Nebria nivalis nivalis (Paykull) . . 854
Fig. 47. Antennal pedicel, Nebria nivalis nivalis (Paykull) . . 854
Fig. 48. Clypeus, Nebria desolata Kavanaugh 854
Fig. 49. Clypeus, Nebria hudsonica LeConte 854
Fig. 50. Labrum, Nebria pallipes Say 854
Fig. 51. Labrum, Nebria hudsonica LeConte 854
Fig. 52. Labrum, Nebria ingens ingens Horn 854
Fig. 53. Labrum, Nebria gregaria Fischer von Waldheim 854
Fig. 54. Left mandible, Nebria virescens Horne 856
Fig. 55. Left mandible, Nebria vandykei vandykei Banninger . . . 856
Fig. 56. Left mandible, Nebria nitidula (Fabricius) 856
Fig. 57. Right mandible, Nebria virescens Horn 856
Fig. 58. Right mandible, Nebria nitidula (Fabricius) 856
Fig. 59. Right mandible, Nebria appalachia Darlington 858
Fig. 60. Right maxilla, Nebria brevicollis (Fabricius) 858
Fig. 61. Labium, Nebria virescens Horn 858
Fig. 62. Labium, Nebria hudsonica LeConte 858
Fig. 63. Labium, Nebria ingens ingens Horn 858
Fig. 64. Mentum, general form and position of setae 858
Fig. 65. Mentum, Nebria hudsonica LeConte 858
Fig. 66. Mentum, Nebria lyelli Van Dyke 860
Fig. 67. Mentum, Nebria gregaria Fischer von Waldheim 860
Fig. 68. Mentum, Nebria charlottae Lindroth 860
Fig. 69. Mentum, Nebria obliqua LeConte 860
Fig. 70. Mentum, Nebria mannerheimii Fischer von Waldheim . . . 860

Fig. 71. Mentum, Nebria desolata Kavanaugh 860
Fig. 72. Mentum, Nebria carri new species 860
Fig. 73. Mentum, Nebria kincaidi kincaidi Schwarz 860
Fig. 74. Mentum, Nebria spatulata spatulata Van Dyke 860
Fig. 75. Mentum, Nebria ovipennis LeConte 860
Fig. 76. Mentum, Nebria ingens ingens Horn 862
Fig. 77. Mentum, Nebria trifaria trifaria LeConte 862
Fig. 78. Mentum, Nebria trifaria catenata Casey 862
Fig. 79. Gula, general form and position of setae 862
Fig. 80. Gula, Nebria zioni zioni Van Dyke 862
Fig. 81. Gula, Nebria purpurata LeConte 862
Fig. 82. Pronotum, general form and associated terms 864
Fig. 83. Pronotum, general form and associated terms 864
Fig. 84. Pronotum, Nebria virescens Horn 864
Fig. 85. Pronotum, Nebria chalceola Bates 864
Fig. 86. Pronotum, Nebria paradisi Darlington 864
Fig. 87. Pronotum, Nebria lacustris lacustris Casey 866
Fig. 88. Pronotum, Nebria lacustris bellorum new subspecies . . 866
Fig. 89. Pronotum, Nebria nivalis nivalis (Paykull) 866
Fig. 90. Pronotum, Nebria nivalis gaspesiana new subspecies . . 866
Fig. 91. Pronotum, fossil specimen, nivalis subgroup 866
Fig. 92. Pronotum, Nebria crassicornis crassicornis Van Dyke . 866
Fig. 93. Pronotum, Nebria crassicornis intermedia Van Dyke . . 866
Fig. 93A. Pronotum, Nebria gyllenhali castanipes (Kirby) 868
Fig. 93B. Pronotum, Nebria gyllenhali lindrothi new subspecies . 868
Fig. 94. Pronotum, Nebria lyelli Van Dyke 868
Fig. 95. Pronotum, Nebria acuta acuta Lindroth 868

Fig. 96. Pronotum, Nebria acuta quileute new subspecies 868
Fig. 97. Pronotum, Nebria sahlbergii modoc new subspecies . . . 868
Fig. 98. Pronotum, Nebria sahlbergii triad new subspecies . . . 868
Fig. 99. Pronotum, Nebria zioni zioni Van Dyke 868
Fig. 100. Pronotum, Nebria suturalis LeConte 868
Fig. 101. Pronotum, Nebria obliqua LeConte 870
Fig. 102. Pronotum, Nebria appalachia Darlington 870
Fig. 103. Pronotum, Nebria pallipes Say 870
Fig. 104. Pronotum, Nebria darlingtoni new species 870
Fig. 105. Pronotum, Nebria mannerheimii 870
Fig. 106. Pronotum, Nebria desolata Kavanaugh 870
Fig. 107. Pronotum, Nebria gebleri gebleri Dejean 870
Fig. 108. Pronotum, Nebria gebleri cascadensis new subspecies . 872
Fig. 109 Pronotum, Nebria gebleri rathvoni LeConte 872
Fig. 110. Pronotum, Nebria gebleri siskiyouensis new subspecies 872
Fig. 110A. Pronotum, Nebria gebleri strawberriensis new subspecies 872
Fig. 111. Pronotum, Nebria carri new species 872
Fig. 112. Pronotum, Nebria kincaidi kincaidi Schwarz 872
Fig. 113. Pronotum, Nebria meanyi meanyi Van Dyke 872
Fig. 114. Pronotum, Nebria meanyi lamarckensis new subspecies . 872
Fig. 115. Pronotum, Nebria meanyi sylvatica new subspecies . . . 874
Fig. 116. Pronotum, Nebria metallica Fischer von Waldheim . . . 874
Fig. 117. Pronotum, Nebria ingens ingens Horn 874
Fig. 118. Pronotum, Nebria piperi Van Dyke 874
Fig. 119. Pronotum, Nebria schwarzi schwarzi Van Dyke 876

Fig. 120. Pronotum, Nebria schwarzi beverlianna new subspecies . 876
Fig. 120A. Pronotum, Nebria purpurata LeConte 876
Fig. 121. Pronotum, Nebria trifaria trifaria LeConte 876
Fig. 121A. Pronotum, Nebria trifaria utahensis new subspecies. . . 876
Fig. 122. Pronotum, Nebria coloradensis Van Dyke 878
Fig. 123. Prothoracic venter, Nebria gouleti new species 878
Fig. 124. Prothoracic venter, Nebria sahlbergii modoc new subspecies 878
Fig. 125. Prosternal intercoxal process, Nebria brevicollis (Fabricius) 878
Fig. 125A. Prosternal intercoxal process, Nebria piperi Van Dyke 878
Fig. 126. Prosternal intercoxal process, Nebria fragilis fragilis Casey 878
Fig. 127. Prosternal intercoxal process, Nebria appalachia Darlington 878
Fig. 128. Prosternal intercoxal process, Nebria charlottae Lindroth 878
Fig. 129. Prosternal intercoxal process, Nebria gregaria Fischer von Waldheim 878
Fig. 130. Prosternal intercoxal process, Nebria ingens riversi Van Dyke 878
Fig. 131. Prosternal intercoxal process, Nebria purpurata LeConte 878
Fig. 132. Prosternal intercoxal process, Nebria arkansana uinta new subspecies 878
Fig. 133. Front coxal cavities, Nebria brevicollis (Fabricius) . 880

Fig. 134. Front coxal cavities, Nebria brevicollis (Fabricius) . 880
Fig. 135. Elytral silhouette, generalized rectangular 880
Fig. 136. Elytral silhouette, generalized subrectangular 880
Fig. 137. Elytral silhouette, generalized subovoid 880
Fig. 138. Elytral silhouette, generalized subovoid-narrowed . . 880
Fig. 139. Elytral silhouette, generalized ovoid 880
Fig. 140. Elytral silhouette, generalized tear-shaped 880
Fig. 141. Elytral silhouette, Nebria gregaria Fischer von Waldheim 880
Fig. 142. Elytral silhouette, Nebria charlottae Lindroth 880
Fig. 143. Elytral silhouette, Nebria desolata Kavanaugh 880
Fig. 144. Elytral silhouette, Nebria piperi Van Dyke 880
Fig. 145. Elytral silhouette, Nebria paradisi Darlington 880
Fig. 146. Elytra, general form and associated terms 882
Fig. 147. Elytral base, Nebria arkansana edwardsi 882
Fig. 148. Elytral base, Nebria altaica Gebler 882
Fig. 149. Elytral base, Nebria kincaidi kincaidi Schwarz 882
Fig. 150. Elytral base, Nebria kincaidi balli new subspecies . . 882
Fig. 151. Elytral base, Nebria meanyi meanyi Van Dyke 882
Fig. 152. Elytral base, Nebria meanyi lamarckensis new subspecies 882
Fig. 153. Elytral base, Nebria piperi Van Dyke 882
Fig. 154. Elytral base, Nebria ingens ingens 882
Fig. 155. Left elytron, Nebria virescens Horn 884
Fig. 156. Left elytron, Nebria frigida Sahlberg 884
Fig. 157. Left elytron, Nebria acuta acuta Lindroth 884
Fig. 158. Left elytron, Nebria sahlbergii sahlbergii Fischer

von Wäldheim 884

Fig. 159. Left elytron, Nebria suturalis LeConte 886

Fig. 160. Left elytron, Nebria vándykei vandykei Banninger . . . 886

Fig. 161. Left elytron, Nebria schwarzi schwarzi Van Dyke. . . . 886

Fig. 162. Elytral apices, Nebria virescens Horn 888

Fig. 163. Elytral apices, Nebria chalceola Bates 888

Fig. 164. Elytral apices, Nebria paradisi Darlington 888

Fig. 165. Elytral apices, Nebria lacustris lacustris Casey . . . 888

Fig. 166. Elytral apices, Nebria pallipes Say 888

Fig. 167. Elytral apices, Nebria meanyi meanyi Van Dyke 888

Fig. 168. Elytral apices, Nebria schwarzi schwarzi Van Dyke . . . 888

Fig. 169. Internal plica, Nebria hudsonica LeConte 890

Fig. 170. Internal plica, Nebria hudsonica LeConte 890

Fig. 171. Elytral base, Nebria gouleti new species 890

Fig. 172. Elytral base, Nebria metallica Fischer von Waldheim . 890

Fig. 173. Elytral base, Nebria trifaria trifaria LeConte . . . 890

Fig. 174. Elytral base, Pterostichus adstrictus Eschscholtz . . 890

Fig. 175. Elytral base, Amara insignis Dejean 890

Fig. 176. Elytral base, Agonum maculicolle Dejean 890

Fig. 177. Elytral base, Patrobus longicornis Say 890

Fig. 178. Elytral fragments, fossil specimens, Nebria nivalis (Paykull) 892

Fig. 179. Elytral fragments, fossil specimens, Nebria lacustris Casey or Nebria pallipes Say 892

Fig. 180. Elytral fragments, fossil specimens, Nebria suturalis LeConte 894

Fig. 181. Hindwing (metathoracic wing), general form and

associated terms 896
Fig. 182. Hindwing, Nebria virescens Horn 896
Fig. 183. Hindwing, Nebria appalachia Darlington 896
Fig. 184. Hindwing, Nebria coloradensis Van Dyke 896
Fig. 185. Hindwing, Nebria charlottae Lindroth 896
Fig. 186. Hindwing, Nebria gregaria Fischer von Waldheim 898
Fig. 187. Hindwing, Nebria purpurata LeConte 898
Fig. 188. Hindwing, Nebria fragilis fragilis Casey 898
Fig. 189. Hindwing, Nebria lyelli Van Dyke 898
Fig 190. Hindwing, Nebria spatulata sierrae new subspecies . . 898
Fig. 191. Hindwing, Nebria gyllenhali castanipes (Kirby) 898
Fig. 192. Hindwing, Nebria gyllenhali lindrothi new subspecies . 898
Fig. 193. Hindwing, Nebria arkansana arkansana Casey 900
Fig. 194. Hindwing, Nebria arkansana uinta new subspecies . . . 900
Fig. 195. Hindwing, Nebria navajo new species 900
Fig. 196. Hindwing, Nebria trifaria utahensis new subspecies . 900
Fig. 197. Oblongum cell, Nebria frigida Sahlberg 902
Fig. 198. Oblongum cell, Nebria trifaria catenata Casey 902
Fig. 199. Oblongum cell, Nebria hudsonica LeConte 902
Fig. 200. Oblongum cell, Nebria obliqua LeConte 902
Fig. 201. Wedge cell, Nebria pallipes Say 902
Fig. 202. Wedge cell, Nebria darlingtoni new species 902
Fig. 203. Wedge cell, Nebria sahlbergii modoc new subspecies . . 902
Fig. 204. Wedge cell, Nebria piperi Van Dyke 902
Fig. 205. Wedge cell, Nebria schwarzi schwarzi Van Dyke 902
Fig. 206. Hindwing, Trachypachus gibbsi LeConte 904
Fig. 207. Relative measure of metasternum length 904

Fig. 208. Metasternum, Nebria piperi Van Dyke 904
Fig. 209. Metasternum, Nebria fragilis teewinot new subspecies . 904
Fig. 210. Metasternum, Nebria kincaidi balli new subspecies . . 904
Fig. 211. Anterior intercoxal process of metasternum, Nebria meanyi lamarckensis new subspecies 906
Fig. 212. Anterior intercoxal process of metasternum, Nebria zioni oasis new subspecies 906
Fig. 213. Anterior intercoxal process of metasternum, Nebria brevicollis (Fabricius) 906
Fig. 214. Anterior intercoxal process of metasternum, Nebria virescens Horn 906
Fig. 215. Metepisternum, Nebria brevicollis (Fabricius) 906
Fig. 216. Metepisternum, Nebria obliqua LeConte 906
Fig. 217. Hindleg, Nebria crassicornis crassicornis Van Dyke . . 906
Fig. 218. Hindleg, Nebria vandykei wyeast new subspecies 906
Fig. 219. Hindleg, Nebria gouleti new species 906
Fig. 220. Front coxa, Nebria obliqua LeConte 906
Fig. 221. Middle coxa, Nebria obliqua LeConte 906
Fig. 222. Middle coxa, Nebria metallica Fischer von Waldheim . . 906
Fig. 223. Hind coxa, Pelophila borealis (Paykull) 908
Fig. 224. Hind coxa, Nebria fragilis fragilis Casey 908
Fig. 225. Hind coxa, Nebria virescens Horn 908
Fig. 226. Hind coxa, Nebria schwarzi schwarzi Van Dyke 908
Fig. 227. Hind coxa, Nebria schwarzi beverlianna new subspecies 908
Fig. 228. Hind coxa, Nebria appalachia Darlington 908
Fig. 229. Hind coxa, Nebria desolata Kavanaugh 908

Fig. 230. Front trochanter, Nebria diversa LeConte 908
Fig. 231. Middle trochanter, Nebria diversa LeConte 908
Fig. 232. Hind trochanter, Nebria diversa LeConte 908
Fig. 233. Front femur, Nebria brevicollis (Fabricius) 910
Fig. 234. Middle femur, Nebria brevicollis (Fabricius) 910
Fig. 235. Hind femur, Nebria brevicollis (Fabricius) 910
Fig. 236. Anterior tibia, Nebria brevicollis (Fabricius) 912
Fig. 237. Middle tibia, Nebria pallipes Say 914
Fig. 238. Middle tibia, Nebria gouleti new species 914
Fig. 239. Middle tibia, Nebria carri new species 914
Fig. 240. Middle tibia, Nebria virescens Horn 914
Fig. 241. Front tarsus, Nebria purpurata LeConte, male 916
Fig. 242. Front tarsus, Nebria ingens ingens Horn, male 916
Fig. 243. Front tarsus, Nebria ovipennis LeConte, male 916
Fig. 244. Hind tarsus, Nebria purpurata LeConte 918
Fig. 245. Hind tarsus, Nebria ingens ingens Horn 918
Fig. 246. Hind tarsus, Nebria ovipennis LeConte 918
Fig. 247. Hind tarsus, Nebria brevicollis (Fabricius) 918
Fig. 248. Hind tarsus, Nebria eschscholtzii Menetries 918
Fig. 249. Fourth tarsomere, hind tarsus, Nebria virescens Horn . 920
Fig. 250. Fourth tarsomere, hind tarsus, Nebria arkansana edwardsi new subspecies 920
Fig. 251. Fourth tarsomere, hind tarsus, Nebria nivalis gaspesiana new subspecies 920
Fig. 252. Fourth tarsomere, hind tarsus, Nebria paradisi Darlington 920
Fig. 253. Abdominal sterna, Nebria frigida Sahlberg, ... 922

Fig. 254. Abdominal sterna, Nebria frigida Sahlberg 922
Fig. 255. Abdominal sterna, Nebria hudsonica LeConte, male . . . 922
Fig. 256. Anal sternum, Nebria hudsonica LeConte, female 922
Fig. 257. Abdominal sterna, Nebria appalachia Darlington 922
Fig. 258. Abdominal sterna, Nebria vandykei wyeast new subspecies, male 924
Fig. 259. Anal sternum, Nebria vandykei wyeast new subspecies, female 924
Fig. 260. Male genitalia, general form and associated terms . . 924
Fig. 261. Orientation of male genitalic structures in in copulatory position 926
Fig. 262. Median lobe, Nebria virescens Horn 926
Fig. 263. Median lobe, Nebria brevicollis (Fabricius) 926
Fig. 264. Median lobe, Nebria paradisi Darlington 926
Fig. 265. Median lobe, Nebria acuta acuta Lindroth 926
Fig. 266. Median lobe, Nebria acuta quileute new subspecies . . 926
Fig. 267. Median lobe, Nebria sahlbergii sahlbergii Fischer von Waldheim 928
Fig. 268. Median lobe, Nebria arkansana edwardsi new subspecies 928
Fig. 269. Median lobe, Nebria arkansana oowah new subspecies . . 928
Fig. 270. Median lobe, Nebria arkansana uinta new subspecies . . 928
Fig. 271. Median lobe, Nebria fragilis fragilis Casey 928
Fig. 272. Median lobe, Nebria desolata Kavanaugh 928
Fig. 273. Median lobe, Nebria navajo new species 930
Fig. 274. Median lobe, Nebria eschscholtzii Menetries 930
Fig. 275. Median lobe, Nebria gebleri gebleri Dejean 930

Fig. 276. Median lobe, Nebria gebleri strawberriensis new subspecies 930
Fig. 277. Median lobe, Nebria carri new species 930
Fig. 278. Median lobe, Nebria kincaidi kincaidi Schwarz 932
Fig. 279. Median lobe, Nebria spatulata sierrae new subspecies . 932
Fig. 280. Median lobe, Nebria ovipennis LeConte 932
Fig. 281. Median lobe, Nebria trifaria trifaria LeConte 932
Fig. 282. Median lobe, Nebria trifaria catenata Casey 934
Fig. 283. Median lobe, Nebria trifaria utahensis new subspecies 934
Fig. 284. Median lobe, Nebria coloradensis Van Dyke 934
Fig. 285. Median lobe, Nebria piute Erwin and Ball 934
Fig. 286. Median lobe, Nebria gouleti new species 936
Fig. 287. Median lobe, Nebria zioni oasis new subspecies 936
Fig. 288. Internal sac of median lobe, Nebria vandykei vandykei Banninger 936
Fig. 289. Internal sac of median lobe, Nebria gyllenhali castanipes (Kirby) 936
Fig. 290. Right paramere, Nebria virescens Horn 938
Fig. 291. Left paramere, Nebria virescens Horn 938
Fig. 291A. Left paramere, Nebria paradisi Darlington 938
Fig. 292. Right paramere, Nebria gouleti new species 938
Fig. 293. Left paramere, Nebria gouleti new species 938
Fig. 294. Parameres, Nebria brevicollis (Fabricius) 938
Fig. 295. Left paramere, Nebria ovipennis LeConte 938
Fig. 296. Right paramere, Nebria schwarzi beverlianna new subspecies 938

Fig. 297. Ring sclerite in relation to median lobe 938
Fig. 298. Ring sclerite in Nebria, generalized 938
Fig. 299. Ring sclerite in Amphizoa lecontei Matthew 938
Fig. 300. Eighth sternum, Nebria virescens Horn, female 940
Fig. 301. Eighth sternum, Nebria metallica Fischer von Waldheim, female 940
Fig. 302. Eighth sternum, Nebria gouleti new species, female . . 940
Fig. 303. Eighth sternum, Nebria paradisi Darlington, female . . 940
Fig. 304. Eighth sternum, Nebria carri new species, female . . . 940
Fig. 304A. Eighth sternum, Trachypachus gibbsi LeConte 940
Fig. 305. Proctiger and paraprocts, Nebria virescens Horn . . . 940
Fig. 306. Proctiger and paraprocts, Nebria diversa LeConte . . . 940
Fig. 307. Paraproct and valvifer, Nebria arkansana edwardsi new subspecies 940
Fig. 308. Paraproct and valvifer, Nebria virescens Horn 940
Fig. 309. Valvifer, Nebria lacustris bellorum new subspecies . . 940
Fig. 310. Valvifer, Nebria lyelli Van Dyke 940
Fig. 311. Valvifer, Nebria gregaria Fischer von Waldheim 940
Fig. 312. Tenth sternum, Nebria paradisi Darlington 942
Fig. 313. Tenth sternum, Nebria suturalis LeConte 942
Fig. 314. Tenth sternum, Amphizoa lecontei Matthew 942
Fig. 315. Coxostylus, Nebria virescens Horn 944
Fig. 316. Coxostylus, Nebria darlingtoni new species 944
Fig. 317. Coxostylus, Nebria piperi Van Dyke 944
Fig. 318. Coxostylus, Nebria gebleri gebleri Dejean 944
Fig. 319. Coxostylus, Nebria gyllenhali castanipes (Kirby) . . . 944
Fig. 320. Coxostylus, Nebria nivalis nivalis (Paykull) 944

Fig. 321. Coxostylus, Nebria zioni zioni Van Dyke 944
Fig. 322. Bursa copulatrix, general form and associated terms . 946
Fig. 323. Bursa copulatrix, general form and associated terms . 946
Fig. 324. Bursa copulatrix, Nebria virescens Horn 946
Fig. 325. Bursa copulatrix, Nebria hudsonica LeConte 946
Fig. 326. Bursa copulatrix, Nebria crassicornis crassicornis Van Dyke 946
Fig. 327. Bursa copulatrix, Nebria frigida Sahlberg 948
Fig. 328. Bursa copulatrix, Nebria acuta acuta Lindroth 948
Fig. 329. Bursa copulatrix, Nebria acuta quileute new subspecies 948
Fig. 329A. Bursa copulatrix, Nebria sahlbergii sahlbergii Fischer von Waldheim 948
Fig. 330. Bursa copulatrix, Nebria sahlbergii modoc new subspecies 948
Fig. 331. Bursa copulatrix, Nebria arkansana edwardsi new subspecies 950
Fig. 332. Bursa copulatrix, Nebria arkansana oowah new subspecies 950
Fig. 333. Bursa copulatrix, Nebria gebleri gebleri Dejean . . . 952
Fig. 334. Bursa copulatrix, Nebria gebleri strawberriensis . . . 952
Fig. 335. Bursa copulatrix, Nebria kincaidi kincaidi Schwarz . . 952
Fig. 336. Bursa copulatrix, Nebria coloradensis Van Dyke 952
Fig. 336A. Bursa copulatrix, Nebria piute Erwin and Ball 952
Fig. 337. Bursa copulatrix, Nebria trifaria trifaria LeConte . . 954
Fig. 338. Bursa copulatrix, Nebria trifaria catenata Casey . . . 954
Fig. 339. Bursa copulatrix, Nebria trifaria utahensis new

subspecies 954

Fig. 340. Bursa copulatrix, Nebria paradisi Darlington 954

Fig. 341. Bursa copulatrix, Nebria darlingtoni new species . . . 954

Fig. 342. Bursa copulatrix, Nebria desolata Kavanaugh 956

Fig. 343. Bursa copulatrix, Nebria obliqua LeConte 956

Fig. 344. Bursa copulatrix, Nebria nivalis nivalis (Paykull) . . 956

Fig. 345. Spermatheca and duct, Nebria virescens Horn 956

Fig. 346. Spermatheca and duct, Nebria hudsonica LeConte 956

Fig. 347. Spermatheca and duct, Nebria frigida Sahlberg 958

Fig. 348. Spermatheca, Nebria subdilatata Motschulsky 958

Fig. 349. Spermetheca and allied structures, Notiophilus sp . . 958

Fig. 350. Spermatheca and duct, Nebria piperi Van Dyke 958

Fig. 351. Spermatheca and duct, Nebria pallipes Say 958

Fig. 352. Spermatheca and duct, Nebria crassicornis intermedia Van Dyke 960

Fig. 353. Oviduct and bursa copulatrix, Nebria brevicollis (Fabricius) 960

Fig. 354. Oviduct and bursa copulatrix, Nebria virescens Horn . 960

Fig. 355. Altitude and latitude components of distribution: Nebria hudsonica LeConte 962

Fig. 356. Altitude and latitude components of distribution: Nebria gyllenhali (Schonherr) 962

Fig. 357. Altitude and latitude components of distribution: Nebria obliqua LeConte 964

Fig. 358. Altitude and latitude components of distribution: Nebria purpurata LeConte 964

Fig. 359. Relationship between proximity to water and altitude

among Nebria, Front Range, Colorado 966
Fig. 360. Cell of Nebria diversa LeConte larva 968
Fig. 361. Life cycle timing: schematic representation 968
Fig. 362. Thoracic venter, Nebria eschscholtzii Menetries, bearing mites 970
Fig. 363. Histiosoma maritimus (Oudemans) (Acarina: Anoetidae) immature 970
Fig. 364. Floating posture, Nebria piperi Van Dyke 972
Fig. 365. Comparison in species group composition between Lindroth's (1961a) classification a two proposed earlier 974
Fig. 366. Comparison in species group composition between Lindroth's (1961a) classification of Nearctic taxa and three proposed later 976
Fig. 367. Sample cladogram reflecting relationships among extant taxa 978
Fig. 368. Hypothetical reconstruction of transformation series . 978
Fig. 369. Cladogram illustrating hypothetical set of relationships among Nebria and allied genera 978
Fig. 370. An example of use of "character correlation" in cladistic analysis 978
Fig. 371. A hypothetical evolutionary sequence 978
Fig. 372. Distribution of character states among Nearctic Nebria species and their Palaearctic relatives 980
Fig. 373. Cladogram illustrating proposed phylogenetic relationships among Nearctic Nebria species and their Palaearctic relatives 991

Fig. 374. Frequency distribution of characters and total number of extra evolutionary steps 993

Fig. 375. Frequency distribution of characters and intrinsic extra steps 993

Fig. 376. Frequency distribution of characters and convergent, intrinsic steps 993

Fig. 377. Frequency distribution of characters and reversed, intrinsic st[illegible] 993

Fig. 378. Frequency di[illegible]tion of character states and convergent, extrinsic steps 993

Fig. 379. Frequency distribution of character states and reversed, extrinsic steps 993

Fig. 380. Geographical distribution map for Nebria brevicollis (Fabricius) records in North America 995

Fig. 381. Geographical distribution map for Nebria virescens Horn 995

Fig. 382. Geographical distribution map for Nebria paradisi Darlington 995

Fig. 383. Geographical distribution map for Nebria gouleti new species 995

Fig. 384. Geographical distribution map for Nebria hudsonica LeConte and Nebria lacustris Casey 995

Fig. 385. Geographical distribution map for Nebria nivalis (Paykull) 997

Fig. 386. Geographical distribution map for Nebria nivalis (Paykull) 997

Fig. 387. Geographical distribution map for Nebria crassicornis

Van Dyke 997
Fig. 388. Geographical distribution map for Nebria gyllenhali (Schonherr) 999
Fig. 389. Geographical distribution map for Nebria frigida Sahlberg 999
Fig. 390. Geographical distribution map for Nebria acuta Lindroth and Nebria lyelli Van Dyke 1001
Fig. 391. Geographical distribution map for Nebria sahlbergii Fischer von Waldheim 1001
Fig. 392. Geographical distribution map for Nebria arkansana Casey 1001
Fig. 393. Geographical distribution map for Nebria gregaria Fischer von Waldheim and Nebria charlottae Lindroth 1001
Fig. 394. Geographical distribution map for Nebria fragilis Casey and Nebria zioni Van Dyke 1001
Fig. 395. Geographical distribution map for Nebria obliqua LeConte 1003
Fig. 396. Geographical distribution map for Nebria pallipes Say 1003
Fig. 397. Geographical distribution map for Nebria appalachia Darlington 1003
Fig. 398. Geographical distribution map for Nebria suturalis LeConte 1003
Fig. 399. Geographical distribution map for Nebria mannerheimii Fischer von Waldheim and Nebria darlingtoni new species 1005

Fig. 400. Geographical distribution map for Nebria eschscholtzii Menetries, Nebria desolata Kavanaugh, and Nebria navajo 1005

Fig. 401. Geographical distribution map for Nebria diversa LeConte 1005

Fig. 402. Geographical distribution map for Nebria gebleri Dejean 1005

Fig. 403. Geographical distribution map for Nebria spatulata Van Dyke 1005

Fig. 404. Geographical distribution map for Nebria ovipennis LeConte 1005

Fig. 405. Geographical distribution map for Nebria kincaidi Schwarz and Nebria carri new species 1005

Fig. 406. Geographical distribution map for Nebria meanyi Van Dyke 1007

Fig. 407. Geographical distribution map for Nebria metallica Fischer von Waldheim 1007

Fig. 408. Geographical distribution map for Nebria vandykei Banninger and Nebria ingens Horn 1007

Fig. 409. Geographical distribution map for Nebria piperi Van Dyke, Nebria schwarzi Van Dyke, and Nebria purpurata LeConte 1007

Fig. 410. Geographical distribution map for Nebria coloradensis Van Dyke and Nebria piute Erwin and Ball 1007

Fig. 411. Geographical distribution map for Nebria trifaria LeConte 1007

Fig. 412. Geographical distribution map for the virescens species

group 1009
Fig. 413. Geographical distribution map for the paradisi species group 1009
Fig. 414. Geographical distribution map for the gregaria species group 1009
Fig. 415. Geographical distribution map for the hudsonica species group 1009
Fig. 416. Geographical distribution map for the gyllenhali species group 1009
Fig. 417. Geographical distribution map for the mannerheimii species group 1011
Fig. 418. Geographical distribution map for the trifaria species group 1011
Fig. 419. Geographical distribution map for the ovipennis species group 1011
Fig. 420. Geographical distribution map for the obliqua species group 1011
Fig. 421. Geographical distribution map for the metallica species group 1011
Fig. 422. Numbers of Nebria species and subspecies represented in 5° latitude and longitude intervals 1013
Fig. 423. Histogram for Nebria diversity in relation to latitude 1013
Fig. 424. Histogram for Nebria diversity in relation to longitude 1013
Fig. 425. Centers of endemism among Nearctic species and subspecies of Nebria 1015

Fig. 426. Diagrammatic representation of Nebria faunal similarities, based on Simpson coefficients, for mountain ranges of central and southern Rocky Mountain regions and for ranges of central and southern Pacific Coast regions 1015

Fig. 427. Diagrammatic representation of Nebria faunal similarities, based on Jaccard coefficients, for mountain ranges of central and southern Rocky Mountain regions and for ranges of central and southern Pacific Coast regions 1015

Fig. 428. Mountain systems and ranges of North America 1017

Fig. 429. Principal drainage systems of North America 1017

Fig. 430. Diagrammatic representation of Nebria faunal similarities, based on Simpson coefficients, among major montane regions 1019

Fig. 431. Diagrammatic representation of Nebria faunal similarities, based on Jaccard coefficients, among major montane regions 1019

Fig. 432. Eastern geographical range patterns 1021

Fig. 433. Rocky Mountain geographical range patterns 1023

Fig. 434. Pacific coastal geographical range patterns 1025

Fig. 435. Northern and transamerican geographical range patterns 1027

Fig. 436. Scattergram relating lower limit of microhabitat range to southern limit of geographical range . . . 1029

Fig. 437. Vicariance patterns among Nearctic Nebria subspecies . 1031

Fig. 438. Vicariance patterns among Nearctic Nebria sister

species or other closely related species 1031

Fig. 439. Vicariance patterns within Nearctic Nebria species groups 1031

Fig. 440. Relationship between geographical range patterns and vicariance in Nebria subspecies 1033

Fig. 441. Relationship between geographical range patterns and vicariance in Nebria species 1035

Fig. 442. Patterns of altitudinal zonation among Nebria taxa: Cascade Range (Mount Rainier) and Sierra Nevada (Yosemite) 1037

Fig. 443 Patterns of altitudinal zonation among Nebria taxa: Rocky Mountains (Front Range, Colorado; and Sangre de Cristo Range, New Mexico) 1039

Fig. 444 The author conferring with his major professor on a point critical to the project 1041

4.2 ZOOGEOGRAPHY

4.21 Introduction

The objective of zoogeography is to describe distributional relationships of and patterns among extant organisms and to reconstruct historical antecedants of these relationships and patterns. Interpretation of present distributions in terms of climatic and geologic (physiographic) history promotes an understanding of the evolutionary history of a group in a context of space and time.

In this section, I first describe distribution patterns among Nearctic Nebria and their Palaearctic relatives and then attempt to reconstruct the distributional history of the group using various clues available. Darlington (1957), Erwin (1970), and Whitehead (1972) discussed the kinds of clues most frequently followed. In my study of Nebria, I relied mainly on "numbers" and "vicariance" clues; and their use is described in discussions of individual analyses.

I consider it important to bear in mind that descriptions and analyses of distribution cannot be divorced from taxonomic interpretation because, necessarily, distributions must apply to groups of organisms, and these groups must be taxonomic units at some level of inclusiveness. Decisions on formal and relative ranking of taxa may then have profound effects on results of zoogeographic analyses and on relationships and patterns perceived. These points were considered when taxonomic levels of comparison were chosen for analyses presented below. Taxa, distributions of which are described and analysed here, are those presented in the classification (section

3.33). The degree to which concordance is demonstrated between present distributions of these taxa and probable consequences of past physiographic and/or climatic events is both a measure and a test of the predictive value and correctness of the phylogeny upon which the classification is based. This concordance (or lack of same) is discussed below in section 4.3.

4.22 Contemporary zoogeography: present patterns of distribution

4.221 Generic, lineage, and species group patterns

General pattern for the genus

Genus Nebria occupies almost the entire Holarctic Region, as well as the south slope of the Himalaya and montane areas on Taiwan. Members are present in Eurasia as far north as the Arctic coast (east and west) and as far south as the Atlas Mountains of Morocco and Algeria and parts of Syria in the west and Taiwan in the east. In North America, members are restricted to areas north of 30° N latitude (see Fig. 422).

Nebria faunas are most diverse in areas rich in montane, riparian habitats, although members of a few species occupy areas with lowland forest or parkland habitats and/or are not associated with water bodies (see section 3.231 above). The ranges of very few species extend into areas with warm climates; and no species are known to occupy tropical or subtropical areas. I am at present unable to accurately define centers of species and subspecies diversity on a world-wide basis, mainly because I cannot yet assess the taxonomic

status of each of the numerous Palaearctic nominal species. Highest diversity in nominal species and subspecies occurs in western Europe, especially in the Alps and Carpathian and Caucasus Mountains.

Other nebriine genera and those of closely related tribes (e.g. Notiophilus, Paropisthius, and Opisthius) occupy ranges which are wholly or in large part sympatric with the range of Nebria. There are, therefore, no readily apparent vicariance patterns among these genera with respect to Nebria. It is possible, however, that a better understanding of phylogenetic relationships within each of these genera and within Nebria on a world-wide basis will permit recognition of some early vicariance relationships as distinct from the massive dispersals which have undoubtedly occurred since the ancestors of these genera first diverged.

Patterns among lineages and species groups

Geographical distributions of species groups which include Nearctic species are illustrated in Figs. 412 - 421. Ranges for lineages of which respective groups are members can be reconstructed by combining the ranges of all included groups. All four lineages (see cladogram, Fig. 373) represented in the Nearctic fauna are shared with the Palaearctic Region; and the respective range of each is broadly sympatric with that of all others. Although four lineages are recognized in the classification presented, only two monophyletic groups are actually represented--(1) the virescens lineage, and (2) the group comprising the remaining lineages (i.e. the gyllenhali, gregaria, and metallica lineages). Together, these two monophyletic groups include a total of 62 species, only 20 of which are restricted to the Palaearctic region and three of which (all in the gyllenhali

group) are shared between both regions. The virescens lineage is more diverse in the Palaearctic Region (two species compared to one) while the group including the other lineages is more diverse in the Nearctic Region (39 species compared to 20).

Of the 10 Nearctic species groups considered, only three are endemic to North America--the hudsonica, mannerheimii, and trifaria groups; and the sister groups of each of these taxa include Palaearctic species. Of the groups shared between the Nearctic and Palaearctic Regions, three--the virescens, paradisi, and gyllenhali groups--are more diverse in the latter region; one--the metallica group--is equally diverse in both regions; and three--the gregaria, obliqua, and ovipennis groups--are more diverse in the Nearctic Region. Among lineages with Nearctic representatives, there are no species groups which are restricted to the Palaearctic Region.

Reference to maps illustrating geographical distributions of species groups (Figs. 412 - 421) reveals the following pattern: Palaearctic representation of groups including Nearctic species is restricted, except for the gyllenhali group, to northeastern Asia, north of the Himalaya and west only to the Altai Mountains of western Mongolia and southcentral Siberia. The ranges of two species, N. nivalis and N. gyllenhali, are almost circumpolar and alone account for the broader range of the gyllenhali group. Therefore, except for the component represented by these two species, groups represented in North America are absent from Europe and western and southern Asia. My limited studies to date on the Palaearctic fauna suggest that the Himalayan Nebria fauna shares many elements with the European fauna but none with the Nearctic fauna. Japan stands out as an area in

which the ranges of Nearctic species groups and European/Himalayan elements overlap [these two faunas are otherwise geographically separate].

In summary then, Nebria lineages and species groups represented in the Nearctic Region comprise a part of the holarctic fauna which is generally restricted to North America and northeastern Asia. Both species and species group diversity in this trans-Beringian fauna is greater in North America than in Asia, although Nebria diversity in general is greater in the Palaearctic than the Nearctic Region. There is no evidence of phylogenetic or faunistic relationship between North American and European groups or lineages.

4.222 Present distributions of Nearctic species and their relatives

Geographical distribution patterns

Members of genus Nebria are widely distributed in North America, north of 30°N and south of 75°N, ranging east/west from Newfoundland to the outermost Aleutian Islands. Analyses of distribution which follow are based on data from Tables 1-13, Appendix B., and distribution maps for included taxa. They represent an attempt to quantify the data for discussion and illustration purposes. Some of the methods used are those introduced or used by Ball and Freitag (in Freitag, 1969), Erwin (1970), Nimmo (1971), and Whitehead (1972). Where appropriate, comparisons are made between my findings and those presented in the above papers. Only Nimmo's study of the Rhyacophilidae and Limnephilidae of Alberta and eastern British Columbia treats a group with predominantly montane distribution and

could therefore be expected to have produced comparable findings.

Patterns of diversity.--The geographical distributions of a Nearctic species and subspecies are illustrated by dot maps (Figs. 380 - 411). In order to describe the overall diversity pattern, I used the technique of Erwin (1970) and Whitehead (1972) and overlaid these maps with a grid map (Fig. 422). I calculated total number of taxa represented in each grid unit (each marking off an area equal to 5° longitude by 5° latitude), number of taxa represented in each latitudinal and longitudinal 5° interval, "total interval values" (TIV) (Ball and Freitag, in Freitag, 1969), and "average landmass interval values" (ALIV) (Erwin, 1970). Number of "landmass units" (LU) per interval was adjusted where necessary (e.g. at sea coasts and lake shores) for the actual amount of land in the grid unit (to nearest 0.1 unit). These data are presented in Table 16; and numbers of taxa represented in each interval are also illustrated by histograms (Figs. 423 and 424).

As the grid map illustrates, greatest Nebria diversity is centered in the West, specifically along the West Coast, from southeastern Alaska to California, with a maximum in western Washington. A second major center of diversity includes the central and southern Rocky Mountain region and the Colorado Plateau. From these centers, diversity decreases in all directions--most gradually to the north, most abruptly southward (e.g. a total of 36 taxa are represented in interval "h" (40-35° N) and only three taxa are represented in interval "i" (35-30° N). A classical subtraction pattern (Darlington, 1957) is apparent in the Alaskan fauna--diversity decreases steadily in a transect from the base of the

Table 16. Total number of species and subspecies, "approximate landmass units" (LU), "average landmass 5° interval values" (ALIV), and "total interval values" (TIV) derived from Fig. 422.

Interval	no. taxa	LU	ALIV	TIV
longitude				
A	1	0.1	10.0	1
B	2	0.1	20.0	2
C	2	0.1	20.0	2
D	3	0.1	30.0	3
E	5	0.5	18.0	9
F	5	1.9	5.3	10
G	5	2.8	3.9	11
H	4	2.6	4.2	11
I	7	2.0	5.0	10
J	8	2.1	5.2	11
K	12	2.1	9.5	20
L	17	2.8	10.4	29
M	15	3.9	7.7	30
N	32	6.7	9.7	65
O	25	8.1	7.0	57
P	23	9.1	4.8	44
Q	15	9.4	3.4	32
R	5	9.1	0.9	8
S	3	8.9	0.4	4
T	3	7.6	0.8	6

Table 16. (continued)

Interval	no. taxa	LU	ALIV	TIV
U	6	7.4	1.4	10
V	6	6.7	1.6	11
W	5	5.8	1.9	11
X	5	5.7	1.8	10
Y	5	4.2	2.6	11
Z	4	2.4	2.1	5
A'	3	1.2	4.2	5
B'	0	0.3	0.0	0
latitude				
a	2	9.9	1.0	10
b	3	17.2	1.9	33
c	12	13.5	4.1	56
d	17	13.7	5.2	71
e	20	14.7	4.8	71
f	30	12.8	5.7	73
g	35	10.8	5.8	63
h	36	9.4	5.2	49
i	3	7.8	0.4	3
j	0	3.7	0.0	0

Alaskan Peninsula to the outer Aleutian Islands. This pattern can be extended further, however, if the Pacific coastal arc from Washington to Alaska is included. The relatively high diversity recorded for grid unit "L/d" reflects the merger of coastal and Rocky Mountain faunas in this area (see also below). A lowpoint in east/west diversity is reached in the Great Plains (intervals "R", "S", and "T"). Although diversity increases slightly in the Appalachian region, only nine taxa (13% of the Nearctic fauna) are represented east of 100° W longitude, and only five of these are restricted to that area.

This pattern of Nebria diversity corresponds quite clearly (and as expected) to the distribution of mountain ranges--the latter are themselves more abundant and complexly distributed in the West than in the East. However, the uniquely high diversity of taxa in western Washington and the sharp truncation of diversity below 35° N cannot be explained on the basis of mountain distributions alone. There are, in fact, numerous mountain ranges south of this area, including the expansive highlands of Mexico. Other explanations (e.g. historical, climatic, etc.) must be sought to account for the pattern.

Low diversity in lowland areas (whether north, south, or central) reflects the small number of Nebria taxa whose members are adapted to occupy these habitats. In contrast with patterns seen among groups with predominantly lowland distributions (e.g. Evarthrus [Ball and Freitag, in Freitag, 1969]; Brachinus [Erwin, 1970]; and Schizogenius [Whitehead, 1972]), it is lowlands rather than mountains which serve as barriers for or limits to Nebria distribution. Those few lowland forms which have evolved are, in every instance, distributed on both

sides of mountain systems (e.g. see distributions of N. eschscholtzii [Fig. 400] in relation to the Sierra Nevada, N. obliqua [Fig. 395] in relation to the Rocky Mountains, and N. pallipes [Fig. 396] and N. lacustris [Fig. 384] in relation to the Appalachian Mountains. These findings suggest that climates of lowland areas are important factors limiting distributions of both montane and lowland Nebria taxa and that mountains do not serve as barriers for distributions of either (see also below).

Centers of endemism.--Centers of diversity may represent areas of overlap in ranges of two or more broadly distributed taxa, or of concentrations of taxa with restricted but congruent ranges. The latter may arise in areas where ancient forms have survived as relicts and exist alongside more recent arrivals, or where a diversity of local environmental factors promote local differentiation and restricted distribution, or where both of the above occur.

I examined the centers of diversity discovered from the grid plot by applying Whitehead's (1972) technique for finding "centers of concentration". I plotted centers of geographical distributions of all species and subspecies for which maximum linear extent of range is less than or equal to 1600 km (based on data from Table 6), and circled each center to enclose all localities within a 250 km radius of it. Results are illustrated in Fig. 425. In effect, by excluding wide-ranging taxa from consideration and focusing on centers of concentration of restricted taxa, I forced recognition of the latter, and thereby determined that, in fact, more than range overlap of wide-ranging taxa is involved. The apparent pattern is consistent with that recognized from the grid plot (Fig. 422) but represents a

refinement of its description. As noted by Whitehead (1972), his "centers of concentration" correspond to centers of endemism and are distinct from centers of diversity per se. This graphic technique demonstrates that, within some centers of diversity outlined above, there are two or more distinct centers of endemism, some of these with very limited extent. The general distributional pattern is also seen to be much more complex that is evident from the grid plot.

The west (Pacific) coastal center of diversity can now be recognized as a complex, north/south series of centers of endemism. The most diverse of these include (1) Cascade Range north of the Columbia River (five endemic taxa) and (2) Sierra Nevada (seven endemic taxa). Each of these centers can be more finely split into subcenters, each with endemic subspecies represented. [A desciption of these is better considered with discussion of vicariance relationships (see below)]. Less diverse centers of endemism in the Pacific coastal area include the Siskiyou and Klamath Mountains (California and Oregon) together (two endemic taxa), Vancouver Island and the Olympic Peninsula together (two endemic taxa), and the Aleutian Islands, Queen Charlotte Islands, Coast Mountains of British Columbia, and Warner Mountains (California) (one endemic taxon each).

Distribution of centers of endemism within the central and southern Rocky Mountain/Colorado Plateau center of diversity is even more complex than that in the west coast center (Fig. 425). Separate centers of endemism can be recognized for (1) the Teton, Wind River, and Gros Ventre Ranges together (two endemic taxa), (2) the Wasatch Mountains (one endemic taxon), (3) the Uinta Mountains (one endemic taxon), (4) the Rocky Mountains of Colorado, southcentral Wyoming,

and northcentral New Mexico together (four endemic taxa), and (5) the southwestern Colorado Plateau (six endemic taxa in distinct subcenters) (see below).

Other centers of endemism include the following: (1) main range of the Rocky Mountains of Alberta and British Columbia (from Peace River to just south of Banff) (one endemic taxon); (2) Salmon River Mountains (central Idaho) (one endemic taxon); and (3) the southern Appalachian Mountains (specifically, parts of the Blue Ridge south of the French Broad River) (two endemic taxa). The northeastern "center" evident in Fig. 425) represents the center of the range of N. nivalis gaspesiana n. ssp., a taxon endemic to the area, but which occupies disjunct parts of same.

Just as with centers of diversity, centers of endemism in Nebria do not correspond to such centers for lowland carabid groups studied to date (e.g. Evarthrus [Ball and Freitag, in Freitag, 1969], Brachinus [Erwin, 1970], and Schizogenius [Whitehead, 1972]). In fact, both diversity and endemism patterns in Nebria are more or less complementary to those of these other groups. Some congruency in patterns of endemism should be found, however, when other montane groups are studied in detail.

Extent of geographical range.--In the above plot (Fig. 425), some distortion of the distributional pattern was introduced by limiting representation of taxon distribution to a maximum radius of 250 km about the range center. Several of the taxa considered have ranges much larger than this, and position and apparent size of centers of their ranges as plotted are somewhat misleading (e.g. as noted above for N. nivalis gaspesiana). An analysis of range size characteristics

of the fauna is therefore important for proper interpretation of the significance of apparent centers of endemism. Based on data from Table 6 on maximum linear extent of range (m.e.r.) in kilometers for Nearctic taxa, I calculated the frequency distribution of ranges in size classes (each representing a 400 km size range). Results are recorded separately for species and subspecies in Table 17. Size classes are the metric equivalents of those of Ball and Freitag (in Freitag, 1969), Erwin (1970) and Whitehead (1972). Direct comparisons are therefore possible between findings of these workers and those for Nebria. Fifty-five percent of all Nebria species and 79% of all subspecies have m.e.r. values less than 1600 km (=1000 mi.). Average m.e.r. values for species and subspecies are 2511 km and 1241 km, respectively. The average value for maximum range extent in Nebria species is larger than for Evarthrus species (1120 km [=700 mi.]), Brachinus species (2080 km [=1300 mi.]), and Schizogenius species (1600 km [=1000 mi.]) (values from Whitehead, 1972). The high average m.e.r. value recorded for Nebria species is due mainly to presence in the Nearctic fauna of two species with extremely large, circumpolar ranges--namely, N. gyllenhali (m.e.r.=22,550 km) and N. nivalis (m.e.r.=17,100 km). Range of the latter is comparable to that of Schizogenius pygmaeus Van Dyke (m.e.r. 16,000 km). Among endemic Nearctic taxa, the largest m.e.r. value is that for N. gyllenhali castanipes (m.e.r.=6900 km).

Percentage of Nebria species with restricted ranges (i.e. m.e.r. values less than or equal to 1600 km) (55%) is higher than that in Brachinus (42%), slightly less than that in Schizogenius (60%), and considerably less than that in Evarthrus (79%) (values from Whitehead,

Table 17. Frequency distribution of maximum linear extent of geographical range in kilometers for Nearctic Nebria species and subspecies (based on data from Table 6).

Range size class	Species no.	Species percentage	Subspecies no.	Subspecies percentage
er 5200	2	10%	2	4.7%
4801-5200	2		0	
4401-4800	1		0	
4001-4400	2	14%	0	4.7%
3601-4000	0		0	
3201-3600	3		1	
2801-3200	4		1	
2401-2800	0	21%	1	11.6%
2001-2400	3		3	
1601-2000	2		0	
1201-1600	4		2	
801-1200	1	55%	1	79.0%
401-800	5		6	
1-400	13		25	
Average maximum extent of range:		2511 km		1241 km

1972). However, if percentages of taxa with very restricted ranges (i.e. those with m.e.r values less than 400 km [=250 mi.]) among these same genera are compared, a different picture emerges. Thirty-one percent of Nebria species are in this category, compared with 27% of Evarthrus species, 19% of Brachinus species, and 18% of Schizogenius species. Sixty percent of Nebria subspecies have m.e.r. values less than or equal to 400 km. A relatively high percentage of Nebria taxa, therefore, occupy very restricted ranges, even compared with Evarthrus members, all of which are flightless. Relative discontinuity of habitat (i.e. of montane area) probably accounts for the higher level of range restriction among Nebria than among lowland groups (e.g. Evarthrus) for which suitable habitats may be more continuous. The centers of endemism recognized above are indeed significant, denoting locations of these restricted ranges and, more importantly, overlap in same. Factors affecting range size and the relationship between range size and taxonomically significant differentiation are discussed below (see also Kavanaugh, in press B).

Faunal similarity among drainage systems and montane regions.--Members of most Nebria taxa are associated with snowfields or streams (see section 3.231 for details). It therefore seems reasonable to search for relationships between geographical distributions of taxa and particular drainage systems. Also, as noted above, distributions of Nebria taxa are clearly related to distributions of mountains. Patterns of endemism and restricted ranges of taxa further suggest relationships between taxa, or groups of same, and certain mountain systems, ranges, or regions. Measures of similarity in Nebria faunas among different drainage systems and/or among different mountain

systems or regions are, therefore, more appropriate for this study than are equivalent measures among centers of diversity or endemism (e.g. Erwin, 1970; Whitehead, 1972) [although these various "centers" may, in fact, correspond to some degree with distributions and/or subdivisions of montane areas]. Using the classifications of drainage systems and of mountain systems and ranges presented in Tables 2 and 1, respectively, and distributional data on Nebria taxa from Tables 2 and 4, I compared faunal similarities between various areas.

1. Drainage systems and Nebria distribution. A review of data presented in Table 4 indicates little if any correlation between distributions of Nebria taxa and particular drainage systems. For example, populations of N. hudsonica and N. obliqua occupy portions of several distinct drainage systems on both sides of the Rocky Mountains-- eastern slope = Mackenzie, Nelson, Missouri, and Arkansas River systems; western slope = Yukon, Fraser, Columbia, Great Basin, and Colorado River systems. This kind of pattern is general rather than unique: different stream systems which drain the same mountain system have similar if not identical Nebria faunas. Faunal similarity among drainage systems appears, therefore, to be due to shared montane source areas rather than, for example, to confluence downstream. Two possible exceptions involve distributions of N. gouleti n. sp. and the species pair, N. desolata and N. navajo n. sp. The range of N. gouleti (Fig. 383) is restricted to the lower Columbia River system, east of the Cascade Range. To date, specimens have been collected only along the lower Columbia River itself, Snake River and its tributaries in western Idaho, and Wenachee River. Ranges of N. desolata and N. navajo (Fig. 400) demonstrate a vicariance pattern

linking opposite sides of the lower Colorado River system, each apparently restricted to tributaries of the Colorado which drain north and south, respectively (see further discussion below).

These findings support the hypothesis proposed above, based on study of microhabitat distributions and preferences (see section 3.231 above), that associations with streams and other water bodies are essentially means of satisfying temperature requirements and only secondarily, if at all, involve an obligate relationship with water.

2. Mountain regions and systems and Nebria distribution. From even a quick review of data presented in Table 2, associations between distributions of individual taxa and certain mountain ranges, systems, or regions are apparent. These distributions are, of themselves, interesting to examine, especially for the clues they provide about the environmental requirements of taxon members. However, of more general interest and importance are patterns, if any, apparent among distributions of taxa. The significance of a distributional pattern increases with the frequency of its replication; and patterns which are repeated among different taxa, even among taxa representing grossly different groups, or among entire faunas, can be trusted to provide clues to their own origins in relation to past historical (climatic and physiographic) events.

One approach which aids in recognition of patterns among distributions is study of regional faunas and of similarities among these. Patterns of faunal similarity integrate data on distributions of individual taxa with data on range overlap or congruence. My intent was to examine faunal similarities among the least inclusive montane units (84 in number) classified in Table 1. However, the

number of calculations required to compare each unit with all others was prohibitively large, surpassing capabilities of computer facilities available to me as well as time available for hand calculation. I therefore compared Nebria faunal similarities among physiographic regions; and, in this way, the number of montane areas compared was reduced to 20.

Two measures of similarity were used, each providing somewhat different information, and each introducing its own particular bias. The first, Simpson's (1960) coefficient of similarity between two faunas, N_1 and N_2, is calculated as follows:

$$S = (C/N_1) \times 100$$

where C is the number of taxa shared between the two areas and N_1 is the smaller fauna (lesser number of taxa represented). The second, Jaccard's coefficient of similarity (as defined by Braun-Blanquet, 1932), is calculated as follows:

$$J = (C/N_2) \times 100$$

where C is as above and N_2 is the larger fauna (greater number of taxa represented). If the faunas compared are equal in diversity, then the two similarity measures are equivalent in value and use. Where faunal sizes are very different, each measure emphasizes a particular aspect of similarity. Simpson coefficients, by relating number of taxa shared to the smaller fauna, emphasize similarity. For example, if the smaller fauna includes only one taxon, but it is shared with the larger fauna which includes 10 taxa, the Simpson coefficient equals 100, or identity, even though only 10% of the larger fauna is represented in the smaller. This measure is especially useful in obtaining clues to the relationship between small,

peripheral, depauperate faunas and possible (larger) source areas and faunas. In contrast, Jaccard coefficients emphasize difference, especially the distinctiveness of large faunas, by relating number of shared taxa to diversity in the larger fauna. For example, if the above example is again used, the Jaccard coefficient equals 10, indicative of very low similarity. This measure effectively ignores similarity due to representation of few wide-ranging taxa in both areas compared if respective faunal diversities are very different. High Jaccard coefficients reflect of approximately equal faunal diversities and/or a high percentage of shared taxa.

Results of these tests for similarity in Nebria faunas of montane physiographic areas are presented in Tables 18 (Simpson coefficients) and 19 (Jaccard coefficients) and are graphically illustrated in Figs. 430 and 431 , respectively. These tables each consist of two triangular matrices. The upper right matrix lists coefficients of similarity for all pairs of areas, the lower left lists numbers of taxa shared by each pair, and the intervening diagonal row lists numbers of taxa for each area. Each montane area is diagramatically represented in Figs. 430 and 431. Areas between which coefficients of similarity (Simpson, Fig. 430; Jaccard, Fig. 431) are greater than or equal to 50 are linked by single lines; and those between which similarity values are equal to or greater than 75 are linked by double lines. For purposes of these analyses, species and subspecies were treated independently and equally.

Comparison of illustrations for Simpson and Jaccard coefficients demonstrates that, as expected, similarities measured by the former are more marked and numerous than those measured by the latter.

Table 18. Measure of Nebria faunal similarities among montane regions (as classified in Table 1): data matrix[1], Simpson coefficents (Simpson, 1960).

	Mountain region[2]																			
	1A	1B	1C	1D	1E	2A	2B	3A	3B	3C	3D	3E	3F	4A	4B	4C	4D	6A	6B	6C
1A	8	63	38	40	0	63	25	50	63	50	38	13	13	100	63	13	13	0	0	0
1B	5	13	46	40	0	69	15	50	67	67	42	18	20	0	62	30	20	0	0	0
1C	3	6	13	60	100	77	15	13	22	22	42	18	0	0	31	0	0	0	0	0
1D	2	2	3	5	100	60	20	20	40	40	60	20	0	0	40	0	0	0	0	0
1E	0	0	1	1	1	100	100	0	0	0	100	100	0	0	0	0	0	0	0	0
2A	5	9	10	3	1	18	36	38	44	44	50	36	10	0	43	20	20	20	0	0
2B	2	2	2	1	1	5	14	13	11	11	25	36	10	0	7	10	10	0	0	0
3A	4	4	1	1	0	3	1	8	88	88	63	25	25	100	88	50	38	20	0	0
3B	5	6	2	2	0	4	1	7	9	89	67	33	22	100	89	44	33	20	0	0
3C	4	6	2	2	0	4	1	7	8	9	78	33	22	50	89	44	33	20	0	0
3D	3	5	5	3	1	6	3	5	6	7	12	45	20	0	58	30	20	20	0	0
3E	1	2	2	1	1	4	4	2	3	3	5	11	30	0	36	30	30	20	0	0

Table 18. (continued)

	Mountain region[2]																		
	1A	1B	1C	1D	1E	2A	2B	3A	3B	3C	3D	3E	3F	4A	4B	4C	4D	6A	6B	6C
3F	1	2	0	0	0	1	1	2	2	2	2	3	10	0	30	30	50	0	0	0
4A	2	0	0	0	0	0	0	2	2	1	0	0	0	2	50	0	0	0	0	0
4B	5	8	4	2	0	6	1	7	8	8	7	4	3	1	14	60	50	40	0	0
4C	1	3	0	0	0	2	1	4	4	4	3	3	3	0	6	10	50	40	0	0
4D	1	2	0	0	0	2	1	3	3	3	2	3	5	0	5	5	10	40	0	0
6A	0	0	0	0	0	1	0	1	1	1	1	1	0	0	2	2	2	5	50	100
6B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	4	100
6C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	2

[1] Data matrix is actually two triangular matrices. The lower left matrix lists species or subspecies shared by any two regions; the upper right matrix lists Simpson coefficients of similarity for any two regions; and the diagonal row between these, corresponding to co-ordinates of identity for each region, lists the number of taxa in the region.

Table 18. (continued)

[2] Units compared here correspond to major physiographic units listed in Table 1. Representation of a taxon in any part of the physiographic unit was recorded, for purposes of this analysis, simply as representation in the whole unit. Data on Nebria distributions from Table 2.

Table 19. Measure of Nebria faunal similarities among montane regions (as classified in Table 1): data matrix[1], Jaccard coefficients (Braun-Blanquet, 1932).

	Mountain region[2]																			
	1A	1B	1C	1D	1E	2A	2B	3A	3B	3C	3D	3E	3F	4A	4B	4C	4D	6A	6B	6C
1A	8	38	23	25	0	28	14	50	56	44	25	9	10	25	36	10	10	0	0	0
1B	5	13	46	15	0	50	14	31	46	46	38	15	15	0	57	23	15	0	0	0
1C	3	6	13	23	8	56	14	8	15	15	38	15	0	0	29	0	0	0	0	0
1D	2	2	3	5	20	17	7	13	22	22	25	9	0	0	14	0	0	0	0	0
1E	0	0	1	1	1	6	7	0	0	0	8	9	0	0	0	0	0	0	0	0
2A	5	9	10	3	1	18	28	17	22	22	33	22	6	0	33	11	11	6	0	0
2B	2	2	2	1	1	5	14	7	7	7	21	29	7	0	7	7	7	0	0	0
3A	4	4	1	1	0	3	1	8	78	78	42	18	20	25	50	40	30	13	0	0
3B	5	6	2	2	0	4	1	7	9	89	50	27	20	22	57	40	30	11	0	0
3C	4	6	2	2	0	4	1	7	8	9	58	27	20	11	57	40	30	11	0	0
3D	3	5	5	3	1	6	3	5	6	7	12	42	17	0	50	25	17	8	0	0
3E	1	2	2	1	1	4	4	2	3	3	5	11	27	0	29	27	27	9	0	0

Table 19. (continued)

	Mountain region[2]																			
	1A	1B	1C	1D	1E	2A	2B	3A	3B	3C	3D	3E	3F	4A	4B	4C	4D	6A	6B	6C
3F	1	2	0	0	0	1	1	2	2	2	2	3	10	0	21	30	50	0	0	0
4A	2	0	0	0	0	0	0	2	2	1	0	0	0	2	7	0	0	0	0	0
4B	5	8	4	2	0	6	1	7	8	8	7	4	3	1	14	43	36	14	0	0
4C	1	3	0	0	0	2	1	4	4	4	3	3	3	0	6	10	50	20	0	0
4D	1	2	0	0	0	2	1	3	3	3	2	3	5	0	5	5	10	20	0	0
6A	0	0	0	0	0	1	0	1	1	1	1	1	0	0	2	2	2	5	40	40
6B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	4	50
6C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	2

[1] Refer to Table 18, footnote [1], for explanation of matrix organization.

[2] See comments in Table 18, footnote [2].

However, both tests contribute to recognition of a single pattern of faunal similarities. (1) The Nebria faunas of various parts of the Rocky Mountain region from Idaho and Montana (area 3D) northward are evidently very similar. High similarities (i.e. Simpson coefficients only) between these faunas and that of the so-called "Alaska Rocky Mountains" of northern Yukon and northern Alaska (area 4A) are apparently due to presence in the latter of few taxa, all of which are shared with areas 1A and 3A. This finding reflects the northward subtraction pattern noted above. (2) Similarity between Rocky Mountain and Coastal faunas is high from area 1B northward, but is drastically reduced south of that area. (3) Areas of the south coastal region, and eastward into the Basin and Range physiographic area; are each moderately to highly distinctive (see also Tables 18 and 19), although a widespread species (N. eschscholtzii) is shared among all these areas. (4) Faunas of the central and southern Rocky Mountains and the Colorado Plateau are all relatively similar; and all are distinct from northern Rocky Mountain faunas, except for representation of a few shared, wide-ranging taxa in all these areas. (5) Similarity between western and eastern North American faunas is low, although that between area 6A and all nearest Rocky Mountain areas is moderate (Simpson coefficient=40; see Table 18) due to representation in the former by two widespread taxa (N. gyllenhali castanipes and N. suturalis). [Area 5, the Ozark highlands region, is noted in both figures but not considered in the analyses. Nebria have not yet been recorded from this area (i.e. N=0).]

In summary of these findings, the overall pattern observed is such that, in a transect from the Arctic southward, especially in the

West, faunas of different montane areas at the same latitude are progressively more distinctive (or conversely, that, for given latitudes, similarities increase along a transect northward). In general this pattern coincides with that for centers of endemism (see above, and Fig. 425).

However, similarities noted among faunas of the Colorado Plateau and the central and southern Rocky Mountain areas (3F, 4C, and 4D) seem to contradict the pattern of high endemism within the general area. I therefore re-examined areas 4C and 4D in detail by repeating the above analyses using data for the individual mountain systems or ranges in each area. Similar analyses were also made for mountain ranges of the southern Pacific coastal region (areas 1C through 1E, 2A and 2B, which also appear to be rich in endemic forms). Results are presented in Tables 20 through 23 and Figs. 426 and 427. Because relatively higher similarities were expected among faunas compared in these analyses than among those compared above, mountain areas represented in the figures were only linked by lines if similarity values were equal to or greater than 75.

Closer examination of faunal similarities among mountain ranges within and between areas 4C and 4D reveal details not apparent from analyses of larger physiographic areas. The similarity noted above between these areas is now shown (Fig. 426) to be based on similarity between area 4Da, Laramie Mountains, and several mountain ranges in area 4C. However, as indicated by relatively low Jaccard coefficients, even this similarity is based only on representation of a few shared, widespread taxa. With exception of area 4Da, various mountain ranges of area 4D demonstrate a relatively high level of

Table 20. Measure of Nebria faunal similarities among mountain ranges of the central and southern Rocky Mountain regions: data matrix[1], Simpson coefficients (Simpson, 1960).

	Mountain ranges[2]																			
	4Ca	4Cb	4Cc	4Cd	4Ce	4Cf	4Cg	4Da	4Db	4Dc	4Dd	4De	4Df	4Dg	4Dh	4Di	4Dj	4Dk	4Dl	4Dm
4Ca	2	100	100	100	50	50	50	100	50	50	50	50	50	50	0	50	50	0	50	50
4Cb	2	7	86	100	100	67	80	100	60	50	57	33	43	40	0	25	25	0	20	25
4Cc	2	6	7	100	100	67	80	100	60	50	43	33	29	40	0	25	25	0	20	25
4Cd	2	6	6	6	100	67	80	100	60	50	50	33	33	40	0	25	25	0	20	25
4Ce	1	5	5	5	5	80	80	67	60	50	60	40	40	40	0	25	25	0	20	25
4Cf	1	4	4	4	4	6	100	67	60	50	50	33	33	40	0	25	25	0	20	25
4Cg	1	4	4	4	4	5	5	67	60	50	60	40	40	40	0	25	25	0	20	25
4Da	2	3	3	3	2	2	2	3	67	67	67	33	33	33	0	33	33	0	33	33
4Db	1	3	3	3	3	3	3	2	5	100	100	80	80	80	50	75	75	0	60	75
4Dc	1	2	2	2	2	2	2	2	4	4	100	75	75	75	50	75	75	0	75	75
4Dd	1	4	3	3	3	3	3	2	5	4	7	83	86	80	50	75	100	0	80	100
4De	1	2	2	2	2	2	2	1	4	3	5	6	100	100	100	75	100	0	80	100

Table 20. (continued)

	Mountain ranges[2]																			
	4Ca	4Cb	4Cc	4Cd	4Ce	4Cf	4Cg	4Da	4Db	4Dc	4Dd	4De	4Df	4Dg	4Dh	4Di	4Dj	4Dk	4Dl	4Dm
4Df	1	3	2	2	2	2	2	1	4	3	6	6	7	100	100	75	100	0	80	100
4Dg	1	2	2	2	2	2	2	1	4	3	4	5	5	5	100	75	75	0	60	75
4Dh	0	0	0	0	0	0	0	0	1	1	1	2	2	2	2	50	50	0	50	50
4Di	1	1	1	1	1	1	1	1	3	3	3	3	3	3	1	4	75	100	100	75
4Dj	1	1	1	1	1	1	1	1	3	3	4	4	4	3	1	3	4	0	100	100
4Dk	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	100	0
4Dl	1	1	1	1	1	1	1	1	3	3	4	4	4	3	1	4	4	1	5	100
4Dm	1	1	1	1	1	1	1	1	3	3	4	4	4	3	1	3	4	0	4	4

[1] Refer to Table 18, footnote [1], for explanation of matrix organization.

[2] Alpha-numeric code used for mountain ranges is presented in Table 1. Data on Nebria distributions used in this analysis are from Table 2.

Table 21. Measure of Nebria faunal similarities among mountain ranges of the central and southern Rocky Mountain regions: data matrix[1], Jaccard coefficients (Braun-Blanquet, 1932)

	Mountain ranges[2]																			
	4Ca	4Cb	4Cc	4Cd	4Ce	4Cf	4Cg	4Da	4Db	4Dc	4Dd	4De	4Df	4Dg	4Dh	4Di	4Dj	4Dk	4Dl	4Dm
4Ca	2	29	29	33	20	17	20	67	20	25	14	17	14	20	0	25	25	0	20	25
4Cb	2	7	86	86	71	57	57	43	43	49	57	29	43	29	0	14	14	0	14	14
4Cc	2	6	7	86	71	57	57	43	43	29	43	29	29	29	0	14	14	0	14	14
4Cd	2	6	6	6	83	67	67	50	50	33	43	33	29	33	0	17	17	0	17	17
4Ce	1	5	5	5	5	67	80	40	60	40	43	33	29	40	0	20	20	0	20	20
4Cf	1	4	4	4	4	6	83	33	50	33	43	33	29	33	0	17	17	0	17	17
4Cg	1	4	4	4	4	5	5	40	60	40	43	33	29	40	0	20	20	0	20	20
4Da	2	3	3	3	2	2	2	3	40	50	29	17	14	20	0	25	25	0	25	25
4Db	1	3	3	3	3	3	3	2	5	80	71	67	57	80	20	60	60	0	60	60
4Dc	1	2	2	2	2	2	2	2	4	4	57	50	43	60	25	75	75	0	60	75
4Dd	1	4	3	3	3	3	3	2	5	4	7	71	86	57	14	43	57	0	57	57
4De	1	2	2	2	2	2	2	1	4	3	5	6	86	83	33	50	67	0	67	67

Table 21. (continued)

	Mountain ranges[2]																			
	4Ca	4Cb	4Cc	4Cd	4Ce	4Cf	4Cg	4Da	4Db	4Dc	4Dd	4De	4Df	4Dg	4Dh	4Di	4Dj	4Dk	4Dl	4Dm
4Df	1	3	2	2	2	2	2	1	4	3	6	6	7	71	29	43	57	0	57	57
4Dg	1	2	2	2	2	2	2	1	4	3	4	5	5	5	40	60	60	0	60	60
4Dh	0	0	0	0	0	0	0	0	1	1	1	2	2	2	2	25	25	0	20	25
4Di	1	1	1	1	1	1	1	1	3	3	3	3	3	3	1	4	75	25	80	75
4Dj	1	1	1	1	1	1	1	1	3	3	4	4	4	3	1	3	4	0	80	100
4Dk	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	20	0
4Dl	1	1	1	1	1	1	1	1	3	3	4	4	4	3	1	4	4	1	5	0
4Dm	1	1	1	1	1	1	1	1	3	3	4	4	4	3	1	3	4	0	4	4

[1] Refer to Table 18, footnote [1], for explanation of matrix organization.

[2] Alpha-numeric code used for mountain ranges is presented in Table 1. Data on Nebria distributions used in this analysis are from Table 2.

similarity, indicative of a relatively homogeneous fauna for the area. Because Jaccard coefficient for similarity between the Black Hills (4Ca) and Laramie Mountains (4Da) is relatively large (=67), and that between the latter and the Medicine Bow Mountains (4Db), a bona fide member of the southern Rocky Mountain (4D) fauna, is equally large, relationships of the faunas of both 4Ca and 4Da may, in fact, be more with area 4D than with 4C as suggested by Simpson coefficients (Fig. 426). This hypothesis is supported by representation of several other carabid taxa in the Black Hills fauna which are shared with the Front Range (area 4Dd) fauna but not with that of other mountain ranges of area 4C. These taxa include Dicaelus sculptilis upioides Ball and Platynus tenuicollis LeConte, both of which are also represented (at least by conspecific populations) in eastern North America. Also, Black Hills and Front Range populations of N. obliqua include both pale- and dark-legged adults. Populations in other mountain ranges of area 4C include only pale-legged adults. Because these different leg color morphs are not recognized taxonomically, and because only Nebria (and not entire carabid) faunas were compared, probable relationships between the Black Hills and the Front and other ranges of area 4D were not immediately apparent from similarity measures alone.

For reasons discussed in sections below, I was particularly interested in comparing faunal similarities between northwestern mountains ranges in area 4D and the Uinta Mountains (area 4Cg) with those between the former and the Wind River Mountains (area 4Cd). Although similarities are generally low between both 4Cd and 4Cg and ranges of area 4D, similarities between faunas of area 4D mountain ranges and the Uinta Mountains are slightly, but consistently, higher

than those between the former and the Wind River Mountains (e.g. Jaccard coefficient [Table 21] for similarity between 4Db and 4Cd = 50, and that between 4Dd and 4Cg = 60). The strongest faunal link, then, between the central and southern Rocky Mountain regions appears to be through the Uinta rather than the Wind River Mountains (if the Black Hills and Laramie Mountains are considered faunistically part of area 4D).

Faunal distinctiveness of various mountain ranges of the southern Pacific coast region noted above is again reflected by the present, more detailed analysis. Faunal connections indicated in Fig. 426 (based on Simpson coefficients) reflect only the broad distribution of N. eschscholtzii throughout the area. High levels of endemism noted above are re-emphasized by reference to generally low values for Jaccard coefficients throughout the area (see Table 23 and Fig. 427). Especially significant are the relatively low similarities between faunas of (1) mountains of Vancouver Island (1Ca) or the Olympic Peninsula (1Cb) and that of the adjacent Cascade Range; (2) portions of the Cascade Range north (2Aa) and south (2Ab) of the Columbia River; (3) portions of the Sierra Nevada north (2Ba) and south (2Bb) of Mammoth Lakes area; and (4) the Siskiyou (1Db) or Klamath (1Dc) Mountains and all other ranges of the Coast Mountain system north and south of these areas.

Unfortunately these analyses, as well as others above, are based solely on Nebria faunas which, although diverse in relation to those of many other genera, represent only fractions of the carabid faunas present in the areas studied. Results presented here therefore give only sample measures of total faunal similarities among these areas.

Table 22. Measure of Nebria faunal similarities among mountain ranges of the central and south Pacific Coast region: data matrix[1], Simpson coefficients (Simpson, 1960)

	Mountain ranges[2]											
	1Ca	1Cb	1Da	1Db	1Dc	1Dd	1Ea	1Eb	2Aa	2Ab	2Ba	2Bb
1Ca	8	78	67	0	0	0	0	0	75	50	13	13
1Cb	6	11	100	50	33	100	100	100	82	45	18	25
1Da	2	3	3	50	33	100	100	100	100	100	33	33
1Db	0	1	1	2	100	100	100	100	50	50	50	50
1Dc	0	1	1	2	3	100	100	100	33	33	33	33
1Dd	0	1	1	1	1	1	100	100	100	100	100	100
1Ea	0	1	1	1	1	1	1	100	100	100	100	100
1Eb	0	1	1	1	1	1	1	1	100	100	100	100
2Aa	6	9	3	1	1	1	1	1	16	83	36	25
2Ab	4	5	3	1	1	1	1	1	10	12	36	25
2Ba	1	2	1	1	1	1	1	1	4	4	11	63
2Bb	1	2	1	1	1	1	1	1	2	2	5	8

[1] Refer to Table 18, footnote [1], for explanation of matrix organization.

[2] Alpha-numeric code used for mountain ranges is presented in Table 1. Data on Nebria distributions used in this analysis are from Table 2.

Table 23. Measure of Nebria faunal similarities among mountain ranges of the central and south Pacific Coast region: data matrix[1], Jaccard coefficients (Braun-Blanquet, 1932).

	Mountain ranges[2]											
	1Ca	1Cb	1Da	1Db	1Dc	1Dd	1Ea	1Eb	2Aa	2Ab	2Ba	2Bb
1Ca	8	55	25	0	0	0	0	0	38	33	9	13
1Cb	6	11	27	9	9	9	9	9	56	42	18	18
1Da	2	3	3	33	33	33	33	33	19	25	9	13
1Db	0	1	1	2	67	50	50	50	6	8	9	13
1Dc	0	1	1	2	3	33	33	33	6	8	9	13
1Dd	0	1	1	1	1	1	100	100	6	8	9	13
1Ea	0	1	1	1	1	1	1	100	6	8	9	13
1Eb	0	1	1	1	1	1	1	1	6	8	9	13
2Aa	6	9	3	1	1	1	1	1	16	63	25	13
2Ab	4	5	3	1	1	1	1	1	10	12	33	17
2Ba	1	2	1	1	1	1	1	1	4	4	11	45
2Bb	1	2	1	1	1	1	1	1	2	2	5	8

[1] Refer to Table 18, footnote [1], for explanation of matrix organization.

[2] Alpha-numeric code used for mountain ranges is presented in Table 1. Data on Nebria distributions used in this analysis are from Table 2.

I should also note again here the importance of choice of taxonomic units ("operational units") used in analyses. If, for example, species only, rather than species and subspecies, were recorded for each area, similarities among certain areas would appear greater than indicated above. Use of more inclusive taxonomic units permits recognition of more general patterns of similarity at the expense of information on distinctiveness of certain faunas (at subspecies or other relatively low taxonomic levels). I attempted analyses similar to the above using taxonomic units at all levels from subspecies through lineages. In general, when units above the least inclusive (i.e. species and subspecies) were used, faunal similarities among various areas were recorded as very high, and an insufficient range of variation in similarity remained to permit meaningful comparisons among faunas of different areas. I therefore made no use of such analyses.

3. Faunal similarities in relation to macrohabitat. Nimmo (1971) examined patterns of relationship between geographical and altitudinal distributions among caddisfly (Trichoptera) species in Alberta and eastern British Columbia; and I have attempted similar comparisons (see below). This approach seems applicable in studying faunal similarities as well; but for reasons discussed above (see also Kavanaugh, in press A and B), life zone distributions, rather than strictly altitudinal distributions per se, are considered. Wherever similarity is noted between faunas of any two areas, it is of interest to know the life zone distributions of shared taxa. This information can provide additional clues to the nature and timing of historical events responsible for observed patterns of similarity.

Reference to data presented in Table 8 on life zone distributions and to results of analyses on faunal similarities discussed above have led me to the following conclusion. The pattern of similarity among Nebria faunas of various regions of North America corresponds well to the distribution of the Canadian Life Zone (see discussion, section 3.2311). Most areas linked by intervening lowlands, macrohabitats of which can be classified as Canadian Zone or higher (i.e. Hudsonian or Arctic/Alpine Zone), have very similar faunas. In western North America, relative east/west geographical continuity of the Canadian Zone is achieved just north of 52° N latitude. This is reflected by the relatively high similarity between coastal and inland Nebria faunas from that latitude northward, in contrast to low similarities among adjacent (east/west) areas south of that latitude. North/south geographical continuity of the Canadian Zone (at least in montane areas) ends at approximately 45° N latitude. Relatively low similarities between the northern and central Rocky Mountain regions (areas 4B and 4C, respectively, in Table 21 and Fig. 431), between northern and southern portions of the Cascade Range (areas 2Aa and 2Ab, respectively, in Table 23 and Fig. 427) (separated by the Columbia River valley), and between most adjacent (north-south) montane areas further south reflect Canadian Zone discontinuity south of that latitude. One reason for the correspondence noted is that maximum Nebria diversity is represented in the Canadian zone (Kavanaugh, in press B); and, therefore, discontinuity in the range of this zone results in discontinuity in the ranges of a maximum number of taxa. Divergence, subspeciation, and speciation have occurred among disjunct populations of Canadian zone species south of the area

of macrohabitat continuity; and these processes result in faunal divergence (i.e. decreased similarity among disjunct areas).

Most taxa which are represented in the faunas of many different montane areas, especially areas with minimal Nebria diversity, have members adapted for life in the Transition Zone. Taxa of this zone are, in general, responsible for high Simpson coefficients of similarity between faunas which are very different in size. Some of these, such as N. eschscholtzii, are well represented only in this zone, while others, such as N. gyllenhali castanipes and N. obliqua, occupy broad life zone and geographical ranges. One notable exception to this generalization is N. suturalis, which is one of only two taxa shared between eastern and western North American mountains. The life zone range of this species is narrow--restricted to the Arctic/Alpine Zone. Possible explanations for this unique combination of geographical and life zone ranges are discussed in section 4.23.

In general Nebria faunal distinctiveness is, as could be expected, most closely related to high-altitude diversity. Again with the exception of N. suturalis, taxa restricted to high altitudes (i.e. Hudsonian and Alpine Zones) at latitudes south of 50° N have limited geographical ranges as well. Such mountain ranges as the Cascade Range (area 2A), Sierra Nevada (area 2B), and ranges of the southern Rocky Mountains (area 4D), all of which are occupied by several such taxa, owe their distinctiveness to this element of their respective faunas. South of 40° N latitude, however, Canadian and even Transition Zone elements are, in some instances, so restricted by distribution of suitable macrohabitat that they occupy similarly limited ranges and thereby contribute to distinctiveness of their

respective faunas (e.g. as in mountain ranges on the west flank of the Colorado Plateau in Utah, area 3F).

Patterns of concordance among geographical ranges of species and subspecies.--Patterns of faunal similarity are dependent on, and therefore related to, patterns of congruence and overlap among ranges of taxa. Once identified, both kinds of patterns function as generalizations which provide additional and, in some instances, independent clues to the history and development of the fauna. Through study of patterns among ranges as well as individual ranges themselves, it may be possible to look beyond those odd or otherwise confusing distributions (due, for example, to extinctions of certain populations of single taxa) which tend to obscure geographical relationships.

Patterns observed among Nearctic Nebria taxa are described here. Analyses and discussion in this section are based on ranges of taxa as illustrated in Figs. 380 to 411. Where possible, relationships between geographical and macrohabitat range patterns are noted; and the number and names of taxa demonstrating each pattern are also reported. Ranges of all taxa named as fitting a particular pattern do not necessarily extend throughout the full extent of the pattern because the limits of each pattern represent a composite of those of all included taxa. In some instances, the combined ranges of two or more subspecies of a polytypic species were found to correspond to a recognized pattern whereas the individual ranges of each subspecies do not so correspond. I therefore treated the subspecies together rather than separately in such instances. Information on vicariance relationships among these subspecies is therefore lost here, but is

considered in the following section.

A total of 23 different range patterns are recognized here, some of which (as noted) represent extensions of other patterns or combinations of two or more less widespread patterns. It is convenient to classify the patterns geographically into one of four groups; namely, (1) eastern, (2) Rocky Mountain, (3) Pacific coastal, and (4) northern and transamerican patterns. These groups are, at present, somewhat arbitrary, as may become apparent; but certainly a jority of patterns in each group are historically related. Hopefully, future studies on other montane carabid groups will demonstrate similar groups of patterns.

1. Eastern patterns (Fig. 432):

Range pattern 1. This pattern is restricted to southern portions of the Blue Ridge of North Carolina and Tennessee. Two taxa, N. lacustris bellorum n. ssp. and N. appalachia demonstrate this pattern; and both have members restricted to higher elevations in the area (equivalent to Canadian Zone macrohabitat).

Range pattern 2. This pattern extends from the western Great Lakes and northeastern Mississippi River drainage areas eastward across the Appalachian highlands to the Piedmont region, but not onto the Coastal Plain. Its northern limit is yet poorly defined, but probably does not extend more than 200 km north of the St. Lawrence River at any point. Its northeastern limit includes the base of Gaspé Peninsula, New Brunswick, and western Nova Scotia; and its southern limit extends just south of (and therefore includes) range pattern 1. Two taxa, N. lacustris lacustris and N. pallipes, demonstrate this pattern, although range of the former does not extend

south of the French Broad River. Both of these taxa exhibit broad macrohabitat ranges (equivalent to Upper Sonoran through Canadian Zone range). This pattern corresponds most closely with Munroe's (1954) pattern "E3", but does not extend as far southwest as the latter.

Range pattern 3. This pattern unites several disjunct areas including the following: extreme north Appalachian highlands (i.e. Mount Katahdin [Maine], the [illegible] mountains of Gaspé Peninsula, western Newfoundland Island, and coastal Labrador, northwest to the east shore of Ungava Bay. Only one Nebria taxon, N. nivalis gaspesiana n. ssp., demonstrates this range pattern; but it is repeated among ranges of a diverse group of other insect species (for examples, see Lindroth, 1957 and 1963a; Howden, 1970). The pattern is similar to, and intermediate between, Munroe's (1954) patterns "NE1" and "NE2". Macrohabitat range of N. gaspesiana includes Hudsonian and Arctic/Alpine Zones.

2. Rocky Mountain patterns (Fig. 433):

Range pattern 4. This pattern includes the northern Rocky Mountain region, from southern Montana and central Idaho northwest to southern Yukon Territory, west to the Pacific Coast at latitudes north of 53° N, but not further south. Also included within limits of the pattern are the Blue Mountains of northeastern Oregon and southeastern Washington and extreme northern ranges of the Basin and Range Province in Nevada (i.e. Jarbridge and Ruby Mountains). Four taxa demonstrate this pattern; namely, N. arkansana edwardsi n. ssp., N. gebleri gebleri and N. gebleri strawberriensis (the latter restricted to a single range in the Blue Mountains), and N. schwarzi schwarzi. The macrohabitat ranges of these taxa are identical, each

being restricted to the Canadian and Hudsonian Zones. This pattern is similar to Nimmo's (1971) pattern "2", but is more resticted both north and south and more extended toward the Columbia Plateau region.

Range pattern 5. This pattern corresponds to pattern 4 in the north, but extends further south, through the central Rocky Mountain region, then southwest through the Wasatch and Uinta Mountains to the northern mountain ranges of the west rim of the Colorado Plateau. Two taxa demonstrate this pattern: N. crassicornis intermedia and N. schwarzi beverlianna. The latter is restricted to the central Rocky Mountain region and is therefore only tentatively assigned to this pattern. Its assignment to pattern 6 or 7 (below) would be equally valid, based on available data. Both taxa are represented in Canadian Zone habitats, but macrohabitat range of the former extends into the Arctic/Alpine Zone. This pattern is different in detail from any described by Munroe (1954) or Nimmo (1971), but is closest to Nimmo's pattern "2".

Range pattern 6. This pattern is similar to pattern 5 except that (1) its southern extension is through the Unita Mountains, then east to the southern Rocky Mountains of Colorado and southern Wyoming, rather than south in central Utah; (2) it extends more widely on the Columbia Plateau, to the base of the Cascade Range; and (3) its eastern limit extends across southern Canada to northwestern Lake Superior (perhaps represents a disjunct occurrence in the latter area). One taxon demonstrates this pattern; namely, N. hudsonica (Fig. 384). Macrohabitat range of this species includes Canadian and Transition Zones. This pattern is similar to Nimmo's (1971) pattern "9".

Range pattern 7. This pattern extends from the Teton Mountains southward in the central Rocky Mountain region (but not in the Black Hills or the northern Wasatch and Uinta Mountains) to the mountain ranges of western and southern portions of the Colorado Plateau. Actually, the pattern is a composite of ranges of seven taxa which are, in general, allopatric with respect to each other (see distribution maps for each taxon). These taxa include: N. fragilis fragilis, N. fragilis teewinot, N. zioni zioni, N. zioni oasis, N. desolata, N. navajo, and N. piute. Macrohabitat ranges of these taxa are diverse; but that of each is relatively restricted. N. desolata and N. navajo are restricted to the Upper Sonoran zone; N. fragilis fragilis, N. zioni zioni, and N. zioni oasis to the Transition and Canadian Zones; and N. fragilis teewinot and N. piute to the Canadian and lower Hudsonian Zones. Relationship between macrohabitat and geographical range among members of this pattern is such that taxa with more southern ranges are, in general, also resticted to lower life zones (e.g. Upper Sonoran and Transition).

Range pattern 8. This pattern includes the southern Rocky Mountain region of southern Wyoming (except for the Laramie Mountains), Colorado, and northern New Mexico, mountain ranges forming the eastern rim of the Colorado Plateau, and the Uinta and northern Wasatch Mountains. As such, it is similar to the southern end of pattern 6, but is extended further south than the latter. Six taxa demonstrate this pattern; namely: N. gyllenhali lindrothi n. ssp., N. coloradensis, N. purpurata, N. arkansana arkansana, N. arkansana oowah n. ssp., and N. arkansana uinta. The first four taxa listed all have macrohabitat ranges which include the Arctic/Alpine zone, but

each has its own lower limit (e.g. lower range limits for N. coloradensis and N. gyllenhali lindrothi are, respectively, in the Canadian and Transition Zones). N. arkansana oowah is known only from Canadian Zone habitats; and N. arkansana uinta ranges from Canadian to Transition Zone.

Range pattern 9. This pattern (not illustrated in Fig. 433) includes the central and southern Rocky Mountain regions (except for the Black Hills) and the Colorado Plateau, with an extension into the Basin and Range Province (i.e. Jarbridge and Ruby Mountains of Nevada). As such, it combines the ranges of patterns 7 and 8. One taxon, N. trifaria, including its three subspecies, demonstrates this pattern (Fig. 411). I have recognized this as a distinct pattern because geographical ranges of N. trifaria subspecies (and vicariance patterns among same) are grossly incongruent with patterns 7 and 8 (that is, the distinction between the latter two patterns is not reflected in the distributions of N. trifaria subspecies). Macrohabitat range of N. trifaria is very broad (from Arctic/ Alpine to Transition Zone), although N. trifaria utahensis is geographically restricted to an area devoid of upper Canadian and high life zones.

Range pattern 10. This pattern is the most extensive of Rocky Mountain patterns. It includes the ranges of patterns 4 through 9, except for the eastern extension of pattern 6 (Fig. 433). In addition, it includes much of the Basin and Range Province and extends westward to the eastern slope of the Sierra Nevada and Cascade Range. One species, N. obliqua, demonstrates this pattern; and, as could be expected, its macrohabitat range is broad (Hudsonian to Upper Sonoran Zone) with a low-alitude lower limit. This pattern is similar

to the western portion of Nimmo's (1971) pattern "8" but does not extend as far east in Canada as the latter.

3. Pacific coastal patterns (Fig. 434):

Range pattern 11. This pattern extends throughout the Cascade Range and Coast Mountains (including ranges on the Olympic Peninsula and Vancouver Island) from southern British Columbia to northern California. As such, it circumscribes the core area of highest Nearctic Nebria diversity. Six taxa demonstrate this pattern: N. paradisi, N. vandykei vandykei, N. vandykei wyeast, N. crassicornis crassicornis, N. gebleri cascadensis, and N. gebleri siskiyouensis. The first four taxa are well represented in the Arctic/Alpine Zone, although only N. paradisi is restricted to that zone. Macrohabitat ranges of N. gebleri subspecies are similar, each centered in the Canadian Zone and slightly extended into the Hudsonian and/or Transition Zone. This pattern is similar to, but less extended north, south, and east than, Nimmo's pattern "4".

Range pattern 12. This pattern is restricted to the Columbia Plateau and adjacent (eastern) mountain ranges (i.e. area 3D, Fig. 428). Two taxa, N. gouleti n. sp. and N. carri n. sp. demonstrate this pattern. The former is restricted to Transition and Upper Sonoran Zone macrohabitats and the latter to the Hudsonian Zone--the highest zone available in the geographical range of the species.

Range pattern 13. This pattern is similar to pattern 11, but extends further north than the latter--to the Yukon/Alaska border; and, south of the Olympic Peninsula, it is confined to the Cascade Range. Two species (four taxa) demonstrate this pattern: N. kincaidi kincaidi, N. kincaidi balli n. ssp., N. meanyi meanyi, and N. meanyi

sylvatica n. ssp. Macrohabitat ranges of all these taxa have their lower limit in the Canadian Zone. The N. kincaidi subspecies also occupy Hudsonian Zone habitats; and N. meanyi meanyi ranges into the Arctic/Alpine Zone in some areas. Neither Munroe (1954) nor Nimmo (1971) described a similar pattern.

Range pattern 14. This pattern (not illustrated in Fig. 434) is strictly coastal, confined to the Pacific seacoast from extreme northern California to the Queen Charlotte Islands, including the west coast of Vancouver Island and certain shore areas inside Puget Sound. Two taxa N. diversa and N. charlottae, may demonstrate this pattern [the placement of N. charlottae is tentative, pending its rediscovery and confirmation of its habitat range]. Members of N. diversa live on open, sandy sea beaches; and in the geographical area of its range, climate of these beaches is roughly equivalent to that of the Canadian Zone. I suggest that members of N. charlottae will also be found to have some association with seacoast habitats.

Range pattern 15. This pattern is restricted to the Aleutian Islands. A single species, N. gregaria, demonstrates this pattern. Members of this species occupy habitats above highest tideline; and in the geographical area of its range, these localities have a climate roughly equivalent to that of the Hudsonian Zone.

Range pattern 16. This pattern includes major portions of patterns 11 and 12. It extends from the Canadian/United States border(or slightly north thereof) south to the San Bernadino Mountains of southern California, and includes the Columbia Plateau, Coast Ranges from Vancouver Island south as well as the Cascade Range and Sierra Nevada. Two taxa demonstrate this pattern: N. virescens and

N. eschscholtzii. The latter is restricted to Transition and Upper Sonoran Zones throughout its geographical range; and the former has a very broad macrohabitat range (from Transition to Arctic/Alpine Zone). This pattern is similar to Munroe's (1954) pattern "W1", but it extends slightly further south and east than the latter and includes the Columbia Plateau (whereas "W1" does not).

Range pattern 17. This pattern is similar to pattern 13 but extends further west along the Alaskan coast (Gulf of Alaska), to the Kenai Peninsula. It also extends further south, to the northern Sierra Nevada. Two taxa, N. acuta and N. gyllenhali lassenensis, demonstrate this pattern. Macrohabitat range of the former is from the Canadian to the Arctic/Alpine Zone, while the latter is restricted to the Hudsonian Zone. This pattern is similar to Munroe's (1954) pattern "W4", but does not extend as far west in Alaska as the latter, and is restricted to the Cascade Range and Sierra Nevada in the south rather than to Coast Mountain ranges.

Range pattern 18. This pattern is similar to pattern 13 with the following exceptions: (1) it extends further west in Alaska to include the Aleutian Islands chain (as far west as Amchitka Island); (2) it includes the Queen Charlotte Islands; (3) its southern limit is broader, including the Warner Mountains of northeastern and the Siskiyou and Klamath Mountains of northwest California; and (4) it extends further east, on the Columbia Plateau and to, and across, the Rocky Mountains in British Columbia and Alberta (as far east as the Swan Hills), and south along these mountains to central Montana. Four species (six taxa) demonstrate this pattern: N. sahlbergii (three subspecies), N. mannerheimii, N. metallica, and N. piperi. All are

well represented in the Canadian Zone. Macrohabitat ranges of N. mannerheimii and all N. sahlbergii sspp. extend also into the Transition Zone, and those of N. piperi, N. metallica, and N. sahlbergii sahlbergii include the Hudsonian Zone. This pattern is similar to Munroe's (1954) pattern "NW2", but it extends further south and is more broadly extended in the plateau regions of central British Columbia and central Washington than the latter. Of particular interest (see section 4.23) is the range of N. metallica (Fig. 407) which extends further west in the Aleutian Islands than that of any other species (except the Aleutian endemic, N. gregaria) and further south in the Rocky Mountains than that of any other taxon whose range has been classified here among Pacific coastal patterns.

Range pattern 19. This pattern is restricted to the Sierra Nevada of California and extreme western Nevada. Nine taxa demonstrate this pattern: N. lyelli, N. darlingtoni n. sp., N. spatulata spatulata, N. spatulata sierrae n. ssp., N. ovipennis, N. gebleri rathvoni, N. meanyi lamarckensis n. ssp., N. ingens ingens, and N. ingens riversi. N. darlingtoni is restricted to the Transition Zone and lower limits of the Canadian Zone. The macrohabitat ranges of all other taxa are more or less restricted to higher life zones. Only N. gebleri rathvoni has a range which extends to the Transition Zone; and only meanyi lamarckensis and N. ovipennis share the Canadian Zone with the former. N. lyelli and N. ingens sspp. are restricted to the Arctic/Alpine Zone, where N. spatulata sspp. are also best represented.

4. Northern and transamerican patterns (Fig. 435):

Range pattern 20. This is a trans-Beringian pattern, which

extends from western Siberia (e.g. Kamchatka, Chukotsk Peninsula) east through Alaska and Yukon Territory to the Anderson River area, and south to extreme northcentral British Columbia. It also extends southwest in Alaska along the Alaskan Peninsula to the inner Aleutian Islands (as far as Unalaska Island). A single species, N. frigida, demonstrates this pattern; and its macrohabitat range is restricted to Arctic/Alpine and Hudsonian Zones. The pattern is similar to Munroe's (1954) pattern "NW3", but its south coastal and eastern limits are more restricted, and its Yukon distribution more extensive, than the latter.

Range pattern 21. This pattern is similar to pattern 20, but it extends further east across arctic Canada to the west shores of Ungava Bay (Labrador) and northeast to Baffin Island. A single taxon, N. nivalis nivalis demonstrates this pattern; and its members occupy habitats only in the Arctic/Alpine and upper Hudsonian Zones. The pattern is intermediate between Munroe's (1954) patterns "A1" and "A2", because it crosses Hudson Bay, but does not reach the Labrador coast. It differs from both these patterns in that it includes interior Alaska, central Yukon Territory, and the Mackenzie River drainage system.

Range pattern 22. This pattern is divided into eastern and Rocky Mountain (disjunct) portions. The eastern part includes the Labrador coast, the east coast of Hudson Bay, summits of the highest mountain peaks in the northern Appalachian ranges of New England (e.g. Mount Washington, New Hampshire), and northern Lake Superior. Degree of continuity between these areas is unknown at present; but areas in New England are certainly isolated from each other and from areas further

north. The western part of the pattern extends from the northern to the southern Rocky Mountain region, although the pattern is certainly discontinuous along this path. A single species, N. suturalis, demonstrates this pattern; and its macrohabitat range is restricted to the Arctic/Alpine zone, except for the population at Black Bay (Lake Superior) which apparently occupies a Hudsonian Zone habitat there.

Range pattern 23. This is a transamerican pattern, which extends from western Newfoundland Island west to the lower Yukon River valley in central Alaska. It extends southeast to the highest peaks of New England and southwest to the central Rocky Mountain region and northern ranges of the Basin and Range Province. Its northern limit corresponds rather well to northern treeline, extending beyond it only in coastal Labrador. A single taxon, N. gyllenhali castanipes, demonstrates this broad pattern. Its members occupy habitats in Transition through Arctic/Alpine Zones; but this subspecies is well-represented only in Canadian and Hudsonian Zones. The pattern is most similar to Munroe's (1954) pattern "CO2", but it extends further northeast and northwest than the latter; and it does not extend as far west (at lower latitudes) or southwest as "CO2".

From a review of the above patterns and relationships among them, I make the observations discussed here and in following paragraphs. As expected, maximum overlap of range patterns occurs in areas of highest faunal diversity, such as in western Washington (interval "Nf", Fig. 422) and northern Utah (interval "Pg", Fig. 422), unless that diversity is based in large part on endemic taxa. Again, as could be expected, centers of endemism may stand out as areas with high diversity, but also as areas with little overlap in range patterns

(see, for example, the southern Sierra Nevada and southwestern Utah, areas rich in endemic taxa).

Range patterns appear to form more or less regular patterns of concentric rings or perimeters extending out in waves from particular centers. Among these centers are: (a) central, interior Alaska Fig. 435), with patterns 20, 21, and (according to one possible interpretation) part of pattern 23 all extending in waves eastward from this area or from some area further west; (b) western Washington (especially portions of the Cascade Range in that region) (Fig. 434), with patterns 11, 13, 15, and 17 extending northward along the Pacific coast of British Columbia and Alaska, patterns 12, 16, and 18 extending eastward across the Columbia Plateau, and patterns 11, 16, 17, and 19 extending southward; (c) central Utah (Fig. 433), with patterns 5 and 7 extending north and northwest; (d) northern Colorado (Fig. 433), with patterns 6 and 8 extending west then northwest; and (e) southern Blue Ridge of eastern North Carolina and western Tennessee (Fig. 432), with pattern 2 extending north, northeast, and northwest from the area (as defined by pattern 1). Conspicuously absent from this list of centers which demonstrate concentric wave patterns are southernmost centers of endemism: namely, the Sierra Nevada and southwestern Utah. The historical significance of these wave patterns and their apparent absence from certain areas is discussed below in section 4.23.

By comparing individual range patterns with the macrohabitat ranges of their respective included taxa, a relationship between the linear extent and direction of extended waves and macrohabitat (life zone) ranges can be observed (refer to descriptions of patterns

above). The general relationship is as follows: (1) South and east or west extensions (waves) from centers appear to be related to the lower limits of macrohabitat ranges of member taxa and are therefore facilitated among taxa with members adapted for life in lower life zones (e.g. Transition and Upper Sonoran). For example, patterns 2 (Fig. 432), 10 (Fig. 433), and 16 (Fig. 434) reflect distributions of taxa so adapted; and the greater southward extent of pattern 16 than of pattern 11 (Fig. 434) (from the central Washington center) appears to reflect relatively lower minimum limits of life zone ranges for taxa demonstrating pattern 16. (2) Northward extensions from centers appear to be related to upper macrohabitat range limits, at least to some extent. For example, compare patterns 6 and 10 (Fig. 433), which reflect the ranges of N. hudsonica and N. obliqua, respectively. The upper life zone range limit for the former is the Canadian Zone, and that of the latter is the Hudsonian Zone. However, many taxa with high upper life zone range limits also have high lower life zone range limits. Distributions of Hudsonian and Arctic/Alpine macrohabitats throughout low- and mid-latitude areas are markedly discontinuous. As a result, many taxa occupying and restricted to Arctic/Alpine and Hudsonian [illegible] lower latitudes do not have geographical ranges extended as far north as expected based on the generalization made above.

One particularly intriguing finding is evidence for a region of cross-over in geographical range patterns in the central Rocky Mountain region (see Fig. 433). This 'Rocky Mountain chiasma' has its point of intersection centered almost exactly over the southwestern corner of Wyoming. The upper-left to lower-right arm of

the "X" is represented by range patterns 6 and 8, which extend from Colorado, New Mexico, and southcentral Wyoming through the Uinta and northern Wasatch Mountains, and then (pattern 6 only) north and northeast into the northern Rocky Mountain region. The other arm of the "X" is represented by range patterns 5 and 7, which extend from southern Utah north through the southern Wasatch Mountains to the northern ranges of the central Rocky Mountain region (e.g. Teton, Wind River, Gros Ventre Mountains) and then (pattern 5 only) north into the northern Rocky Mountain region. For example, if the geographical ranges of N. fragilis (Fig. 394) and N. arkansana (Fig. 392) are superimposed on a single map, the cross-over pattern is readily apparent. This illustration involves taxa with geographical ranges classified in patterns 4, 7, and 8. However, northern arms of the pattern are not always distinct, as ranges of N. hudsonica (pattern 6; and see Fig. 384) and N. crassicornis intermedia (pattern 5; and see Fig. 387) demonstrate if superimposed on a single map. In this example, the pattern is one of simple intersection rather than cross-over. Because (as noted above in appropriate taxon descriptions) the relationships between various populations of N. arkansana and N. fragilis are not yet completely clear, it is possible that the apparent cross-over pattern is merely an artifact of improper assessment of specific identity of members of certain populations (specifically those populations assigned to N. fragilis teewinot n. ssp.). I suggest, however, that the pattern does exist; and I predict that detailed studies on distribution and variation patterns among other groups will also demonstrate it. Possible interpretations of the historical development of the unlikely pattern are discussed in

Table 24. *Nebria* species and subspecies shared between different Nearctic faunas and between Nearctic and Palaearctic faunas.

Faunas[1]	Taxon shared[2]	Pattern no.[3]	Life zone range[4]	Minimum latitude[5]
E/NEF + RMF				
	N. suturalis	22	(H) to A/A	n/a
	N. gyllenhali castanipes	23	(T) to (A/A)	52
RMF + PCF				
	N. crassicornis intermedia	5	C to A/A	52
	N. piperi	18	C to H	55
	N. metallica	18	C to H	52
	N. gebleri gebleri	4	(T) to C	52
	N. gyllenhali castanipes	23	(T) to (A/A)	45
	N. sahlbergii sahlbergii	18	(T) to H	50
	N. mannerheimii	18	(T) to C	50
	N. virescens	16	T to (A/A)	45[6]
	N. hudsonica	6	T to C	45
	N. obliqua	10	US to (H)	36
	N. gouleti	12	US to T	45[6]
	N. eschscholtzii	16	US to T	45[6]

Table 24. (continued)

Faunas[1]	Taxon shared[2]	Pattern no.[3]	Life zone range[4]	Minimum latitude[5]
NAF + PAF				
	N. nivalis nivalis	21	H to A/A	60
	N. frigida	20	H to A/A	60

[1] Abbreviations for faunas are as follows: E/NEF = eastern/northeastern fauna; NAF = Nearctic fauna; PAF = Palaearctic fauna; PCF = Pacific Coastal fauna; and RMF = Rocky Mountain fauna (see text for discussion related to each).

[2] Refer to Figs. 380 - 411 for distribution maps for taxa listed.

[3] Pattern numbers refer to patterns illustrated in Figs. 432 - 435 and discussed in text.

[4] Abbreviations used are as follows: A/A = Arctic/Alpine Zone; H = Hudsonian Zone; C = Canadian Zone; T = Transition Zone; and US = Upper Sonoran Zone (modified from Merriam, 1894a and 1898). Parentheses around an entry denote occurrence of few individuals or populations in a particular zone, or only partial occupation of the zone (i.e. upper or lower extreme only) by taxon members.

[5] "Minimum latitude" refers to a rough estimate of the southernmost latitude (^{o}N) at which contact between faunal areas is maintained in the range of the taxon considered. The entry "n/a" (= not applicable) refers to the broad disjunction (and, therefore, lack of contact at any latitude) in the range of N. suturalis.

Table 24. (continued)

[6] Denotes taxa, ranges of which cross the Columbia Plateau (latitude approximately = 45° N) and are therefore shared by PCF and RMF, but which do not also link these faunas north of that latitude (refer to distribution maps for appropriate taxa).

section 4.23.

Geographical range patterns themselves, and patterns among these patterns, suggest that four different generalized faunas can be recognized in North America; namely, the eastern/northeastern fauna (E/NEF), the Rocky Mountain fauna (RMF), the Pacific Coastal fauna (PCF), and the northwestern (Alaska/Yukon) fauna (NWF). Overlap of geographical range patterns of these respective faunas is very limited, involving relatively few taxa. Data on geographical and macrohabitat ranges of taxa shared between these general faunas are presented in Table 24. Taxa shared by a given pair of faunas are listed in the table in descending order according to the lower limit of their respective life zone ranges (i.e. those taxa with highest lower limits are listed first) and secondarily according to their upper life zone range limits. It is apparent from review of these data that: (1) taxa common to the Palaearctic and Nearctic faunas are restricted to Hudsonian and Arctic/Alpine macrohabitats (life zones); (2) all taxa common to different Nearctic general faunas, with the exception of N. suturalis, have macrohabitat ranges which include the Canadian or lower life zones; and 71% of shared taxa are represented in the Transition Zone; and (3) a direct relationship is apparent between the southernmost limit of the connecting portion of the range of a taxon shared by two general faunas and the lower limit of the life zone range of that taxon (Fig. 436).

These observations agree with those made above in the discussion on similarities among different montane faunas in relation to macrohabitat. Clearly, patterns in both geographical and macrohabitat distributions are apparent among members of the Nearctic Nebria fauna.

Present distributions of taxa may reflect both present distributions of their respective required habitats and effects of various historical events. Geographical and macrohabitat range patterns described above therefore reflect, among included taxa, community in habitat requirements, evolutionary (including distributional) history, or both. Interpretation of these patterns in relation to known details of past geologic and climatic history is attempted in section 4.23.

Patterns of vicariance among Nearctic taxa.--The most generally useful set of clues about distributional histories of taxa and entire faunas are obtained from a study of vicariance patterns. An essential prerequisite to interpretation, or even recognition, of these patterns is an understanding of phylogenetic relationships (particularly sister group relationships) in the group under study, because vicariance patterns based on range disjunctions between other than sister groups are of little, if any, significance (see also Ashlock, 1974; Ball, 1976; and Croizat et al., 1974). Discussion which follows is based on the set of phylogenetic (and sister group) relationships proposed in the cladogram (Fig. 373). Data on the geographical relations of all Nearctic Nebria species and subspecies are summarized in Table 5.

Vicariance relationships are apparent among Nearctic Nebria subspecies, sister species, and sister groups of greater inclusiveness up to and including the species group level. All four lineages represented in North America are broadly sympatric; and, as noted above, ranges of Nebria and all related genera are also sympatric. Below, I discuss vicariance relationships, first among subspecies, and then among species and successively larger groups.

Table 25. Data on vicariance relationships among Nearctic Nebria subspecies.

A. East/West Relationships

Western Vicar		Intervening Gap[1]		Eastern Vicar	
Taxon	Range pattern	Distance(km)	Type	Taxon	Range pattern
N. nivalis nivalis	21	93	?	N. nivalis gaspesiana	3
N. crassicornis crassicornis	11	102	L	N. crassicornis intermedia	5
N. gyllenhali gyllenhali[2]	--	705	W,L	N. gyllenhali castanipes	23
N. gyllenhali lindrothi	8	46	L	N. gyllenhali castanipes	23
N. acuta quileute	17	111	W,L	N. acuta acuta	17
N. arkansana oowah	8	65	L	N. arkansana arkansana	8
N. arkansana uinta	8	204	L	N. arkansana arkansana	8
N. zioni oasis	7	46	L	N. zioni zioni	7
N. gebleri cascadensis	11	83	L	N. gebleri gebleri	4
N. gebleri strawberriensis	4	65	L	N. gebleri gebleri	4
N. gebleri siskiyouensis	11	204	L	N. gebleri rathvoni	19
N. kincaidi balli	13	160	W,L	N. kincaidi kincaidi	13

Table 25. (continued)

Western Vicar		Intervening Gap		Eastern Vicar	
Taxon	Range pattern	Distance(km)	Type	Taxon	Range pattern
N. spatulata spatulata	19	37	?	N. spatulata sierrae	19
N. meanyi sylvatica	13	130	W,L	N. meanyi meanyi	13
N. trifaria trifaria	9	74	L	N. trifaria utahensis	9

B. North/South Relationships

Northern Vicar		Intervening Gap		Southern Vicar	
Taxon	Range pattern	Distance(km)	Type	Taxon	Range pattern
N. lacustris lacustris	2	111	L	N. lacustris bellorum	1
N. gyllenhali castanipes	23	278	L	N. gyllenhali lassenensis	17
N. sahlbergii sahlbergii	18	185	L	N. sahlbergii modoc	18
N. sahlbergii sahlbergii	18	176	L	N. sahlbergii triad	18
N. arkansana edwardsi	4	222	L	N. arkansana uinta	8

Table 25. (continued)

Northern Vicar		Intervening Gap		Southern Vicar	
Taxon	Range pattern	Distance(km)	Type	Taxon	Range pattern
N. fragilis teewinot	7	296	L	N. fragilis fragilis	7
N. gebleri cascadensis	11	223	L	N. gebleri siskiyouensis	11
N. meanyi meanyi	13	629	L	N. meanyi lamarckensis	19
N. ingens riversi	19	93	L	N. ingens ingens	19
N. vandykei vandykei	11	93	L	N. vandykei wyeast	11
N. schwarzi schwarzi	4	962	L	N. schwarzi beverlianna	5
N. trifaria trifaria	9	93	L	N. trifaria catenata	9

[1] "Intervening gap" refers to the area between the closest populations of respective subspecies. Straight-line distance was measured directly from distributional dot maps for taxa. Gap "type" refers to the nature of the gap area: L = lowland; W = water (e.g. sea or gulf); and "?" signifies that critical characteristics of the gap are unclear.

[2] This taxon is restricted to the Palaearctic Region. I have not described range patterns for that region.

1. Vicariance relations among Nebria subspecies. According to my stated criteria for recognition of subspecies (see section 2.29), geographical ranges of subspecies are, necessarily, allopatric with respect to each other. Therefore, all conspecific subspecies demonstrate vicariance relationships with each other. Data pertinent to study of these relationships are presented in Table 25. For ease of comparison, subspecies pairs are classified as either east/west or north/south vicars. Only relationships between adjacent subspecies are examined. The following generalizations are as based on review and use of these data.

North/south and east/west vicariance patterns are approximately equal in number--12 (46%) and 14 (54%), respectively. There appear to be no fundamental differences in the nature of areas which function as gaps between north/south as opposed to east/west vicariant pairs. With only two exceptions (namely, for N. nivalis and N. spatulata subspecies; see descriptive sections for each), disjunctions between subspecies reflect easily recognizable, extant barriers--namely, lowlands and/or water gaps. The Puget lowland, which separates mainland Washington from the Olympic Peninsula and Vancouver Island, is a combined water/lowland barrier which separates the following subspecies pairs: N. acuta acuta and N. acuta quileute; N. kincaidi kincaidi and N. kincaidi balli; and N. meanyi meanyi and N. meanyi sylvatica. Bering Strait presently appears to functions as a barrier separating ranges of N. gyllenhali gyllenhali and N. gyllenhali castanipes. Gaps between all other subspecies pairs correspond to intervening lowlands, or at least to breaks in the continuity of suitable montane habitat. The term lowland as applied here is

relative. For example, the "lowland" gap between N. ingens ingens and N. ingens riversi corresponds to the area around Mammoth Lakes, a lowpoint in the Sierra Nevada south of Yosemite National Park, at an elevation of just over 2750 meters. This is hardly a "low-altitude" area, except in relation to the macrohabitat range of N. ingens, which is restricted to areas above 3400 meters. I have elsewhere (Kavanaugh, in press B) reviewed relationships between macrohabitat ranges of and the nature of gaps between Nebria subspecies.

A statistically significant difference (at P = 0.99; T value = 3.554) can be demonstrated between the average gap width (i.e. linear distance between closest populations of different subspecies) separating north/south vicars (280 km [S.D.=172.8]) and that separating east/west vicars (101 km [S.D.=55.1]) (see also Kavanaugh, in press B). One possible interpretation of this finding is that isolation leading to differentiation of north/south vicars is more difficult (or at least requires greater gap distances) than isolation of east/west vicars. This suggestion is consistent with what could be predicted based on orientation of North American mountain chains (most of which run north/south) and on the apparent relative ease with which past movements of biotas have occurred along these chains with changing climate (e.g. during glacial cycles)(see, for example, Ball, 1970; Burger, 1974; Martin, 1958; Larson, 1975; Nimmo, 1971; and Ross, 1965).

Fig. 437 illustrates, diagrammatically, the positions of gaps between adjacent subspecies. Lines connecting nearest heterosubspecific populations are equivalent to so-called "individual

tracks" (Croizat et al., 1974). Where individual tracks for two or more subspecies pairs coincide, a "generalized track" can be recognized. In general, the pattern of individual tracks is diffuse, with relatively little coincidence. This is especially evident for the Rocky Mountain Region, where, in fact, no generalized tracks can be recognized; and subspeciation patterns in this region are more or less random with respect to each other. In the Pacific coastal region, however, four generalized tracks are apparent. The first, based on two individual tracks (namely, for N. crassicornis subspecies and for N. gebleri gebleri and N. gebleri cascadensis) links faunas on opposite sides of the Okanagan lowland in southcentral British Columbia. The second links opposite sides of the Puget lowland (i.e. The Olympic Peninsula/Vancouver Island with the Cascade Range). It is based on three individual tracks; namely those for N. acuta subspecies, N. kincaidi subspecies, and for N. meanyi meanyi and N. meanyi sylvatica. A third generalized track links portions of the Cascade Range on opposite sides of the Columbia River valley. It is based on two tracks--those for N. gyllenhali castanipes and N. gyllenhali lassenensis and for N. vandykei subspecies. The fourth generalized track, based on individual tracks for N. sahlbergii sahlbergii and N. sahlbergii triad and for N. gebleri cascadensis and N. gebleri siskiyouensis, links the Cascade Range of central Oregon with the Klamath/Siskiyou mountain system of northwestern California. I note with interest that only one instance of subspecies vicariance (i.e. that for N. meanyi meanyi and N. meanyi lamarckensis) is apparent between the Cascade Range and the Sierra Nevada (see comments below for vicariance among more inclusive groups).

Generalized tracks mark locations of barriers which have more general biotic significance than individual tracks (see Croizat et al. [1974] and Platnick and Nelson [1978] for further discussion). Implications of these tracks for the distributional histories of Nebria faunas are discussed in section 6.23.

In an effort to relate patterns in geographical range to vicariance patterns, pertinent data from Table 25 were reorganized and are presented in Fig. 440. From a review of these data, I note the following: (1) A majority of subspecies vicariance relationships (58% of north/south vicars and 64% of east/west vicars) are confined to single recognized range patterns. I suggest that this reflects the relative recency of range discontinuities among these polytypic species (see below for comparison with vicariance patterns among species). (2) Because range patterns described above are composites of ranges of all included taxa, vicariance relationships of individual taxa conform rather poorly to the limits of different patterns. As a result, there are no instances of replicated vicariance between two range patterns, even in areas where generalized tracks have been recognized (see above). For example, the generalized track across the Okanagan lowland involves subspecies of N. crassicornis and N. gebleri. Although western (coastal) vicars (namely N. crassicornis crassicornis and N. gebleri cascadensis) are both members of range pattern 11, ranges of respective eastern (inland) vicars (i.e. N. crassicornis intermedia and N. gebleri gebleri) are classified in different range patterns--patterns 5 and 4, respectively. In this study at least, examination of relationships between vicariance patterns and geographical range patterns have provided less useful

information than analysis of tracks alone.

2. Vicariance relations among sister species. Data on vicariance relationships among Nearctic Nebria sister species are presented in Table 26. These data and their treatment are similar to that above for subspecies.

Vicariance relationships are demonstrated at present by 11 pairs of sister species, of which five pairs (45%) can be classified as east/west vicars and the remainder (55%) as north/south vicars. Just as with subspecies pairs, there appear to be no fundamental differences in the nature of gaps between north/south and east/west species pairs. N. gregaria and N. charlottae are restricted to island archipelagos and therefore separated by an ocean gap. All other species pairs are separated by lowland terrestrial areas, some of which (such as the Great Plains or the Colorado Plateau) are relatively broad. The nature of the gap between N. lyelli and N. acuta is not yet understood; and these species may, in fact, have parapatric or slightly overlapping ranges. I do not know enough about the southern limit to the range of N. frigida to discuss the gap between it the range of N. daisetsuzana.

The relationship between gap width and vicariance orientation described above for subspecies is not apparent among species. Although the sample size is small and variation within it is great (see Table 26), it appears that gaps between east/west species vicars are relatively larger than those between east/west subspecies vicars in relation to respective north/south vicars. This suggests that speciation among these pairs was related to an older, different set of historical events (such as the Illinoian, rather than Wisconsinan,

Table 26. Data on vicariance relationships among Nearctic Nebria sister species.

A. East/West Relationships

Western Vicar		Intervening Gap[1]		Eastern Vicar	
Taxon	Range pattern	Distance(km)	Type	Taxon	Range pattern
N. hudsonica	6	1100	L	N. lacustris	2
N. gregaria	15	2300	W	N. charlottae	14
N. kincaidi	13	440	L	N. carri	12
N. piperi	18	340	L	N. schwarzi	4
N. piute	7	440	L	N. coloradensis	8

B. North/South Relationships

Northern Vicar		Intervening Gap		Southern Vicar	
Taxon	Range pattern	Distance(km)	Type	Taxon	Range pattern
N. frigida	20	? (2000)	?	N. daisetsuzana[2]	--
N. acuta	17	60	?	N. lyelli	19

Table 26. (continued)

Northern Vicar		Intervening Gap		Southern Vicar	
Taxon	Range pattern	Distance(km)	Type	Taxon	Range pattern
N. fragilis	7	120	L	N. zioni	7
N. mannerheimii	18	620	L	N. darlingtoni	19
N. desolata	7	160	L	N navajo	7
N. vandykei	11	780	L	N. ingens	19

1 See Table 25 for explanation of gap "type" code used here.

2 This taxon is restricted to the Palaearctic region. I have not described range patterns for that region.

glaciation) which permitted much broader distribution of cold-adapted organisms than was possible during the last glacial period.

Fig. 438 illustrates, diagrammatically, the gaps separating vicariant sister species. Solid lines connecting nearest populations of respective vicars define individual tracks for sister species. In general, the pattern of these individual tracks is less diffuse than the pattern for subspecies tracks, although the simplicity of the pattern may be due in part to the relative paucity of species tracks. Three generalized tracks are apparent among species pairs, only one of which is as clearly defined as those for subspecies. The first is a track linking that portion of the Cascade Range from central Oregon northward with the Sierra Nevada. It is based on two species pairs: N. darlingtoni//N. mannerheimii and N. ingens//N. vandykei. The former pair demonstrate microhabitat ranges including the Canadian and Transition Zones, and the latter pair are restricted to the Arctic/Alpine Zone. This breadth of representation suggests that this is a significant pattern, one which is likely to appear among sister species in many different montane groups. The second generalized track spans the lowland comprising the northern Great Basin, Columbia Plateau, and the Okanagan valley. The two species pairs forming the track are N. carri//N. kincaidi and N. piperi//N. schwarzi. All four species occupy Hudsonian Zone microhabitats; and ranges of all except N. carri extend also into the Canadian Zone. This is the only generalized track which includes both species and subspecies pairs (two of each, for a total of four individual tracks). The third generalized track is less obvious than the others and may, in fact, include unrelated individual tracks—namely, those for N. desolata//

N. navajo and N. coloradensis//N. piute., The track for the former pair links opposite (north/south) sides of the lower Colorado River lowland, and that for the latter pair links opposite (east/west) sides of the Colorado Plateau, specifically across the Green River lowland. Members of the first species pair are restricted to the Upper Sonoran Zone, and those of the second pair range from the Canadian Zone upward.

Relationships between vicariance patterns and geographical range patterns are illustrated in Fig. 441. Although over half of all vicariance patterns among subspecies are confined to single range patterns, only two pairs of sister species are so restricted. Both of these pairs, N. fragilis//N. zioni and N. desolata//N. navajo, have their combined ranges within the range of pattern 7 (Fig. 433). Just as with subspecies, there are no instances of replicated vicariance between the same two range patterns. However, southern vicars representing three different species pairs have their ranges included in pattern 19. Respective northern vicars of these pairs differ in range pattern assignments; but because these different patterns are based mainly on differences in southward extent, the distinction may be trivial here. If so, tracks of these three species pairs (namely, N. acuta//N. lyelli, N. darlingtoni//N. mannerheimii, and N. ingens//N. vandykei) form a coincident, replicated pattern not demonstrated from analysis of tracks alone.

Four pairs of sister species have geographical ranges which are at present broadly sympatric. These include: N. obliqua//N. suturalis, N. appalachia//N. pallipes, N. diversa//N. eschscholtzii, and N. ovipennis//N. spatulata. In each of these pairs, however,

vicariance in habitat distribution is at least suggested. The macrohabitat ranges of N. obliqua and N. suturalis are, in fact, non-overlapping, the latter being restricted to the Arctic/Alpine Zone and the former absent from only this zone. Altitudinal ranges of N. appalachia and N. pallipes and of N. ovipennis and N. spatulata overlap to some degree (see Table 8); but my field observations suggest that abundance patterns for pair members are complementary rather than coincident--that is, at altitudes where one species is most abundant the other is poorly represented. N. diversa and N. eschscholtzii differ in both macro- and microhabitat ranges. Members of the former species live only on open, sandy sea beaches, which are, climatically, equivalent to a Canadian Zone macrohabitat. Members of the latter species live under stones on streambanks in Transition or Upper Sonoran Zone areas. Very few N. eschscholtzii individuals have been collected on ocean beaches occupied by N. diversa members; and most, if not all, of these records are for rivermouth localities, rather than open beaches per se. It is at least tempting to suggest that selection for reduced competition between these macrosympatric sister species may be a force directing (or at least influencing) development of observed patterns of habitat vicariance. The zoogeographic implications of the observed patterns are discussed below (section 4.23).

3. Vicariance relationships among species groups, subgroups, and infragroups. In general, vicariance relationships among Nearctic Nebria become more obscure when successively more inclusive sister groups are compared. An upper limit of obscurity is reached and maintained at and above the lineage level--all Nearctic lineages are

broadly sympatric. This is no doubt correlated with the fact that the inclusiveness of groups generally reflects their age. "Time of origin" of a group (Hennig, 1966) refers to the point in time when its stem species separated from the stem species of its sister group. The more remote that time, the more time there has been for any evidence of vicariance associated with that separation to have been obliterated by subsequent dispersals, extinctions, etc. Nonetheless, certain relationships and patterns are apparent among some Nebria sister groups at present.

The lowest level of inclusiveness above the sister species level is what we might call "sisters once-removed", where one species, A, is judged to be the sister of the common ancestor of two extant species, B and C. Species A, therefore, has no extant sister species, and stands alone as the sister group of species B and C. A total of seven Nearctic and related Palaearctic species are involved in this kind of relationship (see cladogram, Fig. 373). Of these, two are sympatric with one or both of their respective"sisters once-removed". N. gouleti is sympatric with N. hudsonica but not with N. lacustris; and N. gyllenhali is sympatric with both N. frigida and N. daisetsuzana. The remaining species demonstrate vicariance relationships. Three of these, N. virescens, N. metallica, and N. angustula, have respective sisters once-removed on opposite sides of the Pacific Basin. These relationships are illustrated in Fig. 439, respectively, as tracks linking (1) Oregon with northern Honshu (Japan), (2) Amchitka Island (outer Aleutian Islands) with the Komandorskiye Ostrova (Commander Islands), and (3) Kamchatka with Attu Island (Aleutian Islands) (upper track only). Two remaining species, N. arkansana and N. trifaria,

are each parapatric in relation to one of their respective sisters once-removed and allopatric in relation to the other. The geographical ranges of N. arkansana and N. fragilis approximate, but do not overlap, one another in northern Utah (relationship not illustrated); and ranges of N. trifaria and N. coloradensis have the same relationship in central Colorado (relationship not illustrated). In the absence of recognizable barriers to dispersal in the areas in question, the sigificance of these instances of parapatry is unknown.

The next level of relationship to be considered is that in which a single species is related to a larger groups of species, again as the sister of their common ancestor (stem species) (e.g. see proposed relationships of N. paradisi, Fig. 373). Seven Nearctic and one related Palaearctic species are involved in this kind of relationship. Six of these (namely, N. nivalis, N. crassicornis, N. sahlbergii, N. meanyi, N. gebleri, and N. purpurata) are at present sympatric with one or more members of their sister [illegible] N. gebleri and N. meanyi, however, I think it is still possible to recognize previous vicariance relationships (see section 4.23 below). N. paradisi and N. mellyi have sister groups on opposite sides of the Pacific Basin. These relationships are represented, respectively, in Fig. 439 by tracks linking (1) Washington with Hokkaido and the Kuril Islands (between Hokkaido and Kamchatka), and (2) southeastern (coastal) Alaska with the Altai Mountains of central Asia. I assume that future collecting in the mountainous regions of eastern Siberia will reduce the latter disjunction somewhat.

The last class of relationships to consider are those between sister groups in which diversity is apparent in both groups.

Among Nearctic sister groups and/or their Palaearctic relatives, six instances of vicariance can be recognized. The obliqua subgroup and the gregaria group (see classification, section 3.33) each have sister groups (including, respectively, N. altaica + N. ochotica + N. japonica and N. snowi + N. carbonaria) which are restricted to eastern Asia. These relationships are represented, respectively, in Fig. 439 by the tracks linking (1) the upper Yukon River valley with northeastern Siberia, and (2) Attu Island with Kamchatka (lower track only). These tracks represent the seventh and eighth individual tracks among Nebria which cross the North Pacific. Taken together, these form a significant generalized track; but it is not safe to assume that all these tracks relate to the same historical events and are therefore of equivalent age. Evidence to the contrary is presented in section 4.23.

Within North America, vicariance relationships among sister groups are as follows: (1) The kincaidi and ovipennis infragroups are north/south vicars. A track connecting their respective ranges (Fig. 438, broken line) links the Cascade Range of northern Oregon with the Sierra Nevada. This pattern is coincident with patterns for two sister species pairs (see above). (2) The schwarzi and trifaria subgroups demonstrate north/south (and to some degree coastal/inland) vicariance (this track not illustrated), although the ranges of single species in each group do overlap in northwestern Wyoming. (3) Two pairs of groups demonstrate east/west vicariance relationships. The desolata and eschscholtzii infragroups represent vicars on opposite side of the southern end of the Great Basin. In Fig. 438, this track is represented by the broken line linking the southern Sierra Nevada

with the southwestern corner of the Colorado Plateau. (4) The gregaria subgroup (including N. angustula, known only from Kamchatka) and the arkansana subgroup are sister groups which demonstrate vicariance between continental shelf and inland (Rocky Mountain) areas (this track is not illustrated). This vicariance pattern is unique in that, unlike the generalized track evident across the Okanagan lowland it does not include the coastal ranges of the mainland (e.g. Coast Mountains, Cascade Range, etc.) but, rather, bypasses them entirely.

Nebria fossils and past distributions

Fossil specimens indistinguishable from members of extant taxa provide a unique opportunity for studying past distributions of organisms and paleoenvironments (Coope, 1970a). Based on the assumption that habitat distributions of most taxa remain constant over considerable time intervals (principle of uniformitarianism), we can use our knowledge of present environmental relationships of living taxa to reconstruct past environments. Of greatest importance in present context, however, is the use of fossils in describing past distributions. Known fossil specimens referable to Nearctic Nebria taxa were discussed above (section 3.24). I here review distributional data they provide.

Among fossil specimens discovered to date, adults of the following extant species appear to be represented: N. nivalis, N. suturalis; and either N. pallipes or N. lacustris (see section 3.24 for discussion of these specimens). Two apparent records for N. nivalis are widely separated in time and location. The earliest

record is of Tertiary age (ca. 5.7 million years B.P.), from Lava Camp mine, Seward Peninsula, Alaska (Hopkins et al., 1971)--an area within the present range of this species. The second record is apparently of early Wisconsinan age (ca. 70,000 years B.P.), from the Scarborough Formation (Morgan, 1972), Toronto, Ontario. This locality is well outside the present geographical range of the species (Fig. 385; locality for fossils is marked by an "X"). Implications of the record are that (1) in early Wisconsinan time, the range of N. nivalis extended (and was probably displaced) much further south than at present, at least as far as the lower Great Lakes area; and (2) the regional environment was equivalent to that of Arctic/Alpine or upper Hudsonian Zone areas at present. N. suturalis was also represented in the Scarborough fauna. Limits to its present geographical range (Fig. 398; locality for fossils is marked by an "X") do not include the Toronto area; and the scenario suggested based on its occurrence at Scarborough is identical with that based on the N. nivalis record. It is interesting to note that, although N. nivalis and N. suturalis appear to occur together in the fossil assemblage, they are not yet known to co-exist in any locality at present. This may well be due to incomplete sampling in crucial areas (e.g. in coastal Labrador, where representatives of both species have been found).

Fossil specimens tentatively identified as either N. pallipes or N. lacustris have been recovered from the Don Formation (also in the Toronto area), which apparently represents an assemblage of Sangamon (interglacial) age (ca. 100,000 years B.P.) (A. Morgan, personal communication). Present geographical ranges of both species reach their northern limit in this general area; and it is likely that at

the time the fossils were deposited, regional environment of the area was similar to that at present or slightly warmer.

4.224 Habitat distributions; altitudinal zonation patterns

In preceding sections, I have tried to integrate data on habitat distributions with data on geographical distribution in an attempt to simulate the third dimension to Nebria distribution--namely, altitude. Reasons for reference to life zones rather than to altitude ranges per se in all preceding sections have been discussed above (section 3.231). In this section, I discuss the relationship between life zone range and geographical range in general, and then present examples of altitudinal zonation patterns among Nebria taxa in certain mountain ranges.

Relationship between life zone range and geographical range.--It seems appropriate to assume that, in general, taxa with broad macrohabitat (life zone) ranges should demonstrate broader geographical ranges than taxa with more restricted macrohabitat ranges. To test the validity of this assumption, I examined this relationship statistically, using data from Table 6 (on the maximum linear extent of geographical ranges) and Table 8 (on life zone distributions). Correlation coefficents were calculated (X = maximum linear extent of geographical range in kilometers, and Y = life zone range [number of life zones occupied]) for different samples: first those composed only of species level taxa, then those including species and subspecies level taxa. Results of these tests indicate that the assumed relationship is supported, but very poorly, by Nebria distributions. For example, the

correlation coefficient (r) for these two variables over the sample including all species equals 0.2797 (where N = 42; $mean_x$ = 2439 km, $S.D._x$ = 4255.7; $mean_y$ = 2.26 life zones, $S.D._y$ = 0.964) and $0.1 > p > 0.05$. For the sample including both species and subspeces, r = 0.2358 (N = 68; $mean_x$ = 1339 km, $S.D._x$ = 2342.3; $mean_y$ = 2.09 life zones, $S.D._y$ = 0.958) and $0.1 > p > 0.05$. In an attempt to explain the rather poor test results, I applied the same tests to selected subsets of the data--namely (1) the northern taxa (those restricted to, or most widespread in, high latitude areas) alone; and (2) the southern taxa (those restricted to areas south of 49° N latitude) alone. Tests on samples using southern taxa alone produced slightly higher correlation coefficients (for species only, r = 0.4596 [N = 19; $mean_x$ = 406 km, $S.D._x$ = 471.2; $mean_y$ = 2.05 life zones, $S.D._y$ = 0.970], which is barely significant at $p \leq 0.05$; for species and subspecies, r = 0.5589 [N = 41; $mean_x$ = 286.1, $S.D._x$ = 370.2; $mean_y$ = 1.95, $S.D._y$ = 0.9988], which is significant at $p \leq 0.001$). Results obtained in the test using northern species and subspecies were similar to those for southern species alone; but the test on northern species alone yielded a correlation coefficient equal to 0.8490 (N = 6; $mean_x$ = 9203, $S.D._x$ = 8489.7; $mean_y$ = 2.0, $S.D._y$ = 1.095) and $0.01 > p > 0.001$.

Why is the assumed relationship poorly, or at least unequally, supported by the data in general, and best supported by data from the northern species sample? Is it due to the small sample size of the latter and, hence, not really support at all? No! Northern species are the only taxa which occupy areas which offer relatively continuous macrohabitats (i.e. the Hudsonian and Arctic Life Zones). Only at

high latitudes are the effects of discontinuity in macrohabitat minimized. Taxa which are restricted to lower latitudes, even those which occupy broad life zone ranges in particular mountain ranges, are prevented from attaining broad geographical ranges at present by gaps in the range of the lowest life zone they occupy. The only exceptions are those taxa (e.g. N. obliqua) which have such low limits to their life zone ranges (e.g. in Transition or Upper Sonoran Zones) that gaps are either absent or relatively easily bridged (e.g. with slight shifts in climate). Present geographical and habitat distributions have also been determined, at least in part, by historical events; but because of the physiographic pattern of North America, discontinuities in macrohabitat suitable for most Nebria would be relatively more significant in lower latitudes under any set of climatic events likely to occur.

In summary, I have not been able to adequately demonstrate a direct relationship between extent of geographical range and extent of life zone range, although I still maintain that this relationship must, in general, apply. Failure to clearly demonstrate this relationship is testimony to the complex interplay of past and present factors which have affected distributions of Nearctic Nebria.

Altitudinal zonation patterns.--As noted in section 3.2311, overlap of geographical ranges and diversity in macrohabitat ranges among Nebria taxa result, in some areas, in classic altitidinal zonation patterns. Altitudinal ranges are difficult to define, mainly because they differ significantly with relatively minor shifts in latitude, longitude (i.e. from coastal to inland areas), and exposure (north versus south slopes of mountains). Too many independent environmental factors

affect altitudinal range to make geographically broad generalizations possible (except, as above, by reference to life zone ranges). Patterns such as those recognized below can, therefore, be recognized only for limited geographical areas. Among such studies on altitudinal zonation in insects are those of Armin (1963) and Haubold (1951) on the Carabidae of Boulder County, Colorado; Gregg (1947) on zonation in ants (Formicidae); Nebeker (1971) on various aquatic groups; and Nimmo (1971) on rhyacophilid and limnephilid caddisflies (Trichoptera) in the Alberta/eastern British Columbia Rocky Mountains. I present here altitudinal zonation patterns recognized among Nebria in four different montane areas.

First of these is the southern slope of Mount Rainier (Cascade Range, Washington). The pattern present is illustrated in Fig. 442; upper half). Altitudinal ranges of 12 taxa are represented in the figure; and considerable overlap of altitudinal ranges of different taxa is apparent. At certain altitudes, several taxa are represented. Maximum diversity occurs at the 1300 to 1400 m level, roughly equivalent to the area of transition between Canadian and Hudsonian Zones. The second area is the western slope of the Sierra Nevada in the area within and around Yosemite National Park, California. The zonation pattern present is illustrated in Fig. 442; lower half). The fauna of this area is less diverse (only eight taxa represented) than the Mount Rainier fauna, but it covers a broader altitudinal range (namely, 400 m to about 3600 m) than the latter (0 m to about 2800 m). There are two taxa shared with the Mount Rainier fauna (N. eschscholtzii and N. acuta acuta), both of which have their altitude ranges shifted upward in the Yosemite area. Peak diversity in this

fauna is at the 3400 m level (in the Arctic/Alpine Zone) where four taxa are represented. The third area is the Front Range (eastern slope) of the Rocky Mountains in Colorado. The zonation pattern, illustrated in Fig. 443 (upper half), involves eight taxa. Maximum diversity is at about the 2900 m level (in the Hudsonian Zone). The last area is the Sangre de Cristo Range (north slope) in the Rocky Mountains of northern New Mexico. The zonation pattern is represented in Fig. 443 (lower half). Only four taxa are represented, and all are shared with the fauna of the Front Range. Because given life zones occupy increasingly higher altitudes in transects from north to south (e.g. see Mani, 1962), altitudinal ranges of these taxa should be displaced upward in the Sangre de Cristo Range if the macrohabitat ranges of the taxa are equivalent in all areas. In this instance however, the opposite is true--the respective altitudinal ranges of three of the four taxa are displaced downward in relation to ranges of populations in the Front Range. Of particular interest is the altitudinal range of N. purpurata in New Mexico. It is so far displaced as to be below, and non-overlapping with, that of Front Range representatives. Maximum diversity for the fauna is at the 2500 m level (Canadian Zone), where all four taxa are represented. These same four taxa do not quite overlap in the Front Range; but if the range of N. obliqua extended high enough, the four would co-exist only as low as the 2800 m level.

Clearly, members of the Sangre de Cristo fauna, except N. obliqua (which demonstrates the expected range in relation to Colorado populations), have peculiar altitudinal distributions. In an attempt to interpret the unexpected downward displacement of these ranges, I

can suggest only one scenario consistent with these findings. Populations isolated in this mountain range, when confronted with a trend toward warmer temperatures than at present were forced to retreat upward with other cool-adapted members of the biota. The warming trend suggested may correspond to the so-called "altithermal" (or "hypsithermal") period (variously placed at between 5000 and 7000 years B.P.; see Richmond, 1965). [Existence of this warm period is questioned, however, by some workers for certain parts of the southwest (e.g. Martin and Mehringer [1965] doubted its significance and/or existence in southern Arizona and New Mexico)]. In the face of continued warming, populations already displaced to highest elevations were, in effect, forced right off the tops of the mountains. This could account for the absence of N. suturalis and N. trifaria from the fauna. Apparently populations which were able to survive this period did so by acquiring adaptations to life in a warmer climate. As climate again cooled, these populations were able to shift their ranges down the mountains. If survival in the warm climate had been achieved at the expense of certain genetic variability within the populations, specifically that portion related to adaptation for life in cool climate, resulting altitudinal ranges of these taxa could remain displaced below there original levels. The present altitudinal ranges of N. purpurata, N. gyllenhali lindrothi, and N. arkansana arkansana may well reflect the above sequence of events.

4.225 Range size, disjunction, and dispersal

I have reviewed factors affecting certain aspects of distribution

(especially geographical isolation and extent of geographical range) of Nebria taxa in a separate paper (Kavanaugh, in press B). I here summarize some results of that study--namely those which bear on the relationship between apparent dispersal capability and distribution.

As noted above, members of all taxa appear to have approximately equal ambulatory capabilities. Differential dispersal capability is therefore dependent on differences in either flight capability of individuals or the intrinsic disposition of individuals for ambulatory movement, or on both (assuming that environmental constraints are not completely limiting factors). I have no comparative data at present on the relative dispositions of members of various taxa for movement. I therefore limit discussion here to apparent differences in flight capability (see section 3.234 for detailed discussion of this topic).

A highly significant difference ($P \geq 0.99$) found in mean maximum linear extent of geographical range between taxa with fully-winged members and those with all members having reduced hindwings was noted above (section 3.2342). This suggests that the flight capability of its members, as judged by wing size, may affect (1) the rate at which the range of a taxon may expand (extrinsic dispersal), and/or (2) the maximum size of range that it may occupy yet still maintain minimum genetic continuity (through internal dispersal). Support for hypothesis (1) has already been presented (section 3.2342). Ninety-one percent of the 22 Nebria taxa represented in areas which were completely covered by Wisconsinan ice sheets have members with full-sized hindwings. This implies that these taxa have, in general, been able to invade deglaciated regions more rapidly than taxa with all members having reduced hindwings. A first assumption, therefore,

is that flight capability has been important for the apparent success of rapidly expanding taxa (although explanation for same is undoubtedly not this simple). It is more difficult to test hypothesis (2) above in the absence of data on minimum gene flow required to maintain continuity and on the frequency and duration of and distance covered in flight. For an (admittedly) indirect test, however, I used data from Table 7 on significant disjunctions in the geographical ranges of taxa and tried to relate these to flight capability. I first assumed that taxa whose members have full-sized hindwings would be able to accomodate larger disjunctions within their geographical ranges than taxa those whose members all have reduced hindwings. I based this assumption on the idea that, although some large gaps in present distributions may never be crossed under present climatic conditions, even by strong fliers, shifts in climate which could reduced the gap distance would first (and probably also more frequently) benefit fliers by permitting more frequent gene flow between populations. Statistical treatment of the data indicates that, although mean size of significant disjunctions among the ranges of taxa with fully-winged members (334.6 km) is more than twice as large as the mean disjunction size among taxa with short-winged members only (151.3 km), these sample means are not significantly different (except at $P \leq 0.30$ [T value = 1.082 (with 29 degrees of freedom). Variance in gap size is simply too great to provide support for the assumption.

Factors other than gap size must also influence gene flow between and/or differentiation among isolated populations. This latter point is demonstrated by an observation made elsewhere (Kavanaugh, in press

B), that there is no significant difference between mean gap distance separating significantly disjunct populations assigned to single taxa and mean gap distance between populations assigned to different subspecies. The role of flight in maintaining gene flow between disjunct populations, and in internal dispersal in general, is therefore not clarified by the above test.

4.226 Relationship between life cycle timing and distribution

As noted above (section 3.2322), relationships have been suggested between altitudinal and geographical distributions of carabid species and timing of their life cycle (e.g. Greenslade, 1965; Lindroth; 1949). Overwintering stage appears to be a most critical factor in relation to distribution (see above). Lindroth (1949) noted that species of Scandinavian carabid beetles members of which overwintered as larvae tended to be restricted to coastal regions--that is, to areas with a maritime climate. Such areas experience relatively mild winters, and are, therefore, perhaps more favorable to insects in the larval stage at that time. Similarly, low altitude and low latitude areas provide mild winter conditions compared with such conditions in corresponding high altitude and latitude areas. Similar concentrations of taxa which overwinter as larvae could t[illegible] expected in the former areas. I have tested these hypoth[illegible]earctic Nebria using data presented in Table 13 on life cycle [illegible]ming and data on the geographical and macrohabitat distributions of taxa. Results of these tests are summarized below.

The association noted by Lindroth (1949) between larval

overwintering and maritime climate is demonstrated also among Nearctic Nebria. Of the 17 taxa all or most members of which overwinter as larvae, 15 (88%) have geographical ranges associated with areas having maritime climates. Only 5% of the taxa occupying high altitude areas have members which overwinter as larvae (and this represents only 11.5% of all taxa with larvae which overwinter). Suggested relationships between larval overwintering and both maritime climate and low altitude are supported by data on Nebria taxa. I could find no such relationship, however, between latitude and overwintering stage. Although 64% of the taxa represented in northern areas have members which overwinter as adults, 24% of all taxa in which larvae overwinter are represented in these areas compared with representation by only 18.8% of all taxa in which adults overwinter.

Life cycle timing appears to be related to both altitudinal and longitudinal (coastal versus inland) distribution; but whether or not this relationship is one of cause and effect is yet uncertain. If my interpretation of evolution in Nebria overwintering stage (character no. 171, Table 15 and Fig. 372) is correct, the plesiotypic character state is 'overwintering in the larval stage'. If phylogenetic relationships proposed by the cladogram (Fig. 372) are correct, overwintering in the adult stage by all or most individuals of a taxon has evolved independently at least eight times, and by some individuals of a taxon at least five more times. This suggests that overwintering stage is a character subject to change, perhaps in response to selection for adaptation to life in areas with cold winters. However, shifts from larval to adult overwintering, and vice versa, are not universally as expected. For example, all or most

members of all taxa in the metallica lineage overwinter as adults, even though some member taxa are restricted to coastal (maritime) areas (e.g. N. meanyi meanyi); and N. crassicornis intermedia members overwinter as larvae and yet have a Rocky Mountain (i.e. continental) distribution). In some instances at least, it appears then that overwintering stage characteristics inherited from a common ancestor may be retained unchanged by descendant taxa regardless of their geographical range.

4.23 Historical zoogeography

This section has been omitted from the dissertation, but it will be included in the manuscript for publication. In this section, I will apply clues provided by the preceding study on present Nebria distribution to reconstruction of past distributional history of the genus in North America. I intend to organize the discussion as outlined below.

4.231 Introduction to historical biogeography: goals, principles, techniques, assumptions.

4.2311 "Vicariance" and "dispersal" biogeography--two sides of the same coin.

4.232 Overview of Cenozoic history of the Holarctic Region.

4.2321 Progressive changes in physiography and climate.

4.2322 Cyclic changes in physiography and climate.

4.233 Cenozoic history of Nearctic Nebria.

4.2331 "Post-Glacial" history.

4.23311 Dispersal, and other changes in geographical range

4.23312 Historical development of of present vicariance patterns.

4.23313 Speciation, subspeciation, and differentiation in post-glacial time.

4.23314 Nebria distributions and the "hypsithermal interval.

4.2332 Nebria distribution and Wisconsinan Glaciation

4.23321 "Glacial refugia" and other changes in geographical range.

4.2333 Sangamon interglacial and distributions of Nebria.

4.23331 Speciation and differentiation in post-Illinoian time.

4.2334 Illinoian Glaciation and Nebria distributions.

4.23341 Maximum range extension of cold-adapted organisms.

4.2335 Pre-Illinoian history and the origins of Nearctic Nebria.

4.23351 Vicariance patterns and distributional history of Nearctic Nebria and their Palaearctic relatives.

4.3 Compatibility between proposed phylogeny and historical zoogeography.

This section has also been omitted from the dissertation, but it will be included in the manuscript for publication. If certain phylogenetic relationships suggested by the cladistic analysis do, in fact, accurately reflect evolutionary history, then distributional histories of certain taxa have been more complex than other sets of relationships suggest. In this section, I will examine these complex reconstructions and consider alternative sets of relationships which might permit simpler explanations for observed distributional patterns.

4.4 Evolutionary trends

This section has been omitted from the dissertation. For publication, I will include here discussion of trends in structure, geographical and habitat distributions, and life history among Nearctic Nebria. I have discussed evolutionary rates and factors affecting same elsewhere (Kavanaugh, in press B), but will summarize my findings here also.

5.0 PROSPECTUS

In preceding sections, I have reviewed the history of Nearctic Nebria systematics and presented results of my own studies to date. It seems appropriate in closing to make some suggestions from my present perspective concerning possible directions for future studies on this interesting group of beetles. I hope to follow some of these suggestions myself and will welcome the help of others in doing so. Perhaps what I have presented above will encourage others to take up some studies on Nebria which will utilize their own special skills and interests.

5.1 Geographical distributions and undescribed taxa

Some parts of North America are not yet adequately sampled for presence of Nebria populations; and it is in these areas that future field work and collections may be most profitable. There are probably few if any Nebria species yet to be discovered, even in these areas; but important information on geographical variation patterns and range limits of several species and on the geographical relations of certain subspecies can be obtained from additional work in these areas.

In eastern North America, the Nebria fauna comprises few species, the respective distributions of which are relatively well-known. However, the recent discovery of certain West Virginia populations of N. pallipes, members of which are unusually small and have dark appendages (see species description), suggests that more field work in that state may be needed. Similarly, some of the high mountains of Virginia (e.g. Mount Rogers) have not yet been adequately sampled for

Nebria species, particularly for presence of N. appalachia populations. Additional work on the geographical distribution of this species should also include careful search in all the isolated mountain ranges further south, including on the highest "balds" in northern Georgia.

Representatives of [illegible] species have not yet been found in the Ozark mountain system; but the occurrence of relict populations there is still a possibility. Careful search of suitable habitats in the Ouchita Mountains and Boston Hills may yet disclose their presence in that area.

A search for Nebria populations is needed in several areas of western North America. Sampling in the Capitan and Sacramento Mountains of southcentral New Mexico has been negligible; and more fieldwork is needed in the Sangre de Cristo Range further north. The Chuska Mountains of northeastern Arizona may also yield interesting Nebria specimens; and fieldwork throughout the canyonlands of northern Arizona and southern Utah may better define the geographical range limits and variation patterns of N. desolata and N. navajo. Mountain ranges in Utah which require additional sampling include the Uinta, Pavant, Pine Valley, and central Wasatch Mountains. The Gros Ventre and Wind River Ranges of Wyoming have also been inadquatel[illegible]mpled.

Data on distributions and diversity of species in the Sierra Nevada of California are yet incomplete. Members of several taxa (e.g. N. lyelli and N. meanyi lamarckensis) are known from only one or a few localities; and their respective geographical ranges may be somewhat larger. Additional collections may help to clarify geographical relations of different subspecies of N. ingens and N.

spatulata and the pattern of geographical variation in N. ovipennis.

Areas of particular interest in the Pacific Northwest include the Olympic Peninsula and Vancouver Island, high altitude areas of which have not been adequately sampled, Cascade Range north of Snoqualmie Pass (Washington), Coastal Ranges of British Columbia (north of Vancouver) and southeastern Alaska, and the Queen Charlotte Islands. Geographical relations between N. crassicornis crassicornis and N. crassicornis intermedia and between N. gebleri gebleri and N. gebleri cascadensis are presently unclear; but these may eventually be clarified through sampling in the mountainous area between Vancouver and Terrace, British Columbia. The Nebria fauna of the Queen Charlotte Islands is not yet fully known. Nebria charlottae was described from a single specimen collected over 100 years ago, and its continued presence and (if applicable) its geographical and habitat distributions must be established through field studies in the Islands. High altitude areas in the Coastal Ranges of southeastern Alaska should be sampled for relict Nebria populations, ancestors of which may have survived glacial periods in nearby coastal refugia (see above).

5.2 Future directions in Nebria systematics

Comparative studies which remain to be made on Nearctic Nebria are many and varied, limited only by availability of techniques needed to accomplish them and willingness of workers to begin them. Each additional study should exploit a new set of characters and provide new data on phylogenetic relationships among species; and each should, therefore, permit new tests of hypotheses of relationship based on

results of all previous studies.

Characters of external structure of adults which I have not yet exploited adequately include those of the mandibles, maxillae, and internal sac of the male median lobe; and these should be especially useful in defining and testing relationships among species groups and subgroups. Study of several internal organ systems (especially the digestive and reproductive systems) in adults may also provide pertinent data. I anticipate that comparative studies of external structure of eggs, larvae, and pupae will generate data of use in testing hypotheses of relationship based on characters of adults; but again, I suggest that results will be useful mainly for tests of supraspecific relationships.

External structure of adults is the character system used classically for comparisons among and characterizations of members of different taxa. Unfortunately, data from such studies do not always permit unequivocal determinations of relationships among taxa or populations considered; and at some point in any study, the usefulness of this (or any other) character system is bound to reach its limit. I suggest that this point has been reached in Nearctic Nebria systematics, and that, except for use of mandibular and other characters noted above, little more will be gained from further study of adult external structure. This may be especially true for determination of relationships among populations and subspecies. For example, relationships among various populations of N. arkansana and of N. fragilis are extremely complex; and data on external structure appear inadequate to permit clear choices among alternative sets of relationships.

I am convinced that data from other charact[illegible] systems, such as those derived from comparative biochemical and/or serological studies, will be needed, in many instances, to permit adequate recognition of relationships among populations. In particular, I suggest that comparative biochemical studies (using one of several techniques available) will be very useful in exploring relationships among member species and subspecies of the gregaria lineage (especially relationships between N. gregaria and N. sahlbergii sahlbergii in the Aleutian Islands; between N. arkansana edwardsi and N. sahlbergii sahlbergii in western Alberta and eastern British Columbia [see discussion above under species descriptions]; and between N. arkansana and N. fragilis. Similar studies on populations of members of the trifaria infragroup may help to determine relationships among these taxa also, whereas other studies to date have not led to completely satisfying conclusions (see above).

Comparative natural history studies should yield abundant data, useful in both testing of hypotheses on phylogenetic relationships and in promoting a more complete understanding of the role of these beetles in their environment. Of particular importance are studies on nocturnal microhabitat preferences (see above) and mating behavior, especially possible mechanisms for species recognition. Because members of several different Nebria species are frequently found hiding together during the day in some areas, unique nocturnal foraging areas (microhabitats) or stategies as well as some means of recognizing members on their own species might be expected. If discovered, such [illegible]acteristics might be useful in defining both phylogenetic and [illegible]ironmental relationships among species.

The classification of Nearctic taxa presented here must be considered tentative, pending a reclassification of the genus worldwide. Future comparative studies among members of the genus should, as far as is possible, adopt a worldwide perspective. As noted above, relationships among Nebria, other nebriini genera, and genera in related tribes (e.g. Notiophilus) are not yet clearly defined. Determination of these relationships must be given highest priority among the future goals of Nebria systematics.

LITERATURE CITED

Ali, H. A. 1967. The higher classification of the Carabidae and the significance of internal characters. Bulletin de la Société Royale Entomologique d'Egypte, 51:211-231.

Allen, J. A. 1871. On the mammals and winter birds of east Florida. Bulletin of the Museum of Comparative Zoology, 2:161-450.

Allen, R. P. 1967. The boreal carabid beetle, Nebria riversi Van Dyke. The Pan-Pacific Entomologist, 43:82.

Andersen, J. H. 1968. The effect of inundation and choice of hibernation sites of Coleoptera living on river banks. Norsk Entomologisk Tidsskrift, 15:115-133.

Andersen, J. H. 1970. The larvae of Pelophila borealis Payk., Nebria gyllenhali Schnh. and N. nivalis Payk. (Coleoptera, Carabidae). Astarte, 3:87-95.

Andrewes, H. E. 1923. Coleoptera of the second Mount Everest Expedition, 1922. Part I. Carabidae. The Annals and Magazine of Natural History, Ser. 9, 2:273-278.

Andrewes, H. E. 1935. On the genotypes of British Carabidae II. The Annals and Magazine of Natural History, 15:12-25.

Andrewes, H. E. 1939. The generic names of the British Carabidae, with a check list of the British species. The Generic Names of British Insects, 6 :153-192.

Armin, C. 1963. A study of the family Carabidae (Coleoptera) in Boulder County, Colorado. Unpublished PhD Dissertation, Department of Biology, University of Colorado, Boulder, Colorado, 476 pp.

Armstrong, D. M. 1977. Dispersal vs. dispersion: process vs. pattern. Systematic Zoology, 26:210-211.

Arnett, R. H., and G. A. Samuelson. 1969. Directory of Coleoptera collections of North America (Canada through Panama). Purdue University Press, Lafayette, Indiana, vii + 123 pp.

Ashlock, P. D. 1974. The uses of cladistics. Annual Review of Ecology and Systematics, 5:81-99.

Bailey, N. T. J. 1952. Improvements in the interpretation of recapture data. Journal of Animal Ecology, 21:120-127.

Ball, G. E. 1959. A taxonomic study of the North American Licinini with notes on Old World species of genus Diplocheila Brulle. Memoirs of the American Entomological Society, No. 16, 259 pp.

Ball, G. E. 1960. Carabidae (Latreille, 1810), Fascicle 4. [pp. 55-210] In: Arnett, R. H., Jr. (editor), The beetles of the United States (a manual for identification). Catholic University of America Press, Washington, D. C., xi + 1112 pp.

Ball, G. E. 1966. The taxonomy of the subgenus Scaphinotus Dejean with particular reference to the subspecies of Scaphinotus petersi Roeschke. Transactions of the Americam Entomological Society, 92:687-722.

Ball, G. E. 1970. Barriers to southward dispersal of the holarctic boreo-montane element of the family Carabidae in the mountains of Mexico. Anales de la Escuela Nacional de Ciencias Biologicas, Mexico, 17:91-112.

Ball, G. E. 1975. Pericaline Lebiini: notes on classification, a synopsis of the New World genera, and a revision of the genus Phloeoxena Chaudoir (Coleoptera: Carabidae). Quaestiones

Entomologicae, 11:143-242.

Ball, G. E., and J. Negre. 1972. The taxonomy of the Nearctic species of the genus Calathus Bonelli (Coleoptera: Carabidae: Agonini). Transactions of the American Entomological Society, 98:412-533.

Ball, I. R. 1976 (1975). Nature and formulation of biogeographical hypotheses. Systematic Zoology, 24:407-430.

Bänninger, M. 1923. Versuch einer Bestimmungstabelle der zentral- und östasiatischen Nebria-Arten ohne gelbe Flügeldeckenzeichnung. Koleopterologische Rundschau, 10:129-142.

Bänninger, M. 1925. Neunter Beitrag zur Kenntnis der Carabinae: die Nebriini. Entomologische Mitteilungen, 14:180-195, 256-281, 329-343.

Bänninger, M. 1928. Über die Nebriini. 13. Beitrag zur Kenntnis der Carabinae. Koleopterologische Rundschau, 14:1-7.

Bänninger, M. 1931. Über Carabinae, Ergänzungen und Berichtigungen. (Col.) 17. Beitrag. Deutsche Entomologische Zeitschrift, 1931:177-212.

Bänninger, M. 1933. Über Carabinae, Ergänzungen und Berichtigungen. (Col.) 19. Beitrag. Deutsche Entomologische Zeitschrift, 1933:81-124.

Bänninger, M. 1949. Ueber Carabinae (Col.). Ergänzungen und Berichtigungen III, mit Bemerkungen zu R. Jeannels neuer Einteilung der Carabiden. Mitteilungen der Münchner Entomologischen Gesellschaft, 35-39:127-157.

Bänninger, M. 1960. Die schweizerischen Arten der Gattung Nebria Latr. (Col. Carab.). Mitteilungen der Schweizerischen Entomologischen Gesellschaft, 32:337-356.

Beaulne, J.-L. 1914-16. Les Coléoptères du Canada. Partie II. Carabiques. Le Naturaliste Canadien, 40:152-156, 171-180; 41:28-31, 40-48, 55-62, 71-78, 87-94, 108-111, 120-127, 139-143, 155-160, 171-176, 189-192; 42:13-15, 29-32, 45-47, 59-63, 158-160, 187-191; 43:10-15, 22-26.

Bell, R. T. 1955. Species of the pallipes-group of Nebria in the eastern United States. Proceedings of the Entomological Society of Washington, 57:265-267.

Bell, R. T. 1964. Does Gehringia belong to the Isochaeta? (Coleoptera: Carabidae). The Coleopterists' Bulletin, 18:59-61.

Bell, R. T. 1967. Coxal cavities and the classification of the Adephaga (Coleoptera). Annals of the Entomological Society of America, 60:101-107.

Berggren, W. A., and J. A. van Couvering. 1974. Developments in paleontology and stratigraphy, 2. The Late Neogene: biostratigraphy, geochronology and paleoclimatology of the last 15 million years in marine and continental sequences. Elsevier, Amsterdam, xi + 216 pp.

Bils, W. 1976. Das Abdomenende weiblicher, terrestrisch lebender Adephaga (Coleoptera) und seine Bedeutung für die Phylogenie. Zoomorphologie, 84:113-193.

Blackwelder, R. E. 1939. Fourth supplement to the Leng Catalogue of Coleoptera of America, north of Mexico. John D. Sherman, Mount Vernon, New York, 146 pp.

Blackwelder, R. E. 1967. Taxonomy. A text and reference book. John Wiley and Sons, Inc., New York, xiv + 698 pp.

Blackwelder, R. E., and R. M. Blackwelder. 1948. Fifth supplement to

the Leng Catalogue of Coleoptera of America, north of Mexico. John D. Sherman, Mount Vernon, New York, 87 pp.

Blair, K. G. 1950. Nebria nivalis Paykull (Col., Carabidae) in Scotland. Entomologists' Monthly Magazine, Ser. 4., 86:220-222.

Blake, I. H. 1945. An ecological reconnoissance in the Medicine Bow Mountains. Ecological Monographs, 15:207-242.

Blatchley, W. S. 1910. An illustrated descriptive catalogue of the Coleoptera or beetles (exclusive of Rhynchophora) known to occur in Indiana, with bibliography and descriptions of new species. Indianapolis, Indiana, 1386 pp.

Bonelli, F. A. 1810. Observations entomologiques. 1. Memorie della Reale Accademia della Scienze di Torino, 18:21-78.

Bowditch, F. C. 1896. List of Mt. Washington Coleoptera. Psyche, 7 (Supplement II):1-11.

Braun-Blanquet, J. 1932. Plant sociology. [translated by G. D. Fuller and H. S. Conrad] McGraw-Hill, New York, xviii + 439 pp.

Brothers, D. J. 1975. Phylogeny and classification of the aculeate Hymenoptera, with reference to Mutillidae. University of Kansas Science Bulletin, 50:483-648.

Brown, W. J. 1930. Coleoptera of the north shore of the Gulf of St. Lawrence. The Canadian Entomologist, 62:231-237.

Brown, W. J. 1937. The Coleoptera of Canada's eastern Arctic. The Canadian Entomologist, 69:106-111.

Brown, W. L., Jr., and E. O. Wilson. 1954. The case against the trinomen. Systematic Zoology, 3:174-176.

Brundin, L. 1966. Transantarctic relationships and their significance, as evidenced by chironomid midges, with a monograph

of the subfamilies Podonominae and Aphroteniinae and the austral Heptagyiae. Kunglig Svenska Vetenskapsakademiens Handlingar, Fjärde Serien, 11:1-472.

Brundin, L. 1972. Evolution, causal biology, and classification. Zoologica Scripta, 1:107-120.

Burger, J. F. 1974. The horse flies of Arizona. I. Introduction and zoogeography (Diptera: Tabanidae). Proceedings of the Entomological Society of Washington, 76:99-118.

Bush, A. H. 1914. A trip up Mount Cheam. Proceedings of the Entomological Society of British Columbia, 4:58-60.

Carleton, M. 1936. The anatomy and histology of the alimentary canal of the adult Nebria brevicollis Linn. (Coleopt.). Transactions of the Society of British Entomology, 3:119-127 and plates XII-XVI.

Carter, A. 1976. Wing dimorphism in the insect species Agonum retractum LeConte (Coleoptera: Carabidae). Canadian Journal of Zoology, 54:1375-1382.

Casey, T. L. 1913. Studies in the Cicindelidae and Carabidae of America. Memoirs on the Coleoptera, 4:1-192.

Casey, T. L. 1920. Random studies among the American Caraboidea. Memoirs on the Coleoptera, 9:133-299.

Casey, T. L. 1924. Additions to the known Coleoptera of North America. Memoirs on the Coleoptera, 11:1-347.

Chagnon, G. 1917. A preliminary list of the insects of the Province of Québec. Par III.--Coleoptera. Supplement, Report of the Québec Society for the Protection of Plants, 1916-17:159-277.

Chapman, R. F. 1969. The insects: structure and function. American Elsevier Publishing Co., New York, xii + 819 pp.

Chaudoir, M. 1843. Carabiques nouveaux décrits. Bulletin de la Société Impériale des Naturalistes de Moscou, 16:671-791.

Chaudoir, M. 1850. Memoire sur la famille des Carabiques. II. Bulletin de la Société Impériale des Naturalistes de Moscou, 23:3-85, 349-460.

Chiolino, B. B. 1970. Wing dimorphism in some Vermont Carabidae. Unpublished MSc. Thesis, Department of Zoology, University of Vermont, 139 pp.

Clark, M. E. 1948. An annotated list of Coleoptera taken at or near Terrace, British Columbia. Part I. Proceedings of the Entomological Society of British Columbia, 44:24-27.

Clark, T. H., and C. W. Stearn. 1968. Geological evolution of North America. Second edition. The Roland Press Co., New York, viii + 570 pp.

Coope, G. R. 1968. Fossil beetles collected by James Bennie from Late Glacial silts at Corstorphine, Edinburgh. Scottish Journal of Geology, 4:339-348.

Coope, G. R. 1970a. Interpretations of Quaternary insect fossils. Annual Review of Entomology, 15:97-120.

Coope, G. R. 1970b. Climatic interpretations of Late Weichselian Coleoptera from the British Isles. Revue de Géographie Physique et de Géologie Dynamique, Deuxième Série, 12:149-155.

Coope, G. R., and J. A. Brophy. 1972. Late Glacial environmental changes indicated by a coleopteran succession from North Wales. Boreas, 1:97-142.

Cracraft, J. 1974. Phylogenetic models and classification. Systematic Zoology, 23:71-90.

Criddle, N. 1922. The entomological record, 1921. Fifty-second Annual Report of the Entomological Society of Ontario, 1921:57-70.

Criddle, N. 1926. The entomological record, 1925. Fifty-sixth Annual Report of the Entomological Society of Ontario, 1925:94-107.

Critchley, B. R. 1973. Parasitism of the larvae of some Carabidae (Coleoptera). Journal of Entomology, Series A, 48:37-42.

Croizat, L., G. J. Nelson, and D. E. Rosen. 1974. Centers of origin and related concepts. Systematic Zoology, 23:265-287.

Crowson, R. A. 1970. Classification and biology. Heinemann Educational Books Ltd., London, 350 pp.

Csiki, E. 1927. Pars 92. Carabidae: Carabinae II. [pp. 315-622] In: Junk, W. and S. Schenkling (editors), Coleopterorum Catalogus 1. W. Junk, Berlin, 345 pp. + 648 pp. [1926-33]

Csiki, E. 1933. Pars 127. Carabinae: corrigenda et addenda. [pp. 623-648] In: Junk, W., and S. Schenkling (editors), Coleopterorum Catalogus 1. W. Junk, Berlin, 345 pp. + 648 pp. [1926-1933].

Csiki, E. 1946. Die Käferfauna des Karpaten-Beckens. I Band. allgemeiner Teil und Caraboidea. Budapest, 798 pp.

Curtis, J. 1823-40. British entomology; being illustrations and descriptions of the genera of insects found in Great Britain and Ireland. I. Coleoptera, Part 1. London. [without pagination, plates number in order of publication, not as bound].

Daniel, K. 1903. Bestimmungstabellen der europäischen Koleopteren. LII. (Nebriini, Notiophilini, Trachypachydini, Epactiini, Elaphrini, und Lorocerini). Münchener Koleopterologische

Zeitschrift, 1:155-173.

Daniel, K., and J. Daniel. 1904. Neue paläarktische Koleopteren. Münchener Koleopterologische Zeitschrift, 2:76-93.

Darlington, P. J., Jr. 1930. A new Nebria from Mount Rainier. Psyche, 37:104-105.

Darlington, P. J., Jr. 1931a. A new name for Nebria vandykei Darlington. Psyche, 38:24.

Darlington, P. J., Jr. 1931b. On some Carabidae, including new species, from the mountains of North Carolina and Tennessee. Psyche, 38:145-164.

Darlington, P. J., Jr. 1936. Variation and atrophy of flying wings of some carabid beetles (Coleoptera). Annals of the Entomological Society of America, 29:136-179.

Darlington, P. J., Jr. 1943. Carabidae of mountains and islands; data on the evolution of isolated faunas, and on atrophy of wings. Ecological Monographs, 13:37-61.

Darlington, P. J., Jr. 1957. Zoogeography: the geographical distribution of animals. John Wiley and Sons, Inc., New York, xi + 675 pp.

Darlington, P. J., Jr. 1965. Biogeography of the southern end of the World: distribution and history of far-southern life and land, with an assessment of continental drift. Harvard University Press, Cambridge, Massachusetts, x + 236 pp.

Darlington, P. J., Jr. 1971. The carabid beetles of New Guinea. Part IV. General considerations; analysis and history of fauna; taxonomic supplement. Bulletin of the Museum of Comparative Zoology, 142:129-337.

Davies, M. J. 1953. The contents of crops of some British beetles. The Entomologist's Monthly Magazine, 89:18-23.

Davies, M. J. 1959. A contribution to the ecology of Notiophilus and allied genera (Col., Carabidae). The Entomologist's Monthly Magazine, 95:25-28.

Dejean, P. F. M. A. 1826. Species général des Coléoptères de la Collection de M. le Comte Dejean. 2. Crevot, Paris, viii + 501 pp.

Dejean, P. F. M. A. 1831. Species general des Coléoptères de la Collection de le Comte Dejean. 5. Méquignon-Marvis, Paris, viii + 883 pp.

Dillon, E. S., and L. S. Dillon 1961. A manual of common beetles of eastern North America. Row, Peterson and Co., Evanston, Illinois, viii + 884 pp.

Döbler, H. 1975. Katalog der in den Sammlungen des ehemaligen Deutschen Entomologischen Institutes aufbewahrten Typen--XII (Coleoptera: Carabidae). Beitrage zur Entomologie, Berlin, 25:99-150.

Edwards, J. G. 1951. Amphizoidae (Coleoptera) of the World. The Wasmann Journal of Biology, 8:303-332.

Edwards, J. G. 1954. A new approach to infraspecific categories. Systematic Zoology, 3:1-20.

Edwards, J. G. 1956a. Clarification of certain aspects of infraspecific systematics. Systematic Zoology, 5:92-94.

Edwards, J. G. 1956b. What should we mean by subspecies? Turtox News, 34:200-202, 230-231.

Edwards, J. G. 1975. The Carabidae of Glacier National Park, Montana.

The Coleopterists Bulletin, 29:47-58.

Ekis, G. 1977. Classification, phylogeny, and zoogeography of the genus Perilypus (Coleoptera: Cleridae). Smithsonian Contributions to Zoology, No. 227, 138 pp.

Ekis, G., and A. P. Gupta. 1971. Digestive system of Cleridae (Coleoptera). International Journal of Insect Morphology and Embryology, 1:51-86.

Elliott, E. A., and C. Morley 1907-11. On hymenopterous parasites of Coleoptera. The Transactions of the Entomological Society of London, 1907:7-75; 1911:452-496.

Erwin, T. L. 1967. Bombardier beetles (Coleoptera, Carabidae) of North America: Part II. Biology and behavior of Brachinus pallidus Erwin in California. The Coleopterists Bulletin, 21:41-55.

Erwin, T. L. 1970. A reclassification of bombardier beetles and a taxonomic revision of the North and Middle American species (Carabidae: Brachinida). Quaestiones Entomologicae, 6:4-215.

Erwin, T. L., and G. E. Ball. 1972. Classification of the ovipennis and trifaria groups of Nebria Latreille (Coleoptera: Carabidae: Nebriini). Proceedings of the Biological Society of Washington, 85:77-108.

Eschscholtz, J. F. 1823. Species insectorum novae, descriptae. Mémoires de la Société Impériale des Naturalistes de Moscou, 6:97-108.

Eschscholtz, J. 1829-1833. Zoologischer Atlas, enthaltend Abbildungen und Beschreibungen neuer Thierarten. G. Reimer, Berlin, iv + 17 pp. and plates 1-5 (Erstes Heft, 1829); 13 pp.

and plates 6-10 (Zweites Heft, 1829); 18 pp. and plates 11-15 (Drittes Heft, 1829); 19 pp. and plates 16-20 (Viertes Heft, 1831); viii + 28 pp. and plates 21-25 (Fünftes Heft, 1833).

Evans, J. D. 1906. List of Coleoptera in the collection of J. D. Evans, Trenton, Ont., which have not heretofore been reported as having been taken in Canada. The Canadian Entomologist, 38:96-100.

Evans, M. E. G. 1955a. A comparative account of the feeding methods of the beetles Nebria brevicollis (F.) (Carabidae) and Philonthus decorus (Grav.) (Staphylinidae). Transaction of the Royal Society of Edinburgh, 66:91-109.

Evans, M. E. G. 1965b. The feeding method of Cicindela hybrida L. (Coleoptera: Cicindelidae). Proceedings of the Royal Entomological Society of London, Series A., 40:61-66.

Evans, M. E. G. 1965c. An interpretation of gular size in some adult Coleoptera. Proceedings of the Zoological Society of London, 144:403-413.

Evans, M. E. G. 1977. Locomotion in the Coleoptera Adephaga, especially Carabidae. Journal of Zoology, London, 181:189-226.

Fabricius, J. C. 1792. Entomologia systematica, 1. Hafniae, København, xx + 330 pp. + 538 pp.

Fabricius, J. C. 1801. Systema eleutheratorum, 1. Kiliae, Kiel, xxiv + 506 pp.

Fall, H. C. 1926. A list of the Coleoptera taken in Alaska and adjacent parts of the Yukon Territory in the Summer of 1924. The Pan-Pacific Entomologist, 2:127-154.

Fall, H. C., and T. D. A. Cockerell. 1907. The Coleoptera of New

Mexico. Transactions of the American Entomological Society, 33:145-272.

Fattig, P. W. 1949. The Carabidae or ground beetles of Georgia. Emory University Museum Bulletin, 7:1-62.

Fenneman, N. M. 1931. Physiography of western United States. McGraw-Hill Book Co., New York, xiii + 534 pp.

Fenneman, N. M. 1938. Physiography of eastern United States. McGraw-Hill Book Co., New York, xiii + 714 pp.

Fischer von Waldheim, G. 1820-22. Entomographia imperii russici. I. Moscow, viii + 210 pp.

Fischer von Waldheim, G. 1825-28. Entomographia imperii russici. III. Moscow, vii + 315 pp.

Fletcher, J. 1904. Entomological record, 1903. Thirty-fourth Annual Report of the Entomological Society of Ontario, 1903:85-99.

Fletcher, J. 1906. Entomological record, 1905. Thrity-sixth Annual Report of the Entomological Society of Ontario, 1905:90-105.

Forbes, W. T. M. 1926. The wing folding patterns of the Coleoptera. Journal of the New York Entomological Society, 34:42-68, 91-139.

Forsyth, D. J. 1972. The structure of the pygidial defence glands of Carabidae (Coleoptera). Transactions of the Zoological Society of London, 32:249-309.

Freitag, R. 1969. A revision of the species of the genus Evarthrus LeConte. Quaestiones Entomologicae, 5:89-212.

Friden, A. 1971. Beetle fauna on the borders of some Scandinavian glaciers. Norsk Entomologisk Tidsskrift, 18:29-32.

Fuss, C. A. 1850. Die Siebenbürgischen Arten der Gattung Nebria. Verhandlungen und Mitteilungen des Siebenbürgischen Vereins für

Naturwissenschaften zu Hermannstadt, 1:13-16, 18-20.

Ganagarajah, M. 1965. The neuro-endocrine complex of adult Nebria brevicollis (F.) and its relation to reproduction. Journal of Insect Physiology, 11:1377-1387.

Ganglbauer, L. 1891. Nebria complanata Linn., der Typus einer neuen Gattung. Wiener Entomologische Zeitung, 10:1-34.

Gemminger, M., and E. von Harold. 1868. Catalogus Coleopterorum hucusque descriptiorum synonymicus et systematicus. I.. E. Deyrolle fils, xxxvi + 424 pp.

Gilbert, O. 1958. The life history patterns of Nebria degenerata Schaufuss and N. brevicollis (Fabricius) (Coleoptera, Carabidae). Journal of the Society for British Entomology, 6:11-14.

Gilmour, D. 1970. General anatomy and physiology. [pp. 29-71] In: CSIRO (sponsor), The insects of Australia; a textbook for students and research workers. University of Melbourne Press, Melbourne, xiii + 1029 pp.

Gislén, T., and P. Brinck. 1950. Subterranean waters on Gotland with special regard to the Lummelunda Current. II. Environmental conditions, plant and animal life, immigration problems. Kunglig Fysiografiska Sallskapets Handlingar, Ny Följd, 61:1-81.

Goulet, H. 1974. Classification of the North and Middle American species of genus Pelmatellus Bates (Coleoptera: Carabidae: Harpalini). Quaestiones Entomologicae, 10:80-102.

Greenslade, P. J. M. 1963a. Further notes on aggregation in Carabidae (Coleoptera), with especial reference to Nebria brevicollis (F.). The Entomologist's Monthly Magazine, 99:109-114.

Greenslade, P. J. M. 1963b. A concentration of Carabidae (Coleoptera)

at Fleet in Dorset. The Entomologist's Monthly Magazine, 99:46-48.

Greenslade, P. J. M. 1964a. The distribtuion, dispersal and size of a population of Nebria brevicollis (F.), with comparative studies on three other Carabidae. Journal of Animal Ecology, 33:311-333.

Greenslade, P. J. M. 1964b. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). Journal of Animal Ecology, 33:301-310.

Greenslade, P. J. M. 1965. On the ecology of some British carabid beetles with special reference to their life histories. Transactions of the Society for British Entomology, 16:149-179.

Greenslade, P. J. M. 1968. Habitat and altitude distribution of Carabidae (Coleoptera) in Argyll, Scotland. Transactions of the Royal Entomological Society of London, 120:39-54.

Griffiths, G. C. D. 1972. The phylogenetic classification of Diptera Cyclorrhapha, with special reference to the structure of the male postabdomen. W. Junk, The Hague, 340 pp.

Griffiths, G. C. D. 1974a. On the foundation of biological systematics. Acta Biotheoretica, 23:85-131.

Griffiths, G. C. D. 1974b. Some fundamental problems in biological classification. Systematic Zoology, 22:338-342.

Guppy, R. 1947. Some records of Carabidae collected on Vancouver Island with ecological data. The Coleopterists Bulletin, 1:51-52.

Habu, A. 1958. Genus Nippononebria and its species (Coleoptera, Carabidae). The Bulletin of the National Institute of Agricultural Sciences (Japan), Series C, 10:67-81.

Hågvar, S., and E. Østbye. 1974. Oxygen consumption, caloric values, water and ash content of some dominant terrestrial arthropds from alpine habitats at Frinse, south Norway. Norsk Entomologisk Tidsskrift, 21:117-126.

Hamilton, J. 1889. Catalogue of the Coleoptera common to North America, north Asia and Europe, with the distribution and bibliography. Transactions of the American Entomological Society, 16:88-162.

Hamilton, J. 1894. Catalogue of the Coleoptera of Alaska, with the synonymy and distribution. Transactions of the American Entomological Society, 21:1-36.

Hamilton, K. G. A. 1972. The insect wing, part III. Venation of the orders. Journal of the Kansas Entomological Society, 45:145-162.

Hardy, G. A. 1927. Report on a collecting trip to Garibaldi Park, B. C. Province of British Columbia, Report of Provincial Museum of Natural History, 1926:C15-C32.

Harrington, W. H. 1890. On the lists of Coleoptera published by the Geological Survey of Canada, 1842-1888. The Canadian Entomologist, 22:135-191.

Hatch, M. H. 1933. Records of Coleoptera from Montana. The Canadian Entomologist, 65:5-15.

Hatch, M. H. 1938. Report on the Coleoptera collected by Dr. Victor B. Scheffer on the Aleutian Islands in 1937. The Pan-Pacific Entomologist, 14:145-149.

Hatch, M. H. 1939a. A key to the species of Nebria of northwestern North America. The Pan-Pacific Entomologist, 15:117-121.

Hatch, M. H. 1939b. List of the Coleoptera taken by Mr. George P.

Engelhardt in Alaska in 1938. Bulletin of the Brooklyn Entomological Society, 34:45-50.

Hatch, M. H. 1949. Studies on the Coleptera of the Pacific Northwest 1. The Pan-Pacific Entomologist, 25:113-118.

Hatch, M. H. 1953. The beetles of the Pacific Northwest. Part I: introduction and Adephaga. University of Washington Press, Seattle, Publication No. 16, vii + 340 pp.

Haubold, ., L. 1951. Distribution of the Carabidae (Coleoptera) of Boulder County, Colorado. American Midland Naturalist, 45:683-710.

Hecht, M. K. 1976. Phylogenetic inference and methodology as applied to the vertebrate record. Evolutionary Biology, 9:335-363.

Hecht, M. K., andJ. L. Edwards. 1977. The methodology of phylogenetic inference above the species level. [pp. 3-51] In: M. K. Hecht, P. C. Goody, and B. M. Hecht (editors), Major patterns in vertebrate evolution. NATO Advanced Study Institute Series A, Vol. 14. Plenum Press, New York and LOndon, ix + 908 pp.

Hennig, W. 1966. Phylogenetic systematics. University of Illinois Press, Urbana, 263 pp.

Henshaw, S. 1881. Index to the Coleoptera described by J. L. LeConte, M.D., Transactions of the American Entomological Society, 9:197-272.

Henshaw, S. 1885. List of the Coleoptera of America, north of Mexico. American Entomological Society, Philadelphia, 161 pp.

Henshaw, S. 1887. First s· ›lement to the list of Coleoptera of America, north of Mexico. Brook·n Entomological Society,

Brooklyn, 8 pp.

Henshaw, S. 1895. Third supplement to the list of Coleoptera, north of Mexico. American Entomological Society, Philadelphia, 62 pp.

Heyden, L. von. 1880-81. Catalog der Coleopteren von Sibirien mit Einschluss derjenigen der turanischen Länder, Turkestans und der chinesischen Grenzgebiete. Deutsche Entomologische Zeitschrift (Besonderes Heft), Berlin, xxiv + 224 pp.

Heyden, L. von. 1893-95. Catalog der Coleopteren von Sibirien, mit Einschluss derjenigen des östlichen Caspi-Gebietes, von Turcmenien, Turkestan, Nord-Thibet und des Amur-Gebietes. Nachtrag I. Deutsche Entomologische Gesellschaft, Berlin, 217 pp.

Heyden, L. von. 1896. Catalog der Coleopteren von Sibirien, mit Einschluss derjenigen des östlichen Caspi-Gebietes, von Turcmenien, Turkestan, Nord-Thibet und des Amur-Gebietes. Nachtrag II. Deutsche Entomologische Gesellschaft, Berlin, 84 pp.

Hlavac, T. F. 1971. Differentiation of the carabid antenna cleaner. Psyche, 78:51-66.

Hoffman, R. S., and R. D. Taber. 1968. Origins and history of tundra ecosystems, with special reference to their vertebrate faunas. [pp. 143-170] In: Wright, H. E., Jr. and W. H. Osburn (editors), Arctic and alpine environments. Indiana University Press, Bloomington and London, 308 pp.

Hopkins, D. M., J. V. Matthews, Jr., J. A. Wolfe, and M. L. Silberman. 1971. A Pliocene flora and insect fauna from the Bering Strait region. Palaeogeography, Palaeoclimatology, Palaeoecology,

9:211-231.

Horn, G. H. 1870. Descriptive catalogue of the species of Nebria and Pelophila of the United States. Transactions of the American Entomological Society, 3:97-105.

Horn, G. H. 1876. Synonymy of the Coleoptera of the Fauna Boreali-Americana, Kirby. The Canadian Entomologist, 8:126-130, 150-151, 166-170, 190-193.

Horvatovich, S. 1973. Ergebnisse der zoologischen Forschungen von Dr. Z. Kaszab in der Mongolei. 306. Nebria nivalis changaica ssp. n. aus der Mongolei (Coleoptera: Carabidae). Folia Entomologica Hungarica, Series nova, 26:251-255.

Howden, H. F. 1970. The Coleoptera. [pp. 1-28] In: Fauna of Sable Island and its zoogeographic affinities. National Museum of Natural Sciences (Canada), Publications in Zoology, No. 4, vi + 45 pp.

Humboldt, A. von, and A. Bonpland. 1805. Essai sur la géographie des Plantes; accompagné d'un tableau physique des regions équinoxiales. Levrault, Schoell et Co., Paris, xii + 13-155.

Inger, R. F. 1961. Problems in the application of the subspecies concept in vertebrate taxonomy. [pp. 262-285] In: Blair, W. F. (editor), Vertebrate speciation. Conference on vertebrate speciation, University of Texas, 1958. University of Texas Press, Austin, xvi + 642 pp.

Jeanne, C. 1966. Carabiques de la Peninsule Ibérique. (3e note). Actes de la Société Linnéenne de Bordeaux, 103:3-18.

Jeannel, R. 1925. Morphologie de l'élytre des Coléoptères Adéphages. Archives de Zoologie Experimentale et Générale, 64:1-84 and

plates I-II.

Jeannel, R. 1926. Monographie des Trechinae. Morphologie comparée et distribution géographique d'un groupe de Coléoptères (1re livraison). L'Abeille, 32:221-550.

Jeannel, R. 1937. Notes sur les Carabiques (Première note). Revue Française d'Entomologie, 4:1-23.

Jeannel, R. 1941. Faune de France, 39. Coléoptères Carabiques. Première partie. P. Lechevalier et Fils, Paris, 571 pp.

Kavanaugh, D. H. 1971. A new species of Nebria Latreille from Utah. Journal of the Kansas Entomological Society, 44:40-46.

Kavanaugh, D. H. 1972. Hennig's principles and methods of phylogenetic systematics. The Biologist, 54:1115-127.

Kavanaugh, D. H. 1977. An example of aggregation in the Scaphinotus subgenus Brennus Motschulsky (Coleoptera: Carabidae: Cychrini). The Pan-Pacific Entomologist, 53:27-31.

Kavanaugh, D. H. in press A. Investigations on present climatic refugia in North America through studies on the distributions of carabid beetles: concepts, methodology and prospectus.

Kavanaugh, D. H. in press B. Rates of taxonomically significant differentiation in relation to geographical isolation and habitat: examples from a study of the Nearctic Nebria fauna.

Kavanaugh, D. H. in press C. Hennigian phylogenetics in contemporary systematics: principles, methods and uses.

Kavanaugh, D. H., and E. A. Martinko. 1972. Notes on distribution and a peculiar behavior pattern in Nebria purpurata LeConte (Coleoptera: Carabidae). The Coleopterists Bulletin, 26:147-149.

Keen, J. H., 1895. List of Coleoptera collected at Massett, Queen

Charlotte Islands, B. C. The Canadian Entomologist, 27:165-172, 217-220.

Kirby, W. 1837. Part 4. The insects. [xxxix + 325 pp.] In: Richardson, J., Fauna Boreali-Americana; or the zoology of the northern parts of British America. Josiah Fletcher, Norwich and London.

Kirk, V. M. 1970. A list of the beetles of South Carolina. Part 2.--mountain, piedmont, and southern coastal plain. South Carolina Agricultural Experiment Station Technical Bulletin No. 1038, 117 pp.

Kirk, V. M., and E. U. Balsbaugh, Jr. 1975. A list of the beetles of South Dakota. Agricultural Experiment Station South Dakota State University Technical Bulletin No. 42, 139 pp.

Knobel, E. 1895. Beetles of New England and their kind--a guide to know them readily. Bradlee Whidden, Boston, 48 pp.

Kryzhanovskiy, O. L., and L. P. Molodova. 1973. The faunistic and ecological ground-beetle (Coleoptera, Carabidae) complexes of south Sakhalin. Entomological Review (a translation of Entomologicheskoye Obozreniye), 52:40-48.

La Rivers, I. 1946. An annotated list of Carabinae known to occur in Nevada (Coleoptera: Carabidae). Bulletin of the Southern California Academy of Sciences, 45:133-140.

Larochelle, A. 1972. Notes sur les périodes d'accouplement de quelques Carabidae du Québec. Le Naturaliste Canadien, 99:61-63.

Larochelle, A. 1975. Les Carabidae du Québec et du Labrador. Département de Biologie du Collège Bourget, Rigaud, Bulletin No. 1, 255 pp.

Larochelle, A. 1976a. Dates of egg-production in some carabid beetles (Coleoptera: Carabidae) from Québec. Cordulia, 2:47-49.

Larochelle, A. 1976b. New data on carabid beetles as prey of the American toad. Cordulia, 2:130.

Larochelle, A. 1977. A list of teneral carabid beetles (Coleoptera: Carabidae) from Québec and their dates of capture. Cordulia, 3:109-113.

Larson, D. J. 1975. The predaceous water beetles (Coleoptera: Dytiscidae) of Alberta: systematics, natural history and distribution. Quaestiones Entomologicae, 11:245-498.

Larsson, S. G. 1939, Entwicklungstypen und Entwicklungszeiten der dänischen Carabiden. Entomologiske Meddelelser, 20:277-569.

Larsson, S. G., and G. Gigja. 1959. Coleoptera 1. Synopsis of species. The Zoology of Iceland, 3:1-216.

Latreille, P. A. 1802. Histoire naturelle, générale et particulière des Crustacés et Insectes. 3. F. Dufait, Paris, 467 pp.

Latreille, P. A. 1810. Considérations générale sur l'ordre naturel des animaux composant les classes des Crustacés, des Arachnides, et des Insectes; avec un tableau méthodique de leurs genres, disposés en familles. F. Schoell, Paris, 444 pp.

Lavigne, R. 1977. Checklist of the Carabidae of Wyoming, U. S. A.. Cordulia, 3:43-48.

LeConte, J. L. 1848. A descriptive catalogue of the geodephagous Coleoptera inhabiting the United States east of the Rocky Mountains. Annals of the Lyceum of Natural History of New York, 4:173-474.

LeConte, J. L. 1850. General remarks upon the Coleoptera of Lake

Superior. [pp. 201-242] In: Agassiz, J. L. R., Lake Superior, Natural History 4. Gould, Kendall, and Lincoln, Boston, x + 248 pp. + 8 plates.

LeConte, J. L. 1853. Notes on the classification of the Carabidae of the United States. Transactions of the American Philosophical Society (new series), 10:363-403.

LeConte, J. L. 1859a. Catalogue of the Coleoptera of Fort Tejon, California. Proceedings of the Academy of Natural Sciences of Philadelphia, 11:69-90.

LeConte, J. L. 1859b. Additions to the coleopterous fauna of northern California and Oregon. Proceedings of the Academy of Natural Sciences of Philadelphia, 11:281-292.

LeConte, J. L. 1860. Report upon insects collected on the survey. In: Reports of explorations and surveys to ascertain the most practical and economical route for a railroad from the Mississippi River to the Pacific Ocean. 1853-5. Vol. XII. Book II. Part III. Zoological Report No. 1., pp. 1-72.

LeConte, J. L. 1863a-66a. List of the Coleoptera of North America. Smithsonian Miscellaneous Collections, No. 140, 6:1-49 (1863), 50-70 (1866).

LeConte, J. L. 1863b-66b. New species of North American Coleoptera. Part 1. Smithsonian Miscellaneous Collections, No. 167, 6:1-86 (1863), 87-168 (1866).

LeConte, J. L. 1866c. Additions to the coleopterous fauna of the United States. I. Proceedings of the Academy of Natural Sciences of Philadelphia, 1866:361-394.

LeConte, J. L. 1869. List of Coleoptera collected in Vancouver's Island by Henry and Joseph Matthews, with descriptions of some new species. The Annals and Magazine of Natural History, 4:369-386.

LeConte, J. L. 1873. Synonymical remarks upon North American Coleoptera. Proceedings of the Academy of Natural Sciences of Philadelphia, 1873:321-336.

LeConte, J. L. 1878. The Coleoptera of the alpine regions of the Rocky Mountains. Bulletin of the United States Geological and Geographical Survey of the Territories, 4:447-480.

LeConte, J. L. 1879. The Coleoptera of the alpine Rocky Mountain regions. Part II. Bulletin of the United States Geological and Geographical Survey of the Territories, 5:499-520.

Leng, C. W. 1920. Catalogue of the Coleoptera of America, north America. John D. Sherman, Mount Vernon, New York, x + 470 pp.

Leng, C. W., and A. J. Mutchler. 1927. Supplement to Catalogue of the Coleoptera of America, north of Mexico. John D. Sherman, Mount Vernon, New York, 78 pp.

Leng, C. W., and A. J. Mutchler, 1933. Second and third supplements to Catalogue of the Coleoptera of America, north of Mexico. John D. Sherman, Mount Vernon, New York, 112 pp.

Leonard, M. D. 1928. A list of the insects of New York with a list of the spiders and certain allied groups. Cornell University Agricultural Experiment Station, Memoir 101, 1121 pp.

Lindroth, C. H. 1939. Zur Systematik fennoskandischer Carabiden. 2. Nebria nivalis Payk. und gyllenhali Schönh. Entomologisk Tidskrift, 60:54-62.

Lindroth, C. H. 1945-49. Die fennoskandischen Carabidae, eine tiergeographische Studie. I-III. Göteborgs Kunglig Vetenskaps-och Vitterhets-Samhalles Handlingar, Sjatte Följden (Serien B), 4: (I) 709 pp. (1945), (II) 277 pp. (1945), (III) 911 pp. (1949).

Lindroth, C. H. 1953a. Kirby's types of North American Carabidae (Coleoptera). Proceedings of the Royal Entomological Society of London, Series B, 22:167-177.

Lindroth, C. H. 1953b. Influence of Pleistocene climate changes on the insect fauna of northern Europe. Transaction of the IXth International Congress of Entomology, Amsterdam, August 17-24, 1952, 2:145-153.

Lindroth, C. H. 1954a. Carabid beetles from Nova Scotia. The Canadian Entomologist, 86:299-310.

Lindroth, C. H. 1954b. Random notes on North American Carabidae. Bulletin of the Museum of Comparative Zoology, 111:117-161.

Lindroth, C. H. 1954c. Carabid beetles from eastern and southern Labrador. The Canadian Entomologist, 86:364-370.

Lindroth, C. H. 1954d. Carabidae common to Europe and North America. The Coleopterists Bulletin, 8:35-52.

Lindroth, C. H. 1955a. The carabid beetles of Newfoundland including the French islands St. Pierre and Miquelon. Opuscula Entomologica, Supplement 12, 160 pp. + 9 plates.

Lindroth, C. H. 1955b. Dejean's types of North American Carabidae. Opuscula Entomologica, 20:10-34.

Lindroth, C. H. 1957. The faunal connections between Europe and North America. John Wiley and Sons, New York, 344 pp.

Lindroth, C. H. 1961a. The ground-beetles of Canada and Alaska, Part 2. Opuscula Entomologica, Supplement 20, pp. 1-200.

Lindroth, C. H. 1961b. Verbindungen und Barrieren in der zirkumpolaren Verbreitung der Insekten. XI. Internationaler Kongress für Entomologie, Wien, 17. bis 25. August 1960, Verhandlungen, 1:438-445.

Lindroth, C. H. 1963a. The fauna history of Newfoundland illustrated by carabid beetles. Opuscula Entomologica, Supplement 23, 112 pp.

Lindroth, C. H. 1963b. The Aleutian Islands as a route for dispersal across the North Pacific. [pp. 121-131] In: Gressitt, J. L. (editor), Pacific Basin biogeography. Bishop Museum Press, Honolulu, ix + 563 pp.

Lindroth, C. H. 1965. Skaftafell, Iceland--a living glacial refugium. Oikos, Supplement 6, 142 pp.

Lindroth, C. H. 1969a. The theory of glacial refugia in Scandinavia. Comments on present opinions. Notulae Entomologicae, 49:178-192.

oth, C. H. 1969b. The biological importance of Pleistocene refugia. [pp. 7-17] In: Karlstrom, T. N. V., and G. E. Ball (editors), The Kodiak Island refugium: its geology, flora, fauna and history. Ryerson Press, Toronto, xvi + 262 pp.

Lindroth, C. H. 1969c. An analysis of the carabid fauna of the refugium. [pp. 195-210] In: Karlstrom, T. N. V., and G. E. Ball (editors), The Kodiak Island Refugium: its geology, flora, fauna and history. Ryerson Press, Toronto, xvi + 262 pp.

Lindroth, C. H. 1969d. The ground-beetles of Canada and Alaska, Part 6. Opuscula Entomologica, Supplement 35, pp. 945-1192.

Lindroth, C. H. 1971. On the occurrence of a continental element in the ground-beetle fauna of eastern Canada (Coleoptera: Carabidae). The Canadian Entomologist, 103:1455-1462.

Lindroth, C. H. 1974. Handbook for the identification of British insects, 4(2). Coleoptera, Carabidae. Royal Entomological Society of London, London, 148 pp.

Lindroth, C. H. 1975. Designation of holotypes and lectotypes among ground beetles (Coleoptera, Carabidae) described by Thomas L. Casey. The Coleopterists Bulletin, 29:109-147.

Lindroth, C. H., and R. Freitag. 1969. North American ground-beetles (Coleoptera, Carabidae, excluding Cicindelinae) described by Thomas Say: designation of lectotypes and neotypes. Psyche, 76:326-361.

Linnaeus, C. 1758. Systema naturae. Tenth edition. Part 1. Stockholm, 824 pp.

Linnaeus, C. 1767. Systema naturae. Twelfth edition. Part 1(2). Stockholm, 795 pp. [= pp. 533-1327].

Löding, H. P. 1945. Catalogue of the beetles of Alabama. Monograph No. 11, Geological Survey of Alabama, University of Alabama, 172 pp.

Luff, M. L. 1972. The larvae of the British Carabidae (Coleoptera) II. Nebriini. The Entomologist, 105:161-179.

Luff, M. L. 1976. Notes on the biology of the developmental stages of Nebria brevicollis (F.) (Col., Carabidae) and on their parasites, Phaenoserphus spp. (Hym., Proctotrupidae). The Entomologist's Monthly Magazine, 111:249-255.

Luff, M. L., and L. Davies. 1972. Ecological observations on some

Carabidae (Col.) from St. Kilda, with notes on other beetles new to the island. The Entomologist's Monthly Magazine, 108:46-51.

Machard, P. 1970. Les Carabiques au bord des nèves. L'Entomologiste, 26:7-9.

Madge, R. B. 1967. A revision of the genus Lebia Latreille in America north of Mexico (Coleptera, Carabidae). Quaestiones Entomologicae, 3:139-244.

Mani, M. S. 1962. Introduction to high altitude entomology. Insect life above the timber-line in the North-west Himalaya. Methuen and Co., London, xix + 302 pp.

Mani, M. S. 1968. Ecology and biogeography of high altitude insects. W. Junk, The Hague. xiv + 527 pp.

Mank, E. W. 1934. The Coleoptera of Glacier Park, Montana. The Candian Entomologist, 66:73-81.

Mann, D. H. 1978. Ecological studies of snowfield foraging arthropods on Mount Rainier. Unpublished MSc. Thesis, University of Washington, vii + 87 pp.

Mannerheim, C. G. 1843. Beitrag zur Kaefer-Fauna der Aleutischen Inseln, der Insel Sitkha und Neu-Californiens. Bulletin de la Société Impériale des Naturalistes de Moscou, 16:175-314.

Mannerheim, C. G. 1852. Zweiter Nachtrag zur Kaefer-Fauna der nord-amerikanischen Laender des russischen Reiches. Bulletin de la Société Impériale des Naturalistes de Moscou, 25:283-387.

Mannerheim, C. G. 1853. Dritter Nachtrag zur Kaefer-Fauna der nord-amerikanischen Laender des russischen Reiches. Bulletin de la Société Impériale des Naturalistes de Moscou, 26:96-273.

Marr, J. W. 1967. Ecosystems of the east slope of the Front Range in

Colorado. University of Colorado Studies, Series in Biology, No. 8, 134 pp.

Martin, P. S., and P. J. Mehringer, Jr. 1965. Pleistocene pollen analysis and biogeography of the southwest. [pp. 433-451] In: Wright, H. E., Jr., and D. G. Frey (editors), The Quaternary of the United States. A review volume for the VII Congress of the International Association for Quaternary Research. Princeton University Press, Princeton, New Jersey, x + 922 pp.

Maslin, T. P. 1952. Morphological criteria of phylogenetic relationships. Systematic Zoology, 1:49-70.

Matthews, J. V., Jr. 1970. Two new species of Micropeplus from the Pliocene of western Alaska with remarks on the evolution of Micropeplinae (Coleoptera: Staphylinidae). Canadian Jouranl of Zoology, 48:779-788.

Matthews, J. V., Jr. Evolution of the subgenus Cyphelophorus (Genus Helophorus, Hydrophilidae, Coleoptera): description of two new fossil species and discussion of Helophorus tuberculatus Gyll. Canadian Journal of Zoology, 54:652-673.

Matthews, J. V., Jr. 1977. Tertiary Coleoptera fossils from the North American arctic. The Coleopterists Bulletin, 31:297-308.

Mayr, E. 1969. Principles of systematic zoology. McGraw-Hill Book Co., New York, xi + 428 pp.

Melsheimer, F. E. 1853. Catalogue of the described Coleoptera of the United States. Smithsonian Institution, Washington, D. C., xvi + 174 pp.

Ménétriés, M. 1844. Sur un envoi d'Insectes de la côte N. O. d'Amérique. Bulletin de la Classe Physico-Mathématique de

l'Académie Im[illegible]iale des Sciences de Saint-Petersbourg, 2:50-63.

Merriam, C. H. 1892. The geographical distribution of life in North America with special reference to mammals. Proceedings of the Biological Society of Washington, 7:1-64.

Merriam, C. H. 1894a. The geographical distribution of animals and plants in North America. United States Department of Agriculture Yearbook, 1894:203-214.

Merriam, C. H. 1894b. Laws of temperature control of geographical distribution of terrestrial mammals and plants. National Geographic Magazine, 6:229-238.

Merriam, C. H. 1898. Life zones and crop zones of the United States. United States Department of Agriculture Division of Biological Survey, Bulletin No. 10, 79 pp.

Morgan, A. 1972. The fossil occurrence of Helophorus arcticus Brown (Coleoptera: Hydrophilidae) in Pleistocene deposits of the Scarborough Bluffs, Ontario. Canadian Journal of Zoology, 50:555-558.

Morgan, A. 1973. Late Pleistocene environmental changes indicated by fossil insect faunas of the English midlands. Boreas, 2:173-212.

Motschulsky, V. 1846. Insectes de la Sibérie, rapportés d'un voyage fait en 1839-1840. Mémoires presentés à l'Academie Impériale des Sciences de St.-Petersbourg par divers savans et lus dans ses assemblées, 5:1-274.

Motschulsky, V. 1850. Die Kaefer Russlands. I. Insecta Carabica. Gautier, Moscow, vii + 91 pp.

Motschulsky, V. 1859. Coléoptères du Gouvernement Iakoutsk, recuellis par M. Pavlofski. Mélanges Biologiques Tirés du Bulletin de

l'Académie Impériale des Sciences de St.-Petersbourg, 3:221-238.

Motschulsky, V. 1860. Coléoptères de la Sibérie orientale et en particulier des Rives de l'Amour. [pp. 79-257] In: Schrenck, L. von, Reisen und Forschungen im Amur-Lande in den Jahren 1854-1856, II. St. Petersburg.

Motschulsky, V. 1865. Enumération des nouvelles espèces de Coléoptères. IV. Bulletin de la Société Impériale des Naturalistes de Moscou, 38:227-380.

Munroe, E. 1954. Canada as an environment for insect life. The Canadian Entomologist, 88:372-476.

Munster, T. 1933. Tillaeg og Bemaekninger til Norges Koleopterfauna. III. Norsk Entomologisk Tidsskrift, 3:267-278.

Nakane, T. 1963. Carabidae. [pp. 5-52 and plates 3-26] In: Iconographia insectorum Japonicorum colore naturali edita. II. (Coleoptera). Hokurykan, Tokyo.

Nakane, T. 1971. Notes on the Coleoptera from the alpine zone of the Daisetsu Mountains. [pp. 179-183] In: Faunal Survey of the Mt. Daisetsu area, JIBP Main area--XII. Annual Report of JIBP-CTS for Fiscal Year 1970.

Nebeker, A. V. 1971. Effect of temperature at different altitudes on the emergence of aquatic insects from a single stream. Journal of the Kansas Entomological Society, 44:26-35.

Nelson, G. J. 1974. Classification as an expression of phylogenetic relationship. Systematic Zoology, 22:344-359.

Nelson, G. J. 1975. Historical biogeography: an alternative formalization. Systematic Zoology, 23:555-558.

Nimmo, A. P. 1971. The adult Rhyacophilidae and Limnephilidae (Trichoptera) of Alberta and eastern British Columbia and their post-glacial origin. Quaestiones Entomologicae, 7:3-234.

Noonan, G. R. 1973. The anisodactylines (Insecta: Coleoptera: Carabidae: Harpalini): classification, evolution, and zoogeography. Quaestiones Entomologicae, 9:266-480.

Oberthur, R. 1883. Coleopterorum novitates. Recueil specialement consacre a l'etude des Coléoptères. Ier. R. Oberthur, Rennes, 48 pp. + 2 plates.

Östbye, E., and L. Sömme 1972. The overwintering of Pelophila borealis Payk. I. Survival rates and cold-hardiness. Norsk Entomologisk Tidsskrift, 19:165-168.

Packard, A. S., Jr. 1872. List of the Coleoptera collected in Labrador. Fourth Annual Report of the Peabody Academy of Sciences, 1872:92-94.

Packard, A. S., Jr. 1888. List of spiders, myriapods and insects of Labrador. The Canadian Entomologist, 20:143-149.

Panzer, G. W. F. 1797. Faunae insectorum Germanicae initia oder Deutschlands Insecten. Hefte 37-48. Felssecker, Nürnberg, 14 pp.

Papp, R. P. 1978. A nival aeolian ecosystem in California. Arctic and Alpine Research, 10:117-131.

Paykull, G. 1790. Monographia Caraborum Sueciae. J. Edman, Uppsala, 138 pp.

Paykull, G. 1798. Fauna Suecica. Insecta. I. Uppsala, x + 234 pp.

Penney, M. 1966. Studies on certain aspects of the ecology of Nebria brevicollis (F.) (Coleoptera, Carabidae). Journal of Animal Ecology, 35:505-512.

Penney, M. 1969. Diapause and reproduction in Nebria brevicollis (F.) (Coleoptera: Carabidae). Journal of Animal Ecology, 38:219-233.

Perrault, G. G. 1972. New and interesting records of Carabidae from the Olympic Peninsula (Washington). The Coleopterists Bulletin, 26:62.

Peyerimhoff, P. de. 1911. Nouveaux Coléoptères du Nord-Africain (quatorzième note: faune cavernicole du Djurdjura). Bulletin de la Société Entomologique de France, 16:359-361.

Platnick, N. I. 1976. Concepts of dispersal in historical biogeography. Systematic Zoology, 25:294-295.

Platnick, N. I. 1977. The hypochiloid spiders: a cladistic analysis, with notes on the Atypoidea (Arachnida, Araneae). American Museum Novitates, 2627:1-23.

Platnick, N. I., and G. J. Nelson. 1978. A method of analysis for historical biogeography. Systematic Zoology, 27:1-16.

Poppius, B. 1905. Kola-Halfons och Enare Lappmarks Coleoptera. Festschrift für Palmén, No. 12, 200 pp.

Poppius, B. 1910. Die Coleopteren des arktischen Gebietes. Fauna Arctic, 5:289-447 + 5 plates.

Pratt, R. Y., and M. H. Hatch, 1938. The food of Black Widow spiders on Whidby Island, Washington. Journal of the New York Entomological Society, 46:191-193.

Provancher, L. 1877. Petite faune entomologique du Canada. I. Les Coléoptères. C. Darveau, Québec, viii + 785 pp.

Putnam, J. D. 1876a. Report on the insects collected by Captain Jones' expedition to northwestern Wyoming in 1873. Proceedings of the Davenport Academy of Natural Sciences, 1876:187-191.

Putnam, J. D. 1876b. Report on the insects collected in the vicinty of Spring Lake Villa, Utah Co., Utah, during the Summer of 1875. Proceedings of the Davenport Academy of Natural Sciences, 1876:193-205.

Ramaley, F. 1907. Plant zones of the Rocky Mountains of Colorado. Science, 26:642-643.

Reitter, E. 1908. Fauna Germanica. Die Käfer des deutschen Reiches. I. Stuttgart, viii + 248 pp.

Richards, O. W. 1946. An observation on Nebria brevicollis (F.) (Col., Carabidae). The Entomologist's Monthly Magazine, 82:225.

Richmond, G. M. 1965. Glaciation of the Rocky Mountains. [pp. 217-231] In: Wright, H. E., Jr., and D. G. Frey (editors), The Quaternary of the United States. A review volume for the VII Congress of the International Association for Quaternary Research. Princeton University Press, Princeton, New Jersey, x + 922 pp.

Rosen, D. E. 1976. A vicariance model of Caribbean biogeography. Systematic Zoology, 24:431-464.

Ross, H. H. 1965. Pleistocene events and insects. [pp. 583-596] In: Wright, H. E., Jr., and D. G. Frey (editors), The Quaternary of the United States. A review volume for the VII Congress of the International Association for Quaternary Research. Princeton University Press, Princeton, New Jersey, x + 922 pp.

Ross, H. H. 1974. Biological systematics. Addison-Wesley Publishing Co., Inc., Reading Massachusetts, Menlo Park, California, London, Don Mills, Ontario, Preface, Acknowledgements, Contents, 345 pp..

Rossi, P. 1792-94. Mantissa insectorum, exhibens species nuper in

Etruria collectas, adjectis faunae Etruscae illustrationibus ac emendationibus. Pisa, 148 and 154 pp.

Ruette, R. de. 1970. A catalogue of types of Coleoptera in the Canadian National Collection of Insects. Memoirs of the Entomological Society of Canada. No. 72, 134 pp.

Sahlberg, J. 1885. Coleoptera och Hemiptera insamlade af Vega Expeditionens medlemmar å Berings Sunds amerikanska kust uti omgifningarna af Port Clarence, vid Grantley Harbour och sjön Iman-Ruk den 23-26 Juli 1879. Ur DVega-expeditionens Vetenskapliga Iakttagelserd, 4:43-71.

Sahlberg, R. E. 1844. In faunam insectorum rossicam symbola, novas ad Ochotsk lectas Carabicorum species continens. Frenckel, Helsingfors, 63 pp.

Say, T. 1823. Descriptions of insects of the families of Carabici and Hydrocanthari of Latreille inhabiting United States. Transactions of the American Philosophical Society, new series, 2:1-109.

Schaeffer, B., M. K. Hecht, and N. Eldredge, 1972. Phylogeny and paleontology. Evolutionary Biology, 6:31-46.

Schaupp, F. G. 1878. Synoptic table. Nebria Latreille. Bulletin of the Brooklyn Entomological Society, 1:45-46.

Schiller, W. 1973. Die Carabiden-Fauna des Naturschutzgebietes Hl. Meer, Kr. Tecklenburg. Natur und Heimat (Münster), 33:111-118.

Schiller, W., and F. Weber 1975. Die Zeitstruktur der ökologischen Nische der Carabiden. Abhandlungen aus dem Landesmuseum für Naturkunde zu Münster in Westfalen, 37:1-34.

Schiødte, J. C. 1867. De metamorphosi Eleutheratorum Observationes:

Bidrag til Insekternes Udviklingshistorie (Fortsaettelse). Naturhistorisk Tidsskrift, Series 3, 4:415-522.

Schönherr, C. J. 1806. Synonymia insectorum, oder: Versuch einer Synonymie aller bisher bekannten Insecten; nach Fabricii Systema Eleutheratorum geordnet. I. H. A. Nordstrom, Stockholm, xii + 293 pp.

Schøyen, W. M. 1880. Coleopterologiske notitser. Entomologisk Tidskrift (Stockholm), 1:177-185.

Schuler, L. 1960. La spermathèque dans la tribu des Bembidiini Jeannel (Col. Trechidae). Revue Française d'Entomologie, 27:24-47.

Schuler, L. 1962. La spermathèque des Chlaenius de France (Callistomorphi Jeannel) (Coleoptera). L'Entomologiste, 18:77-86.

Schuler, L. 1965. Les organes génitaux femelles chez les Coléoptères Carabiques de France. Une définition du genre, le principe de la relativité, résultats généraux. Bulletin de la Société Entomologique de France, 70:110-120.

Schwarz, E. A. 1900. Papers from the Harriman Alaska Expedition. XVII. Entomological results (12): Coleoptera. Proceedings of the Washington Academy of Sciences, 2:523-537.

Scudder, S. H. 1879. Appendix A. The fossil insects collected in 1877, by Mr. G. M. Dawson, in the interior of British Columbia. [pp. 175B-185B] In: Dawson, G. M., Preliminary report of the physical and geological features of the southern portion of the interior of British Columbia. Report on Progress of the Geological Survey of Canada, 1877-78:1B-187B.

Scudder, S. H. 1890. The fossil insects of North America with notes on some European species. 2. The Tertiary insects. Report of the United States Geological Survey of the Territories, Volume 13, 734 pp. (including 28 plates)

Scudder, S. H. 1895a. The Coleoptera hitherto found fossil in Canada. Geological Survey of Canada, Contributions to Canadian Paleontology, 2:27-56 + 2 plates.

Scudder, S. H. 1895b. Additions to the coleopterous fauna of the interglacial clays of the Toronto district. Appendix by A. D. Hopkins on scolytid borings from the same deposits. Geological Survey of Canada, Contributions to Canadian Paleontology, 2:67-92 + 8 plates.

Scudder, S. H. 1900. Adephagous and clavicorn Coleoptera from Tertiary deposits at Florissant, Colorado with descriptions of a few other forms and a systematic list of the non-rhynchophorous Tertiary Coleoptera of North America. Unites States Geological Survey Monongraph No. 40, 148 pp. + 11 plates.

Semenov Tian-Shanskij, A., and D. Znojko. 1928. De Eonebria, subgenere novo generis Nebria Latr., ejusque speciebus (Coleoptera, Carabidae). Revue Russe d'Entomologie, 22:213-215.

Sharp, D., and F. Muir. 1912. The comparative anatomy of the male genital tube in Coleoptera. Transactions of the Entomological Society of London, 1912:477-642 + plates XLII-LXXVIII.

Sherman, J. D., Jr. 1910. A list of Labrador Coleoptera. Journal of the New York Entomological Society, 18:173-197.

Shilenkov, V. G. 1974. Fauna zhuzhelits (Coleoptera, Carabidae) yugo-zapadnogo Pribaikal'ya. [pp. 42-76] In: Mezhetskikh, Z. P.

(editor), Fauna Nasekomykh Vostochoi Sibiri i Dalnego Vostoka. State University of Irkutsk.

Shilenkov, V. G. 1975a. Taksonomicheskii obzor zhuzhelits roda Nebria Latr. (Coleoptera, Carabidae) Sibiri i Dalnego Vostoka SSSR. Entomologicheskoye Obozreniye, 54:830-845.

Shilenkov, V. G. 1975b. O sistematike i geographicheskom rasprostranenii zhuzhelits roda Nebria Latr. (Coleoptera, Carabidae) Uralskikh gor. Permskii Gosudarstvbennyi Pedagogiuskii Instutut, Uchenye Zapiski, Tom 131, Biogeografiya i Krayevedeniye, Vypusk 3, 64 pp.

Shilenkov, V. G. 1976. Ground-beetles of the genus Nebria Latr. (Coleoptera, Carabidae) of the Mongolian People's Republic and adjacent regions. [in Russian, with English title only]. Insects of Mongolia, 4:115-132.

Simpson, G. G. 1960. Notes on the measurement of faunal resemblance. American Journal of Science, Bradley Volume, 258a:300-311.

Simpson, G. G. 1961. Principles of animal taxonomy. Columbia University Press, New York, xii + 247 pp.

Smith, J. B. 1910. Catalogue of the insects of New Jersey, Third edition. Annual Report of the New Jersey State Museum for 1909: 1-888.

Sokal, R. R., and P. H. A. Sneath. 1963. Principles of numerical taxonomy. W. H. Freeman and Co., San Francisco, xvi + 359 pp.

Solsky, S. 1875. Matériaux pour l'entomographie des provinces asiatique de la Russie. Horae Societatis Entomologicae Rossicae, 11:253-299.

Spence, J. R. 1974. The comparative biology of Nebria lacustris

(Casey) and Nebria pallipes (Say) in Vermont. Unpuiblished MSc. Thesis, Department of Zoology, University of Vermont, vii and 118 pp.

Spence, J. R., R. T. Bell, and J. R. Bell. 1976. The larvae of Nebria lacustris Casey and Nebria pallipes Say (Coleoptera, Carabidae). The Coleopterists Bulletin, 30:81-83.

Spence, J. R., and R. T. Bell. Taxonomy and comparative ecology in waterside Nebria (Carabidae). Unpublished manuscript.

Stephens, J. F. 1828. Illustrations of British entomology; or, a synopsis of indigenous insects: containing their generic and specific distinctions; with an account of their metamorphoses, times of appearance, localities, food, and economy, as far as practicable. Mandibulata, 1. Baldwin and Cradock, London, 186 pp. + 9 plates.

Strøm, H. 1768. Beskrivelse over Norske insecter. II. Det Kongelige Norske Videnskabers Selskab Skrifter, 4:313-371.

Sturm, J. 1826. Catalog meiner Insecten-Sammlung, erster Theil, Käfer. Nürnberg, 207 pp. + 4 plates

Sturm, J. 1843. Catalog der Käfersammlung von Jacob Sturm. Nürnberg, xiii + 386 pp. + 6 plates

Tanner, V. M. 1927. A preliminary study of the genitalia of female Coleoptera. Transactions of the American Entomological Society. 53:5-50 + plates II-7.

Tanner, V. M. 1928. The Coleoptera of Zion National Park, Utah. Annals of the Entomological Society of America, 21:269-280.

Taylor, G. W. 1886. The entomology of Vancouver Island. Notes on seventy-six species of Cicindeliade and Carabidae collected near

Victoria, Vancouver Island. The Canadian Entomologist, 18:34-37.

Thiele, H.-U. 1968. Was bindet Laufkäfer an ihre Lebensräume? Naturwissenschaftliche Rundschau, 21:57-65.

Thiele, H.-U. 1969a. Zusammenhänge zwischen Tagesrhythmik, Jahresrhythmik und Habitatbingung. Oecologia (Berlin), 3:227-229.

Thiele, H.-U. 1969b. The control of larval hibernation and adult aestivation in the carabid beetles Nebria brevicollis F. and Patrobus atrorufus Stroem. Oecologia (Berlin), 2:347-361.

Thiele, H.-U. 1971. Die Steuerung der Jahresrhythmik von Carabiden durch exogene und endogene Faktoren. Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere, 98:341-371.

Thiele, H.-U., and F. Weber. 1968. Tagesrhythmen der Aktivität bei Carabiden. Oecologia (Berlin), 1:315-355.

Tipton, J. D. 1960. Some aspects of the biology of the beetles Nebria (L.) and Feronia caerulescens (L.). Unpublished PhD. Dissertation, Reading University.

Tolbert, W. W., V. R. Tolbert, and R. E. Ambrose. 1977. Distribution, abundance and biomass of Colorado alpine tundra arthropods. Arctic and Alpine Research, 9:221-234.

Udvardy, M. D. F. 1969. Dynamic zoogeography, with special reference to land animals. Van Nostrand Reinhold Co., New York, xviii + 445 pp.

Ueno, S.-I. 1953. Carabidae. Shin-Konchu (Tokyo), 6:52-60.

Ueno, S.-I. 1955. Two new species of the genus Nebria. The Entomological Review of Japan, 6:45-50.

Ulke, H. 1902. A list of the beetles of the District of Columbia. Proceedings of the United States National Museum, 25:1-57.

United States Federal [redacted] of Surveys and Maps, Map Information Office. 1929. The mountains of the United States. United States Government Printing Office, Washington, D. C., 31 pp.

Van Dyke, E. C. 1919. The distribution of insects in western North America. Annals of the Entomological Society of America, 12:1-12.

Van Dyke, E. C. 1921. Coleoptera from the Pribilof Islands, Alaska. Proceedings of the California Academy of Sciences (Fourth series), 11:156-166.

Van Dyke, E. C. 1924. The Coleoptera collected by the Katmai Expedition. National Geographic Society, Contributed Technical Papers, Katmai Series, 2:1-26.

Van Dyke, E. C. 1925. Studies of western North American Carabinae with descriptions of new species. The Pan-Pacific Entomologist, 1:111-125.

Van Dyke, E. C. 1926. Certain peculiarities of the coleopterous insect fauna of the Pacific Northwest. Annals of the Entomological Society of America, 19:1-12.

Van Dyke, E. C. 1940. The origin and distribution of the coleopterous fauna of North America. [pp. 255-268] In: Proceedings of the Sixth Pacific Science Congress (Berkeley, Stanford and San Francisco, July 24 to August 12, 1939), Volume 4. University of California Press, x + 993 pp.

Van Dyke, E. C. 1943. New species and subspecies of North American

Carabidae. The Pan-Pacific Entomologist, 19:17-30.

Van Dyke, E. C. 1949. New species of North American Coleoptera. The Pan-Pacific Entomologist, 25:49-56.

Van Dyke, E. C. 1953. New Coleoptera from western North America. The Pan-Pacific Entomologist, 29:98-101, 102-107.

Venable, E. P. 1913. Notes on some Coleoptera of the Okanagan Valley. The Canadian Entomologist, 45:267-268.

Whitehead, D. R. 1972. Classification, phylogeny, and zoogeography of Schizogenius Putzeys (Coleoptera: Carabidae: Scaritini). Quaestiones Entomologicae, 8:131-348.

Whitehead, D. R. 1976. Classification and evolution of Rhinochenus Lucas (Coleoptera: Curculionidae: Cryptorhynchinae), and Quaternary Middle American zoogeography. Quaestiones Entomologicae, 12:118-201.

Wickham, H. F. 1893. Report on an entomological reconnaissance of southern Alaska and adjacent portions of British Columbia. Bulletin from the Laboratories of Natural History of the State University of Iowa, 2:202-233 + 2 plates.

Wickham, H. F. 1902. A catalogue of the Coleoptera of Colorado. Bulletin from the Laboratories of Natural History of the State University of Iowa, 5:217-310.

Wickham, H. F. 1903. The beetles of an Oregon beach. The Ottawa Naturalist, 17:49-52.

Wickham, H. F. 1909. A list of the Coleoptera of Iowa. Bulletin from the Laboratories of Natural History of the State University of Iowa, 6:1-40.

Wickham, H. F. 1923. Coleoptera of the Pribilof Islands, Alaska. [pp.

150-157] In: A biological survey of the Pribilof Islands, Alaska. North American Fauna No. 46. United States Department of Agriculture, Bureau of Biological Survey, iv + 255 pp.

Williams, G. 1959. Seasonal and daily activity in Carabidae, with particular reference to Nebria, Notiophilus and Feronia. Journal of Animal Ecology, 28:309-330.

Wilson, E. O., and W. L. Brown, Jr. 1953. The subspecies concept and its taxonomic application. Systematic Zoology, 2:97-111.

APPENDIX A. DISPOSITION OF PRIMARY TYPES OF NEARCTIC *NEBRIA*

SPECIES NAME	DESCRIBER	DATE:PAGE	STATUS	COLLECTION
Nebria acuta	Lindroth	1961:71	holotype	MCZ
Nebria aleuta	Van Dyke	1924:5	holotype	CAS
Nebria appalachia	Darlington	1931:153	holotype	MCZ
Nebria arkansana	Casey	1913:52	lectotype	USNM
Nebria balli	Kavanaugh	n. ssp.	holotype	CAS
Nebria bellorum	Kavanaugh	n. ssp.	holotype	CAS
Nebria beverliannä	Kavanaugh	n. ssp.	holotype	CAS
Nebria bifaria	Mannerheim	1853:120	lectotype	ZILR
Carabus brevicollis	Frabricius	1792:150	lectotype	ZMKD
Nebria brevis	Casey	1913:55	lectotype	USNM
Nebria carri	Kavanaugh	n. sp.	holotype	CAS
Nebria cascadensis	Kavanaugh	n. ssp.	holotype	CAS
Helobia castanipes	Kirby	1837:20	lectotype	BMNH
Nebria catenata	Casey	1913:49	lectotype	USNM
Nebria charlottae	Lindroth	1961:67	holotype	CNC

SPECIES NAME	DESCRIBER	DATE:PAGE	STATUS	COLLECTION
Nebria coloradensis	Van Dyke	1943:19	holotype	CAS
Nebria columbiana	Casey	1913:48	holotype	USNM
Nebria corvallis	Casey	1924:20	lectotype	USNM
Nebria crassicornis	Van Dyke	1925:121	holotype	S
Nebria cuneata	Casey	1913:50	lectotype	USNM
Nebria curtulata	Casey	1924:20	lectotype	USNM
Nebria darlingtoni	Kavanaugh	n. sp.	holotype	CAS
Nebria desolata	Kavanaugh	1971:41	holotype	CAS
Nebria diversa	LeConte	1863:2	lectotype	MCZ
Nebria edwardsi	Kavanaugh	n. ssp.	holotype	CAS
Nebria elias	Motschulsky	1865:275	type lost	ZMUM
Nebria eschscholtzii	Menetries	1844:55	lectotype	ZILR
Nebria expansa	Casey	1913:56	lectotype	USNM
Nebria femoralis	Motschulsky	1859:244	lectotype	ZILR
Nebria femorata	Motschulsky	1865:275	lectotype	ZILR
Nebria formalis	Casey	1920:153	lectotype	USNM

SPECIES NAME	DESCRIBER	DATE:PAGE	STATUS	COLLECTION
Nebria fragilis	Casey	1924:21	lectotype	USNM
Nebria frigida	Sahlberg (R.F.)	1844:11	lectotype	UMTF
Nebria gaspesiana	Kavanaugh	n. ssp.	holotype	CAS
Nebria gebleri	Dejean	1831:573	holotype	MHNP
Nebria gouleti	Kavanaugh	n. sp.	holotype	CAS
Nebria gregaria	Fischer v. Wald.	1821:72	lectotype	ZMUM
Carabus gyllenhali	Schönherr	1806:196	lectotype	NRSS
Nebria hippisleyi	Casey	1924:21	holotype	USNM
Nebria hudsonica	LeConte	1863:3	lectotype	MCZ
Nebria incerta	Casey	1913:53	lectotype	USNM
Nebria ingens	Horn	1870:98	lectotype	MCZ
Nebria intermedia	Van Dyke	1949:49	holotype	CAS
Nebria kincaidi	Schwarz	1900:525	holotype	USNM
Nebria labradorica	Casey	1920:151	lectotype	USNM
Nebria lacustris	Casey	1913:56	lectotype	USNM
Nebria lamarckensis	Kavanaugh	n. ssp.	holotype	CAS
Nebria lassenensis	Kavanaugh	n. ssp.	holotype	CAS

SPECIES NAME	DESCRIBER	DATE:PAGE	STATUS	COLLECTION
Nebria lindrothi	Kavanaugh	n. ssp.	holotype	CAS
Nebria livida	LeConte	1859:84	lectotype	MCZ
Nebria longula	LeConte	1878:478	holotype	MCZ
Nebria lyelli	Van Dyke	1925:120	holotype	CAS
Nebria mannerheimii	Fischer v. Wald.	1828:253	lectotype	ZMUM
Nebria meanyi	Van Dyke	1925:118	holotype	CAS
Nebria melanaria	Hatch	1949:115	holotype	UWBM
Nebria metallica	Fischer v. Wald.	1821:71	lectotype	ZMUM
Nebria mobilis	Casey	1913:50	lectotype	USNM
Nebria modoc	Kavanaugh	n. ssp.	holotype	CAS
Nebria moesta	LeConte	1850:209	lectotype	MCZ
Nebria mollis	Motschulsky	1865:274	lectotype	ZMUM
Nebria navajo	Kavanaugh	n. sp.	holotype	CAS
Nebria nimbosa	Casey	1920:150	holotype	USNM
Carabus nivalis	Paykull	1790:52	lectotype	NRSS
Nebria oasis	Kavanaugh	n. ssp.	holotype	CAS
Nebria obliqua	LeConte	1866:363	lectotype	MCZ

SPECIES NAME	DESCRIBER	DATE:PAGE	STATUS	COLLECTION
Nebria obtusa	LeConte	1878:478	holotype	MCZ
Nebria oowah	Kavanaugh	n. ssp.	holotype	CAS
Nebria oregona	Casey	1913:52	lectotype	USNM
Nebria ovipennis	LeConte	1878:477	holotype	MCZ
Nebria pacifica	Chaudoir	1850:424	holotype	MHNP
Nebria pallidissima	Casey	1924:19	lectotype	USNM
Nebria pallipes	Say	1823:78	neotype	MCZ
Nebria paradisi	Darlington	1931:24	holotype	MCZ
Nebria parvula	Sahlberg (J.)	1885:47	lectotype	NRSS
Nebria piperi	Van Dyke	1925:117	holotype	CAS
Nebria piute	Erwin & Ball	1972:95	holotype	USNM
Nebria prominens	Casey	1920:151	lectotype	USNM
Nebria pugetana	Casey	1924:19	lectotype	USNM
Nebria purpurata	LeConte	1878:477	holotype	MCZ
Nebria quileute	Kavanaugh	n. ssp.	holotype	CAS
Nebria rathvoni	LeConte	1853:400	holotype	MCZ
Nebria raveni	Van Dyke	1953:102	holotype	CAS

SPECIES NAME	DESCRIBER	DATE:PAGE	STATUS	COLLECTION
Nebria reducta	Casey	1920:150	lectotype	USNM
Nebria riversi	Van Dyke	1925:115	holotype	CAS
Carabus rufescens	Strŏm	1768:331	no type	----
Nebria sahlbergii	Fischer v. Wald.	1828:254	lectotype	UMHF
Nebria schwarzi	Van Dyke	1925:116	holotype	USNM
Nebria sierrae	Kavanaugh	n. ssp.	holotype	CAS
Nebria siskiyouensis	Kavanaugh	n. ssp.	holotype	CAS
Nebria spatulata	Van Dyke	1925:119	holotype	CAS
Nebria strawberriensis	Kavanaugh	n. ssp.	holotype	CAS
Nebria suturalis	LeConte	1850:209	lectotype	MCZ
Nebria sylvatica	Kavanaugh	n. ssp.	holotype	CAS
Nebria teewinot	Kavanaugh	n. ssp.	holotype	CAS
Nebria tenuipes	Casey	1913:51	lectotype	USNM
Nebria testaceipes	Casey	1913:54	holotype	USNM
Nebria tetonensis	Erwin & Ball	1972:95	holotype	USNM
Nebria texana	Casey	1913:54	holotype	USNM
Nebria townsendi	Casey	1924:19	lectotype	USNM

SPECIES NAME	DESCRIBER	DATE:PAGE	STATUS	COLLECTION
Nebria transversa	Casey	1920:152	holotype	USNM
Nebria triad	Kavanaugh	n. ssp.	holotype	CAS
Nebria trifaria	LeConte	1878:478	lectotype	MCZ
Nebria uinta	Kavanaugh	n. ssp.	holotype	CAS
Nebria utahensis	Kavanaugh	n. ssp.	holotype	CNC
Nebria vandykei	Bänninger	1928:5	lectotype	ETHZ
Nebria vandykei	Darlington	1930:104	holotype	MCZ
Nebria violacea	Motschulsky	1850:73	lectotype	UMHF
Nebria virescens	Horn	1870:100	holotype	MCZ
Nebria viridis	Horn	1870:101	lectotype	MCZ
Nebria wyeast	Kavanaugh	n. ssp.	holotype	CAS
Nebria zioni	Van Dyke	1943:20	holotype	CAS

APPENDIX B: MATERIAL EXAMINED

Geographical and temporal specimen data are presented here to supplement the distributional maps and discussions for each species. In order to assist biologists interested in any studies of *Nebria* species, I have tried to present data in a manner which will facilitate location of appropriate populations. A number of comments should be made on the format and content of the data to allow for effective use of this appendix.

For convenience, the species and all data (including countries, states or provinces, counties, and localities) are arranged alphabetically. I agree with Lindroth (1969: xxix) that this format by itself fails to readily provide coherent pictures of species distributions. In concert with distributional maps, however, this format offers obvious advantages in ease of data retrieval.

All records are from specimens I have personally studied. Records solely from the literature are not included here. Certain literature records are, however, discussed in the text.

The use of the geographical subdivisions *county* (written "Co." in the listing) or *comté* ("Cté" in the listing) are used where possible as an aid in organizing the data. Provinces and states for which these subdivisions are not used include Alberta, British Columbia, Manitoba, Saskatchewan, Yukon Territory, and Alaska. In this appendix, all national parks are treated as counties; and all localities within park boundaries are listed under the park rather than under their appropriate counties.

Because altitude data are often important in defining the habitat

ranges of *Nebria* species, these data are recorded here where possible. No attempt has been made, however, to present altitude data not actually recorded on the specimen labels. Where necessary, altitude values have been converted to their metric equivalents.

Only the months in which specimens were actually collected at a given locality have been noted here. This level of exactness adequately describes the temporal distributions of most samples. The addition of year and day data would have expanded this already large appendix tremendously and for minimal added value. For similar reasons, collectors' names have been omitted. In this latter omission, I do not intend to ignore the essential contributions of the many collectors whose personal efforts have added greatly to the scope of this study; and I regret that recognition of their assistance must be confined to the Acknowledgments section of the text.

The collections in which specimens are deposited are noted, but holdings for each are not itemized. Some specimens reported here to be in my personal collection have actually been distributed among vario[illegible]nd institutions; and no mention is made of these t[illegible]nsfers except wh[illegible]ype series are involved (refer to descriptive sec[illegible]on under each taxo[illegible]

A n[illegible]ber of specime[illegible] were found to be inadequately or ambiguously la[illegible]lled. Where possible I have clarified these records, without making note of t[illegible] co[illegible]ions in the listing. In each instance, however, there is no [illegible]ot in my mind as to the correctness of my assign[illegible]nt. Speci[illegible]s with illegible or essentially meaningless locali[illegible]re grouped with specimens bearing no locality labels in the category *No Data*.

Specimens listed in the category *Doubtful Records* are of two types: (1) those labelled as from localities outside the known and probable ranges of the taxon; and (2) those labelled as from localities within the known range of the species but from areas where I am certain no ble habitat exists. However, for some specimens in category (: e appropriate habitat can be found within reasonable proximity of the stated locality, I have chosen to add the word *area* after the entry (as in Portland *area*). Although imprecise, this convention accommodates the common practice among some collectors of simply recording the nearest city or town on specimen labels rather than more precise locality data.

Nebria acuta Lindroth

Map: Figure 390

Nebria acuta acuta Lindroth

Specimens examined: 2224 (1040♂, 1184♀)

CANADA

BRITISH COLUMBIA: Chilkat Pass [June] (1; CNC), Clear Creek (Haines Highway mi. 61.3) [Aug.] (28; UASM), Garibaldi Provincial Park (south slope of Black Tusk [1830m-2040m], Whistler Mountain [1830m]) [July-Aug.] (181; CAS, CNC, DHKa), Lake Alice Provincial Park (0.2 mi. n. of Stump Lake at CheeKye River [100m]) [Aug.] (6; CAS, DHKa), Vedder River [July] (1; INHS).

UNITED STATES OF AMERICA

ALASKA: Big Boulder Creek (Haines Highway mi. 34) [June] (2; UASM), Cape Yakataga [June] (5; CAS, DHKa), Cooper Landing (Stetson Creek [670m]) [Aug.] (7; CNC), Little Boulder Creek (Haines Highway mi. 31) [June] (19; MCZ, UASM), Valdez (14 and 16 mi. e.) [Aug.] (55; CAS, MCZ, UASM, USNM), Worthington Glacier (Richardson Highway mi. 28.7) [Aug.] (24; MCZ, UASM). CALIFORNIA: Lassen Volcanic National Park, Mount Lassen (Lost Creek at Highway 87 [1840m]) [Aug.] (1; DHKa); Siskiyou Co., Mount Shasta (Mud Creek at Clear Creek [1880m]) [May, Aug.] (271; CAS, DHKa, USNM); Tuolumne Co., Chipmunk Flat [Aug.] (1; UCD). OREGON: Clackamas Co., Mount Hood (south slope near Timberline Lodge at headwaters of Salmon River [1830m-1950m]) [Aug.] (18; CAS, DHKa); Deschutes Co., Middle Sister Peak (east slope at North Fork Squaw Creek [1950m-2190m])[Aug.] (112; CAS, DHKa), Soap

Creek ([1750m]) [Aug.] (15; CAS, DHKa), South Fork Squaw Creek (below Camp Lake [2130m]) [Aug.] (16; CAS, DHKa); Hood River Co., Elliot Branch Hood River (0.5 mi. w. of Cloud Cap Inn [1800m]) [Aug.] (6; OSUO), Hood River [July] (1; CAS), Mount Hood ([1740m], Sand Creek Tillie Jane Creek, White River [1380m], White River Glacier) [June-Aug.] (107; CAS, DHKa, KUSM, MCZ, UIMI, UWBM); Marion Co., Mount Jefferson (north slope [1860m-1920m], northwest slope at Russell Creek [1680m-1740m], South Fork Breitenbush River in Jefferson Park [1770m], West Branch Whitewater River [1830m-1890m]) [Aug.] (62; CAS, DHKa, LRus). WASHINGTON: King Co., Snoqualmie (1; UWBM); Kittitas Co., Teanaway Ridge ([910m]) [July] (3; LRus); Lewis Co., White Pass (1.5 mi. w. at Millridge Creek [1280m]) [July] (18; DHKa); Mount Rainier National Park ([1830m]) [July-Sept.] (59; CAS, CUIC, JSch, LACM, MCZ, SJSC, UBC, USNM, UWBM, WSU), Carbon River (at Carbon Glacier) [Sept.] (1; UWBM), Fryingpan Creek ([1160m-1190m]) [July-Aug.] (43; CNC, DHKa, SJSC), Louise Lake ([1400m]) [July] (1; DHKa), Longmire [July-Sept.] (4; CAS, UWBM), McClure Rock ([2130m]) [Aug.] (2; CAS), Narada Falls ([1370m]) [July] (9; USNM, UWBM), Nisqually River (Cougar Rock Campground [960m], near Longmire, at toe of Nisqually Glacier [1190m-1520m], 0.1 mi. above Paradise River [980m]) [July-Sept.] (524; CAS, DHKa, MCZ, MSU, UWBM), North Fork Puyallup River ([1130m], at toe of Puyallup Glacier [1100m-1650m]) [Aug.] (249; CNC, DHKa), Ohanapecosh [June] (1; ROM), Paradise area (Edith Creek Basin [1710m-1920m], Paradise Glacier, Paradise Park [1830m-2130m], Paradise River [1400m-1830m] (above Narada Falls [1400m-1460m], and below Sluskin Falls, Paradise Valley [1520m-1830m]) [June-Sept.] (225; CAS, CNC, DHKa, FMNH, LRus, UASM, USNM, UWBM), Sluskin

Falls [July] (15; UWBM), South Fork Puyallup River ([1070m]) [July] (2; UWBM), Stevens Creek ([1190m-1220m]) [June-July] (22; DHKa, USNM), Sunrise area [July] (36; CAS, LRus, USNM), Tahoma Creek ([840m]) [June] (1; USNM), Van Trump Creek (above Christine Falls [1220m-1280m]) [July] (8; DHKa), West End Road [July] (2; CAS), White River (at White River Campground [1190m-1520m]) [July-Aug.] (32; DHKa, FMNH, UWBM), Yakima Park [Aug.] (3; MCZ); Pierce Co., Ashford (4 mi. e. at Goat Creek on Nisqually River [590m]) [July] (4; DHKa), White River (at Silver Springs Campground [790m]) [Aug.] (1; DHKa); Skamania Co., Mount St. Helens (northeast slope above Timberline Campground [1340m-1500m]) [Aug.] (8; CAS, DHKa); Whatcom Co., Glacier [July] (1; CAS), Mount Baker (Austin Pass area [1190m-1310m], Chain Lakes, Heather Meadows area [1190m]) [Aug.] (18; CAS, DHKa, WSU); Yakima Co., Tieton Dam [Aug.] (1; PURC).

Doubtful Records. CANADA, YUKON TERRITORY: Swift River (Alaska Highway mi. 733.3) [Aug.] (1; LRus). UNITED STATES OF AMERICA, IDAHO: Bonneville Co., Idaho Falls (1; ICCM).

Nebria acuta quileute Kavanaugh, NEW SUBSPECIES

Specimens examined: 134 (80♂, 54♀)

UNITED STATES OF AMERICA

WASHINGTON: Olympic National Park [Aug.] (5; LACM, MCZ), Dosewallips River (at Mascott Campground) [July] (10; UWBM), Eagle Point ([1830m]) [July] (1; CNC), Olympic Hot Springs (Boulder Creek [610m-780m]) [May-Aug.] (117; CAS, CNC, DHKa, UIMI, UWBM), Sol Duc Hot Springs [June] (1; CAS).

Nebria appalachia Darlington

Map: Figure 397

Specimens examined: 274 (164♂, 110♀)

UNITED STATES OF AMERICA

NORTH CAROLINA: Great Smoky Mountains National Park, Fork Ridge ([1620m]) [Aug.] (1; DRWh); Newfound Gap ([1520m-1580m]) [Aug.] (32; AMNH, CAS, MCZ), Smokemont Loop Trail ([760m-910m]) [July] (1; UAFA); Haywood Co., Retreat [May] (1; USNM); Jackson Co., Fork Ridge (at Blue Ridge Parkway [1620m]) [June-July] (5; NMDo, RTBe), Waterrock Knob (3 mi. se. of Soco Gap [1620m-1680m], Scott Creek Overlook [1620m]) [May-July] (124; DHKa, HoKn, NMDo), Yellow Face ([1770m]) [July] (1; RCGr); Mitchell Co., Roan Mountain (1 mi. s. of Carver's Gap on Highway 261 [1550m]) [Sept.] (3; DHKa); Yancey Co., Mount Mitchell ([1520m-2040m] and southwest slope [1710m-1740m], summit) [May-June, Sept.] (79; DHKa, MCZ, USNM). TENNESSEE: Great Smoky Mountains National Park, Alum Cave Creek ([1160m-1310m]) [May] (7; DHKa), Chimneys area ([910m] and Chimney Tops Trail [1070m]) [May] (5; MCZ, USNM), Mount Leconte (and summit [2010m]) [May, Aug.] (8; AMNH, CUIC, USNM), Mount Guyot ([1200m] and Ramsey Cascade [1370m]) [Aug.-Sept.] (2; DHKa, USNM), West Prong Little Pigeon River ([1070m-1220m]) [May] (5; DHKa).

Nebria arkansana Casey

Map: Figure 392

Nebria arkansana arkansana Casey

Specimens examined: 2155 (1083♂, 1072♀)

UNITED STATES OF AMERICA

COLORADO: (1; INHS); Archuleta Co., East Fork San Juan River (3 mi. se. of Highway 160) [Aug.] (1; DHKa), Upper San Juan Valley ([2130m-3200m]) [Aug.] (4; AMNH, ANSP, MCZ, UASM); Boulder Co., Allenspark area (Big Gulch Mountain Brook [2930m]) [Aug.] (10; CArm, CUB), ArapahoePass ([2740m-3350m]) [Aug.] (8; ALar, RTBe), Brainard Lake [July] (2; DHKa), Lake Isabelle ([3170m]) [July] (1; CArm), Middle St. Vrain Creek ([2990m]) [July] (5; CArm), Niwot Ridge [July] (7; CArm, CUB, DHKa), South St. Vrain Creek ([3200m], above Mitchell Lake 3290m]) [July] (17; CArm, CUB), Ward ([3170m] and 5 mi. e. on Left-hand Creek) [July-Aug.] (81; CArm, DHKa, USNM), Yankee Doodle Lake ([3260m]) [Aug.] (2; UAFA); Clear Creek Co., Graymont (Clear Creek) [July] (8; DHKa, USNM), Leavenworth Valley ([3050m-3350m]) [June-July] (49; DHKa, USNM), Silver Plume ([2740m-3050m]) [June] (3; USNM), Stevens Gulch [July] (12; DHKa, USNM); Conejos Co., Cumbres Pass ([3050m]) [June] (1; CAS), Monkhaven (Conejos River) [June] (5; CAS); Costilla Co., Blanca Peak ([3810m]) [July] (14; BRot), Pass Creek (near La Veta Pass) [June] (1; BRot), San Francisco Canyon [June] (1; BRot); Custer Co., San Isabel (1.9 mi. sw. at St. Charles River [2710m-2830m]) [June] (147; DHKa); Dolores Co., Rico (Scotch Creek [2680m]) [July] (1; CNC); Eagle Co., Vail (5 mi. e. at Gore Creek [2740m]) [July] (11; DHKa, USNM); El Paso Co., South Cheyenne Creek (at Gold Camp Road [2530m-2650m]) [June, Aug.] (64; DHKa); Garfield Co., Hauskins Creek (23 mi. ne. of Buford [2910m]) [Aug.] (99; DHKa), Picket Pin Creek (21 mi. ne. of Buford [2870m]) [Aug.] (172; DHKa), Trappers Lake ([2990m]) [Aug.]

(14; DHKa); Gilpin Co., Pinecliffe (and 2.5 mi. w. at South Boulder Creek) [Aug.] (15; DHKa, UAFA), Rollinsville (9.1 mi. w.) [Aug.] (5; UAFA); Grand Co., Fraser River (above Robbers Roost Campground) [Aug.] (1; USNM); Huerfano Co., Blue Lake [June] (1; EAMa), Cucharas River (1.3 mi. w. of Highway 111) [June] (3; DHKa); Jackson Co., Agnes Lake [Aug.] (11; MSU, PURC), Cameron Pass ([3140m]) [Aug.] (2; UASM), Walden (4.9 mi. [2740m-3050m] and 7.4 mi. [3120m] se.) [Aug.] (2; UAFA); Lake Co., Independence Pass (5 mi. e. on Highway 82) [Aug.] (1; UAFA), Leadville [June] (3; CAS), North Fork Lake Creek ([3410m]) [Aug.] (115; DHKa), Twin Lakes (and 7 to 12 mi. w. on Lake Creek) [June, Aug.] (32; CAS, DHKa); La Plata Co., Durango area ([1680m-2130m]) [July-Aug.] (1; MCZ), Gold King Mill (Tirbircio Creek [2830m]) [Aug.] (10; UASM), Junction Creek [July] (2; USNM); Larimer Co., Cameron Pass [Aug.] (18; MSU, RTBe), West Fork Sheep Creek (at Crown Point Road [2900m]) (3; DHKa); Las Animas Co., Stonewall Gap (Middle Fork Purgatoire River [2500m]) [June] (10; DHKa); Mineral Co., Pagosa Springs (20 mi. n.) [June] (1; USNM), South Fork (4 mi. w. on Rio Grande River) [Aug.] (6; DHKa, EAMa), Wolf Creek Pass ([3350m-3410m] and 2 mi. w.) [June-Aug.] (101; BRot, CAS, DHKa, EAMa); Montezuma Co., Dolores River (at Highway 45) [Sept.] (3; CAS); Ouray Co., Ouray (and vicinity [2740m-3050m]) [July] (53; CAS, USNM); Park Co., Alma (South Platte River) [July] (1; EAMa), Como (5 mi. [3200m] and 7 mi. [3350m] w. at Tarryall Creek) (31; DHKa, EAMa), Middle Fork South Platte River (near Hoosier Pass [3510m]) [July] (26; DHKa); Pitkin Co., Aspen (and 8 mi. e. at Roaring Fork River) [July-Aug.] (4; AMNH, DHKa); Rio Grande Co., Summitville ([3050m-3510m]) [Aug.] (2; MCZ); Rocky Mountain National Park, Blue Lake [July] (12; RTBe), Chasm Fall Trail ([2870m]) [Aug.] (2; UAFA), Fall River

([2620m] and at Endovalley Campground) [Aug.] (40; RTBe, UASM), Fall River Road (1.7 mi. w. of Chasm Trail) [Aug.] (48; UAFA), Hang Lake [July] (13; RTBe), North St. Vrain Creek (at Ouzel Falls [2740m-3050m]) [July-Aug.] (52; CArm, DHKs, USNM); Routt Co., Rabbit Ears Pass [Aug.] (1; USNM), Steamboat Springs ([2070m]) [Sept.] (1; CAS); San Juan Co., Molas Divide ([3050m]) [Aug.] (10; PMCh, RDav), Red Mountain Pass (1 to 2 mi. s.) [Sept.] (3; CAS), Silverton area ([3050m]) [Aug.] (9; MCZ); San Miguel Co., South Fork San Miguel River ([2590m]) [July] (16; AMNH, ANSP, KSUC, MCZ, UMRM, USNM), Trout Lake (on Rico Road [2590m-3050m]) [July] (2; MCZ, USNM); Summit Co., Blue River (near Hoosier Pass) [Aug.] (4; USNM), Frisco (Tenmile Creek) [Aug.] (1; RDav), Monte Cristo Creek ([3350m]) [July] (9; DHKa), Quandary Peak (east slope [3410m-3960m]) [July-Aug.] (126; DHKa, USNM); County unknown, La Plata Mountains [July] (8; BRot), Whiskey Pass [June] (2; CAS). NEW MEXICO: (11; ANSP, CAS, ICCM, KUSM, MCZ, OSUC, USNM); Rio Arriba Co., Rio Puerco (at Rio Puerco Campground [2350m-2440m]) [June] (80; DHKa); San Miguel Co., Sapello (15.7 mi. w. on Highway 266 [2440m]) [June] (4; UASM), Winsor Creek ([2590m]) [June] (18; DHKa); Taos Co., Angostura Creek (0.3 mi. s. of Highway 3 [2710m]) [June] (3; DHKa), Red River (8 mi. s. on Red River [2870m]) [June] (8; DHKa), Tres Ritos [July] (3; CAS), Wheeler Peak ([3050m-3260m], Middle Fork Lake [3340m], Middle Fork Red River [3260m3640m]) [June] (186; DHKa). UTAH: San Juan Co., Abajo Mountains [July] (1; BRot), Monticello (5 mi. [2590m] and 7.1 mi. [2830m] w. at North Creek, 5 mi. w. at Spring Creek [2500m], 10.1 mi. w. [3020m]) [July-Aug.] (134; DHKa, MCZ, UASM, USNM), Mount Linnaeus (east slope 12 mi. w. of Monticello [2740m-3050m]) [July-Aug.] (40;

DHKa, UASM, USNM). WYOMING: Albany Co., Centennial (2.0 mi. nw. at Libby Creek Campground [2620m], 7.5 mi. nw. at Nash Fork Little Laramie River [2990m], University of Wyoming Science Camp) [July-Aug.] (56; DHKa, MSU); Carbon Co., Haskins Creek (26 mi. ne. of Savery [2740m]) [July] (7; DHKa), Hidden Treasure Gulch (11.5 mi. wsw. of Encampment [2870m]) [July] (6; DHKa), Lake Marie ([3230m] and 8 mi. sw. [2740m]) [July] (27; DHKa).

Doubtful Records. UNITED STATES OF AMERICA, ARKANSAS: (2; USNM). COLORADO: Denver Co., Denver (1; ICCM). IDAHO: Nez Perce Co., Lewiston (1; ICCM). INDIANA: (2; USNM).

No Data. (1; USNM).

Nebria arkansana edwardsi Kavanaugh, NEW SUBSPECIES

Specimens examined: 1863 (1058♂, 805♀)

CANADA

ALBERTA: Banff National Park, Banff [Aug.-Sept.] (3; CUIC, UASM), Boom Lake ([1830m]) [July] (1; CNC), Bow Lake [Aug.] (1; UASM), Bow River ([1830m]) [Aug.] (6; CNC), Johnson Creek Trail (at Johnson Creek Campground) [July] (1; ROM), Lake Agnes [Aug.] (1; PMNH), Lake Louise [June-Sept.] (16; AMNH, CAS, CNC, MCZ, UBC), Ptarmigan Mountain ([2590m]) [Aug.] (13; CNC), Spray Lake [July] (1; JVMa), Sunset Pass ([1950m]) [Aug.] (4; CNC); Jasper National Park [Aug.] (2; AMNH), Amethyst Lake (and Amethyst Lake Trail [1710m]) [July] (10; DHKa, UASM), Angel Glacier [Sept.] (1; RTBe), Hardisty Creek (1 mi. s. on Highway 93) [July] (1; RFre), Miette Hot Springs [Aug.] (1; RTBe), Miette River (at Meadow Creek [1100m]) [July-Aug.] (22; DHKa, UASM),

Mount Edith Cavell ([1360m] and below Angel Glacier) [July] (3; DHKa, UAFA), Portal Creek Trail ([1950m]) [July] (3; USNM); Waterton Lakes National Park [July-Aug.] (5; UASM, UWBM), Red Rock Canyon [July] (2; CAS), Waterton Park (Cameron Creek)[July] (36; CNC, MCZ, UASM); Other localities, Bellevue (2 mi. w. at Gold Creek [1370m]) [July] (1; DHKa), Blackstone Gap [Aug.] (2; CNC), Blairmore (1; USNM), Blakiston Brook [July] (10; UASM), Carbondale River (near Lost Creek) [Sept.] (1; DJLa), Cline River (at Highway 11) [Aug.] (2; DHKa), Gap [Aug.] (1; CAS), Gorge Creek [July] (2; UASM), Happy Valley (Pincher Creek) [Aug.] (11; CAS, UASM), Highwood Pass ([2380m]) [July] (15; CNC), Highwood River [Aug.] (1; CAS), Marmot Creek (10 mi. sw. of Kananaskis Forest Experiment Station [1520m]) [Aug.] (10; CNC), Mill Creek Ranger Station [Aug.] (2; CAS), Pincher Creek ([1620m]) [July] (3; DJLa), Ram River area [July] (2; BFCa), Sheep River (4.5 mi. above Gorge Creek) [Aug.] (7; DHKa), West Branch Castle River ([1340m]) [Aug.] (6; DJLa). BRITISH COLUMBIA: Glacier National Park, Asulkan Glacier area [Aug.] (1; CUIC), Glacier [July-Aug.] (6; CAS, CNC, PURC), Rogers Pass ([1370m]) [Aug.] (2; ANSP, CAS); Kootenay National Park [Aug.] (3; CNC), Kimpton Creek ([1220m]) [July] (2; CNC), Kindersley Pass ([2130m]) [July] (4; CNC), Kootenay River (at Highway 1B) [Aug.] (1; UASM), Marble Canyon [July] (1; CNC), Sinclair Creek ([1830m] and at Highway 13) [June-Aug.] (25; CAS, CNC, UASM, UBC), Vermillion Creek [July] (4; CAS, MSU, UBC); Yoho National Park [July] (3; CAS), Amiskwi River (and at Amiskwi Falls [1830m]) [Aug.] (34; CNC), Field (and 3 mi. e. on Kicking Horse River) [June, Aug.] (4; CAS, USNM), Lake Oesa ([2130m]) [July] (18; CNC), Lake O'Hara [July] (10; CAS, CNC, UBC), Otterhead River ([1680m]) [Aug.-Sept.] (29; CNC, DHKa), Yoho River

([1400m], 4 to 12 mi. e. of Field, at Takakkaw Falls [1520m]) [July-Aug.] (25; CNC, DHKa, UASM); Other localities, Bosewell [Aug.] (1; UASM), Cabin Creek (ne. of Fernie, near Michel) [July] (13; CNC, UASM), Creston (8 mi. w.) [June] (3; CNC), Crowsnest Pass (2 mi. [1280m] and 5 mi. w. on Elk River [1220m]) [July] (51; DHKa), Edgewood [July-Aug.] (3; CAS), Elk Creek (e. of Fernie) [July] (4; UASM), Elk River (10.7 mi. w. of Fernie) [July] (3; ROM), Erickson (Arrow Creek) [Aug.] (12; CAS, UBC), Fernie (Coal Creek [1680m], Fairy Creek, Lizard Creek) [July-Aug.] (63; BFCa, CAS, CNC, DBUM, FMNH, MSU, UBC), Flathead [June] (1; CUIC), Fort Steele [June, Sept.] (2; CAS, UBC), Fortysixmile Camp (at Hope Trail) [July] (4; CAS, CNC, UBC), Hope Mountains [July-Sept.] (6; CNC, INHS, MCZ), Hosmer (Elk River) [July] (1; CAS), Lorna [June] (2; CAS, UBC), Manning Provincial Park (Nicomen Ridge) [July] (10; CAS, CNC, MSU, UBC), Michel (5; UASM), Mount Copeland ([1980m]) [Aug.] (21; CNC), Radium Hot Springs [Aug.] (6; CAS, CNC, UBC), Slocan [Aug.] (2; BFCa), South Fork Creek [Aug.] (1; UWBM), Summit Creek (near Creston) [Aug.] (5; UASM), Tetsa River (Alaska Highway mi. 378 and 390) [Aug.] (3; DHKa, MSU), Vernon [July] (1; CAS), Whipsaw Creek (at Hope Trail [1460m]) [July] (1; UBC), Wyndel [Sept.] (1; CNC). YUKON TERRITORY: Rancheria (Swift River) [Aug.] (6; CNC, UASM).

UNITED STATES OF AMERICA

IDAHO: Blaine Co., Alturas Lake (at Alturas Inlet Campground [2130m]) [Aug.] (11; DHKa), Cherry Creek (0.1 mi. nw. of Highway 93 [2230m]) [Aug.] (6; DHKa), Dollarhide Summit (2 mi. e. at North Fork Warm Springs Creek [2350m-2410m]) [Aug.] (9; DHKa), Galena [July] (1; BFCa), Galena Summit (2.4 mi. ne. [2320m]) [Aug.] (12; DHKa), Hyndman Creek [July] (22;

UWBM), Ketchum (2 mi. wnw. at Big Wood Creek [1830m]) [Aug.] (28; DHKá), North Fork Warm Springs Creek (10 mi. w. of Ketchum [1890m]) [Aug.] (92; DHKa), Sun Valley [Sept.] (2; JSch); Camas Co., Carrie Creek (32 mi. [2440m] and 36 mi. [2100m] ese. of Ketchum) [Aug.] (106; DHKa), South Fork Boise River (14 mi. e. of Featherville at Skeleton Creek [1550m], 34 mi. e. of Featherville at Bear Creek [1830m]) [Aug.] (157; DHKa); Cassia Co., Rock Creek (15 mi. s. of Hansen, at Rock Creek Ranger Station) [June-July] (6; UIMI); Custer Co., Bayhorse Creek (7 mi. nw. of Highway 93 [2440m]) [Aug.] (3; DHKa), Fourth of July Creek (3 mi. e. of Highway 93 [2230m]) [Aug.] (58; DHKa), Stanley [July] (1; UWBM), Trail Creek Summit (2 mi. ne. at Summit Creek [2320m]) [Aug.] (9; DHKa); Fremont Co., Island Park [July] (3; BFCa); Shoshone Co., Avery (7 mi. e.) [July] (1; UIMI); Valley Co., Dagger Falls [July] (2; BFCa), Middle Fork Salmon River (near Boundary Creek) [Aug.] (7; RTBe); County unknown, Twin Creek Forest Camp ([1520m]) [July] (57; UWBM). MONTANA: Carbon Co., Quad Creek (17 mi. sw. of Red Lodge [3050m]) [July] (66; DHKa); Fergus Co., East Fork Rock Creek ([1710m]) [July] (42; DHKa); Flathead Co., Marias Pass (10 mi. w. of Summit [1370m]) [July] (11; LRus), South Fork Flathead River at Hungry Horse Reservoir [1220m]) [July] (3; LRus); Gallatin Co., Fairy Lakes [Aug.] (1; CUIC); Glacier National Park [July-Aug.] (6; CUIC), Baring Creek (at St. Mary Lake) [Aug.] (3; UWBM), Grinnell Falls ([1860m]) [Aug.] (1; SJSC), Grinnell Glacier ([1860m-1890m]) [Aug.] (21; DHKa, SJSC, USNM), Grinnell Lake (at inlet [1540m]) [Aug.] (1; DHKa), Lake McDonald (and at Sprague Creek Campground) [July-Aug.] (4; CAS, RTBe), Lake Sherburne (at Canyon Creek) [July] (1; CAS), Logan Pass ([2030m-2130m] and 5 mi. w. [1770m]) [July-

Sept.] (16; DHKa, JSch, RTBe, UASM), Morning Eagle Falls ([1680m]) [July] (1; SJSC), Mount Clemens (northeast slope [2160m]) [July] (5; DHKa), Piegan Pass ([2410m]) [Aug.] (1; SJSC), St. Mary [Aug.] (8; SJSC, UASM); Madison Co., Beaver Creek ([1920m]) [Aug.] (1; KUSM), Ennis [July] (2; UIMI); Mineral Co., Haugan [Aug.] (14; KUSM), Lookout Pass ([1280m]) [July] (1; LRus), Saltese [July, Sept.] (3; MSU, SJSC); Sweetgrass Co., Big Timber Creek (at Half Moon Campground [2230m-2290m]) [July] (1; DHKa). NEVADA: Elko Co., Lamoille Creek (at Lower Lamoille Campground [1920m]) [Aug.] (35; DHKa), Thomas Creek (at Thomas Creek Campground [2320m-2380m]) [Aug.] (130; DHKa). OREGON: Baker Co., Cornucopia [June-July] (35; BFCa, UWBM); Union Co., Elgin (and 9 mi. nw. at Little Phillips Creek [1300m]) [May, Aug.] (6; DHKa), Langdon Lake area (se. of summit) [Aug.] (2; UWBM), Tollgate-Elgin Road [June] (3; UWBM); Wallowa Co. [Aug.] (1; JSch), Aneroid Lake ([2320m]) [July] (2; FMNH), East Fork Eagle Creek [July] (9; UWBM), Indian Crossing (Imnaha River) [Aug.] (2; MSU, OSUO), Lostine River ([1310m], at French Campground, at Two Pan Campground [1710m-1980m]) [Aug.] (112; DHKa, USNM, UWBM), Lost Lake [Aug.] (1; UWBM), Wallowa Lake [July-Aug.] (10; DHKa, UWBM), Wallowa River (above inlet to Wallowa Lake) [May] (1; DHKa). WASHINGTON: Walla Walla Co., Walla Walla [Aug.] (1; UWBM). WYOMING: Big Horn Co., Granite Pass (8 mi. sw. on Granite Creek [2380m]) [July] (5; DHKa), Shell Creek (11 mi. sw. of Granite Pass [2130m]) [July] (14; DHKa), West Tensleep Creek ([3140m-3200m]) [July] (17; DHKa); Johnson Co., Clear Creek (12 mi. w. of Buffalo [2190m]) [July] (1; DHKa), South Fork Clear Creek (16 mi. w. of Buffalo [2350m], at South Fork Campground [2350m]) [July-Aug.] (6; DHKa, FMNH); Sheridan Co., Little Tongue River

(13 mi. wsw of Dayton [2380m]) [July] (22; DHKa); Washakie Co., Tensleep (6 mi. [1550m] and 11 mi. [1890m] ne. on Tensleep Creek) [July] (4; DHKa); Yellowstone National Park [Aug.] (25; USNM); County unknown, Bighorn Reserve (1; MCZ).

Nebria arkansana oowah Kavanaugh, NEW SUBSPECIES

Specimens examined: 77 (55♂, 22♀)

UNITED STATES OF AMERICA

UTAH: Grand Co., Mill Creek (at Oowah Lake [2680m]) [Aug.] (74; DHKa); San Juan Co., Mill Creek Valley ([2900m]) [Aug.] (3; UASM).

Nebria arkansana uinta Kavanaugh, NEW SUBSPECIES

Specimens examined: 94 (45♂, 49♀)

UNITED STATES OF AMERICA

UTAH: Cache Co., Logan River (13.7 mi. e. of Logan at Cottonwood Creek [1740m]) [Aug.] (65' DHKa); Summit Co., Lost Lake ([2990m]) [Aug.] (7; DHKa), Upper Provo River (20.8 mi. e. of Kamas [2660m], at Highway 150) [Aug.] (6; DHKa, USNM); Uintah Co., Big Brush Creek (7 mi. wnw. of Highway 44 [2620m]) [Aug.] (14; DHKa); Weber Co., Ogden (6 mi. e. on Ogden River [1490m]) [Aug.] (2; DHKa).

Nebria brevicollis Fabricius

Map: Figure 380

Specimens examined: 2 (2♂)

CANADA

QUEBEC: Cte de Rouville, St-Cesaire [June] (1; DBUM).

SAINT PIERRE AND MIQUELON

MIQUELON: Langlade (1; MHNP).

Nebria carri Kavanaugh, NEW SPECIES

Map: Figure 405

Specimens examined: 153 (63♂, 90♀)

UNITED STATES OF AMERICA

IDAHO: Adams Co., Towsley Springs (9 mi. nne. of Cuprum [2070m]) [July-Aug.] (4; BFCa, DHKa); Blaine Co., Dollarhide Summit (1.0 to 2.0 mi. e. on North Fork Warm Springs Creek [2350m-2500m]) [Aug.] (138; DHKa), Twin Lakes Trail (w. of Petit Lake) [July] (2; BFCa); Camas Co., Carrie Creek (32 mi. wsw. of Ketchum [2440m]) [Aug.] (9; DHKa).

Nebria charlottae Lindroth

Map: Figure 393

Specimens examined: 1 (1♂)

CANADA

BRITISH COLUMBIA: Queen Charlotte Islands (1; CNC).

Nebria coloradensis Van Dyke

Map: Figure 410

Specimens examined: 55 (35♂, 20♀)

UNITED STATES OF AMERICA

COLORADO: Delta Co., Grand Mesa [July] (2; CUB); Eagle Co., Redcliff

[Aug.] (2; MSU, USNM); Garfield Co., Picket Pin Creek (21 mi. ne. of Buford [2870m]) [Aug.] (14; DHKa); Gunnison Co., Mexican Cut Lake (1 mi. nw. of Elko Park [3440m]) [Aug.] (2; PMNH), Rustlers Gulch Trail ([3200m]) [July] (1; SJSC); Lake Co., Lake Creek (7 mi. and 12 mi. w. of Twin Lakes) [Aug.] (5; DHKa, EAMa), Leadville ([3050m-3350m]) [July] (3; DHKa, MCZ, USNM), Twin Lakes [June] (1; CAS); Mesa Co., (1; USNM); Park Co., Middle Fork South Platte River (near Hoosier Pass [3510m]) [July] (9; DHKa), Mount Bross (near Alma [3510m]) [July] (1; CAS), Tarryall Creek (8 mi. w. of Como) [July] (2; EAMa); Summit Co., Monte Cristo Creek ([3350m]) [July] (1; DHKa), Quandary Peak (east slope [3350m-3960m]) [July-Aug.] (11; DHKa, USNM).

Nebria crassicornis Van Dyke

Map: Figure 387

Nebria crassicornis crassicornis Van Dyke

Specimens examined: 1907 (878♂, 1029♀)

CANADA

BRITISH COLUMBIA: (2; AMNH, INHS); Copper Mountain [May] (1; UBC), Fraser River Valley (2; ANSP, CAS), Hope Pass (summit [1830m]) [July] (12; UBC), Manning Provincial Park ([1370m] and Blackwall Peak [1830m-2060m], Nicomin Ridge) [June-Sept.] (101; CAS, CNC, DHKa, KSUC, KUSM, MCZ, UASM, UBC, UMMZ), Welch Peak [=Mount Wahleach] ([1520m-1680m]) [July] (3; INHS, UBC).

UNITED STATES OF AMERICA

WASHINGTON: Chelan Co. ([1830m]) [July] (12; CAS); Clallam Co.,

Indian Creek (s. of Lake Sutherland) [Aug.] (2; CAS); Mount Rainier National Park ([1520m-2130m]) [July-Aug.] (170; ALar, AMNH, CAS, CUIC, DHKa, ICCM, JSch, KSUC, LACM, MCZ, MSU, NMDo, OSUC, OSUO, UASM, UBC, UCR, USNM, UWBM, WSU), Berkeley Park [Aug.] (1; MCZ), Chinook Pass ([1680m]) [July-Aug.] (20; CAS, LRus, USNM), Fryingpan Creek ([1190m]) [July] (1; DHKa), McClure Rock ([2130m]) [Aug.] (2; CAS, DHKa), Narada Falls ([1370m]) [July] (1; UWBM), Nisqually River ([1160m-1420m]) [July] (5; DHKa, UWBM), Paradise area (Edith Creek Basin [1710m-1920m], Golden Gate [1920m-1980m], Paradise Park [1520m-2130m], Paradise River [1460m-1830m], Paradise Valley [1520m-2440m]) [July-Aug.] (401; CAS, CNC, CUIC, DHKa, FMNH, ICCM, KSUC, LRus, MCZ, MSU, NMDo, OSUO, UASM, UBC, UCB, UCD, UMRM, USNM, UWBM), Reflection Lake [July-Aug.] (6; CAS, FMNH, UWBM), Snow Lake ([1520m]) [Aug.] (1; CNC), Spray Park ([1980m]) [Aug.] (2; LRus), Sluskin Falls [July] (8; UWBM), Sunrise area (east slope Burroughs Mountain [1890m-2190m], Shadow Lake [1860m], Sunrise Park [2040m]) [July-Sept.] (599; CAS, CNC, DHKa, LRus, SJSC, UIMI, USNM, UWBM), Tipsoo Lake ([1620m-1650m]) [July-Sept.] (71; AMNH, ANSP, CAS, CUIC, GRNo, ICCM, KSUC, MCZ, PURC, UASM, UIMI, UMMZ, USNM, UWBM), Van Trump Park ([1830m]) [Aug.] (20; CNC), Yakima Park ([1950m-2290m]) [July-Aug.] (40; FMNH, MCZ, RTBe, UIMI, UWBM); Olympic National Park [July-Aug.] (14; CAS, CUIC, ICCM, MCZ), Boulder Peak ([1520m]) [Aug.] (1; CNC), Eagle Point ([1830m]) [July] (31; CNC), Hurricane Ridge ([1220m]) [July-Aug.] (4; LRus, UWBM), Obstruction Peak ([1830m-1970m]) [July-Aug.] (201; CAS, CNC, DHKa), Soleduck High Divide ([1520m]) [Aug.] (5; LRus); Pierce Co., Ashford (1; USNM), Summit Lake [Aug.] (1; EMUS); Whatcom Co., Glacier [July] (1; USNM), Harts Pass ([1890m]) [July] (20; USNM), Mount Baker (Austin Pass [1190m-1310m], Chain Lakes, The Dome,

Heather Meadows [1200m], Kulshan Ridge [1430m]) [July-Aug.] (135; CAS, DHKa, UWBM, WSU), Shuksan [Aug.] (1; OSUO); Yakima Co:, American River [July-Aug.] (7; UIMI, USNM); County unknown, Miners Ridge [July] (1; UWBM).

Doubtful Records. CANADA, ALBERTA: Banff National Park, Lake Louise [Aug.] (18; KUSM). MANITOBA: Cedar Lake [July] (1; MCZ). UNITED STATES OF AMERICA, ARIZONA: Cochise Co., Portal (5 mi. w. [1650m]) [Sept.] (1; CAS).

Nebria crassicornis intermedia Van Dyke

Specimens examined: 2222 (1070♂, 1152♀)

CANADA

ALBERTA: [July] (2; BFCa); Banff National Park [July] (2; UWBM), Banff [May-Aug.] (63; CAS, CUIC, BFCa, PMNH, UBC, USNM), Boom Lake ([1830m]) [July] (1; CNC), Bow Lake [Aug.] (11; UASM), Bow Pass ([2070m-2130m]) [July-Sept.] (26; CNC, RTBe, UWBM), Bow River ([1830m]and 2 mi. w. of Lake Louise) [May, Aug.-Sept.] (4; CNC, DRWh, RTBe), Cascade Creek (near Banff) [Sept.] (1; BFLa), Consolation Lake ([1950m-2130m]) [June] (7; CNC), Eisenhower Junction (12 mi. w.) [June] (3; CNC), Glacier Lake ([2130m]) [July] (2; ANSP) Johnston Creek (2.5 mi. above Johnston Canyon Campground) [July] (1; ROM), Lake Agnes [June-Aug.] (29; CUIC, PMNH, USNM), Lake Helen ([2380m]) [Aug.] (3; CNC), Lake Louise ([2040m] and 2 mi. w. [1630m]) [June-Aug.] (72; AMNH, CAS, CNC, CUIC, KUSM, MCZ, UASM, UBC, USNM), Moraine Lake (and Larch Valley [2290m]) [June-Aug.] (42; CAS, CNC, CUIC, PMNH), Mount Fairview ([2440m-2740m]) [July] (2; CAS), Mount St. Piran [Aug.] (1; ANSP), Ptarmigan Lake

([2290m]) [Aug.] (4; CNC), Ptarmigan Pass ([2130m-2440m]) [July] (11; CAS), Ptarmigan Peak ([2590m]) [Aug.] (4; CNC, UASM), Redoubt Lake ([2380m]) [Aug.] (1; CNC), Simpson Pass [July] (2; ROM), Sulphur Mountain ([1520m-2130m]) [Aug.] (9; UASM), Sunshine Ski Area [Sept.] (1; DRWh), Waterfowl Lake [Aug.] (2; SJSC), Wenkchemna Peak [June] (8; PMNH); Jasper National Park [Aug.] (2; AMNH), Alpine Meadows ([1980m-2290m]) [Aug.] (10; UASM), Amethyst Lake ([1970m-2030m]) [July-Aug.] (61; DHKa, DJLa, GRNo, SJSC, USNM), Angel Glacier ([1710m]) [July-Aug.] (7; DHKa, RTBe), Bald Hills ([2130m-2260m]) [June-Aug.] (15; DHKa), Columbia Icefield Campground [July, Sept.] (34; CUIC, USNM), Geraldine Lakes [July] (5; USNM), Jasper area ([2130m]) [Aug.] (4; CNC, MCZ), Jonas Campground [Aug.] (1; UASM), Maligne Lake ([1680m] and Shovel Pass) [July] (5; CAS, CUIC, MCZ), Miette Hot Springs [July-Aug.] (2; MCZ, UASM), Mount Edith Cavell([1370m-1830m] and Alley Brook) [June-July, Sept.-Oct.] (34; DHKa, ROM, UAFA, USNM), Portal Creek Trail (mi. 4 [1950m])[July] (1; DJLa), Signal Mountain [Sept.] (1; RTBe), Tangle Creek [June] (1; USNM), Whirlpool River [June] (7; DHKa); Waterton Lakes National Park, Bertha Lakes ([1620m]) [July] (1; SJSC), Cameron Lake area ([1660m-1980m]) [July] (12; UASM), Rowe Brook ([1830m]) [July] (1; SJSC), Twin Lakes ([1950m]) [July] (6; DJLa), Upper Rowe Lake [July] (4; SJSC), Waterton Park [July] (6; CNC, MCZ); Other localities, Barnaby Lakes ([2040m]) [Aug.] (3; DJLa), Cadomin [June] (1; UASM), Cardinal River [May] (1; DHKa), End Mountain [July] (1; UASM), Entrance (40 mi. wnw. at North Fork Wildhay River [1430m]) [July] (1; DHKa), Highwood Pass ([2320m-2410m]) [June, Aug.] (2; CNC), Highwood River [July] (2; BFCa), Jumpingpound Creek (20 mi. sw. of Highway 1) [June] (6; DHKa), Kananaskis Forest Experiment Station area

[June] (1; CNC), Kananaskis Lakes [Aug.] (1; BFCa), Loaf Mountain ([2290m]) [July] (3; DJLa), Marmot Creek Basin ([1980m]) [July] (13; CNC), Mercoal [Aug.] (1; UASM), Nordegg (South Creek Bridge, 20 mi. s. on Forestry Trunk Road) [July] (10; DHKa, UASM), North Saskatchewan River (near Nordegg) [July] (5; RFre, UASM), Oyster Creek Pass [Aug.] (7; CAS, UBC), Pembina River (20 mi. se. of Robb [1300m]) [Sept.] (1; UASM), Pinto Lake [July] (2; CAS), Pocaterra Creek [Aug.] (3; BFCa), Prospect Mountain (at Prospect Creek [1670m]) [Sept.] (2; UAFA), Sheep River (4.5 mi. above Gorge Creek) [Aug.] (1; DHKa), Snow Ridge (20 mi. sw. of Kananaskis Forest Experiment Station [2130m]) [July] (1; CNC), Ware Creek (5 mi. nw. of R. B. Miller Research Station) [Aug.] (2; DHKa); Location unknown, Boulder Pass [Aug.] (4; UASM). BRITISH COLUMBIA: (5; ALar, ANSP, LEMC, MCZ); Glacier National Park, Mount Abbott Trail ([2350m]) [Aug.] (1; [illegible]JSC), [illegible]ers Pass ([1370m]) [June, Aug.] (4; ANSP, CAS, CUIC, RFre); Kootenay National Park, Kindersley Pass ([2130m]) [July] (12; CNC), Sinclair Creek ([1830m]) [June] (20; CNC), Vermillion Creek [July] (1; UBC), Vermillion Pass [June] (9; BFCa); Mount Revelstoke National Park ([1980m]) [Aug.] (4; CNC), Eva Lake ([1980m] and Eva Lake Trail [1770m]) [July] (19; CNC), Millar Lake ([1920m]) [Aug.] (4; CNC), Mount Revelstoke ([1650m-1980m]) [June-Aug.] (133; CAS, CNC, KUSM, MCZ, MSU, ROM, UASM, UBC, UWBM); Yoho National Park [June-July] (5; BFCa, CAS, USNM), Amiskwi River ([1830m] and at Amiskwi Falls [1830m]) [Aug.] (5; CNC), Emerald Lake [Aug.] (6; CUIC, MCZ), Field [July-Aug.] (7; ANSP, USNM), Kicking Horse Campground [July] (2; UBC), Lake McArthur ([2130m]) [July] (21; CNC), Lake Oesa ([2130m]) [July] (3; CNC), Lake O'Hara ([2040m]) [July-Aug.] (10; CAS, CNC, CUIC, UBC), Linda Lake ([2040m]) [July] (1; CNC), Mount

Burgess [Sept.] (7; ALar, RTBe), Takakkaw Falls ([1490m]) [Oct.] (2; UASM), Yoho River ([1520m] and 4 to 12 mi. ne. of Field) [Aug.] (6; MCZ, UASM); Other localities, Barkerville (and Grouse Creek [1280m], Round Top Mountain [1830m-1890m]) [Aug.-Sept.] (75; CAS, CNC, CUIC, UASM, UBC, UWBM), Beavermouth [Aug.] (2; ANSP), Cariboo Heart Range ([1370m]) [Sept.] (1; UBC), Donald (8; CUIC, ICCM, ISUI, SDSU, UMMZ, USNM), Dunn Peak ([2130m]) [Aug.] (1; CNC), Gold River [Aug.] (2; ANSP), Grave Creek (15 mi. n. of Michel [1800m]) [Aug.] (1; UBC), Hunters Range [Sept.] (1; CAS), Invermere [Aug.] (1; CAS), Liard Hot Springs (Alaska Highway mi. 496 [460m]) [Aug.] (1; CNC), Lightning Peak ([1830m]) [Sept.] (2; UBC), Lisadele Lake ([1220m]) [July] (3; ALar, CNC), Lorna (and Little White Mountain) [June-Aug.] (26; CAS, INHS, KSUC, MCZ, MSU, UBC, UIMI), Manson River [Aug.] (1; UBC), Morrissey (Bighorn Creek [1529m]) [Aug.] (1; UBC), Mount Copeland ([1980m]) [Aug.] (5; CNC), Mount Murray ([2070m]) [Aug.] (1; CAS), Mount Robson Provincial Park (Jade Lake Trail [2230m], Mount Robson [1830m]) [July] (29; ANSP, CAS, CNC, MCZ, OSUC, UBC, USNM), Mount Thompson (near Canoe River [2440m]) [Aug.] (5; CNC), Okanagan Landing [June] (2; UBC), Osoyoos area (1; MCZ), Pine Pass (Hart Highway [930m]) [June] (2; UASM), Prairie Hills [July] (5; ANSP, CAS, CUIC), Quesnel Lake [May] (1; CAS), Raft Mountain ([2590m]) [June] (3; UBC, UWBM), Rawlings Lake (near Lumby) [Sept.] (1; UBC), Skookumchuk area [Aug.] (1; RGM), Smoky Creek (at headwaters) [Aug.] (2; USNM), Stanley [July-Aug.] (5; UBC), Summit Lake (Alaska Highway mi. 392 [1280m-1620m]) [June-July] (12; CNC, UASM), Tetsa River (Alaska Highway mi. 383) [June] (3; CNC, UASM), Terrace (9; CAS, DHKa, UBC), Thornhill Mountain (near Terrace [1520m]) (6; MCZ), Two Sisters

Mountain (15 mi. e. of Barkerville [1680m-1980m]) [June] (5; CNC); Location unknown, Bowman Lake [Sept.] (1; UWBM), Paradise Mine [Aug.] (4; CAS, UWBM), Park Mountain [June] (3; CAS, UBC), Waterloo Mine [Aug.] (3; INHS, MSU).

UNITED STATES OF AMERICA

IDAHO: [redacted] New Meadows area [June] (1; UIMI); County unknown, "southeastern Idaho" [July] (1; UWBM). MONTANA: Carbon Co., Rosebud Lake [June] (1; DHKa); Glacier National Park [July-Aug.] (23; CUIC, UCR, USNM), Boulder Pass ([2410m]) [July] (4; SJSC), Chaney Glacier ([2290m]) [Aug.] (1; USNM), Fallen Leaf Lake (Allen Mountain [2040m]) [July] (1; SJSC), Grinnell Glacier ([1920m]) [Aug.] (1; SJSC), Grinnell Lake ([1540m]) [July] (1; SJSC), Gunsight Pass ([1980m]) [July] (1; SJSC), Hidden Lake ([1950m]) [July] (2; GRNo, SJSC), Hidden Pass ([2160m])[Aug.] (3; SJSC), Iceberg Lake ([1840m])[July] (1; USNM), Lake McDonald [July] (4; CAS), Logan Pass ([1840m-2100m]) [June-Sept.] (175; CAS, CUIC, DHKa, LRus, MCZ, NMDo, RTBe, SJSC, UASM, UCB), Many Glacier ([1370m]) [July] (2; LRus), Mount Clements (northeast slope [2160m]) [July] (28; DHKa), Piegan Pass ([2420m]) [July] (2; SJSC), Reynolds Mountain (west slope) [Aug.] (2; SJSC), Shangri-La Lake (north of Mount Wilbur [2040m]) [June] (1; SJSC), Sperry Chalets ([2010m]) [July] (2; SJSC, USNM), Sperry Glacier ([2590m]) [Aug.] (1; RTBe), Swiftcurrent Lake ([1480m] and at Canyon Creek) [July] (2; CAS, SJSC); Granite Co., Stony Lake [July] (1; DZEC); Park Co., Cooke City [Aug.] (1; SJSC). OREGON: Baker Co., Anthony Lake ([2130m-2150m]) [June-Aug.] (89; DHKa, FMNH, OSUO, UASM, UWBM), Antone Creek ([2100m]) [May] (1; DHKa); Grant Co., Strawberry Lake ([2620m]) [Sept.] (1; OSUO);

Wallowa Co. [Aug.] (2; JSch), Aneroid Lake ([2290m-2320m]) [July] (83; CAS, FMNH, INHS, UWBM), Dollar Lake ([2500m-2620m]) [July] (20; FMNH, UWBM), Eagle Cap ([2930m]) [Aug.] (1; PUCA), Ice Lake [July] (4; ODA), Lostine River (above Two Pan Campground [1710m-2000m]) [Aug.] (94; DHKa), Wallowa Lake [July] (10; UWBM). UTAH: Cache Co., Logan area [Sept.] (1; EMUS); Duchesne Co., Butterfly Lake ([2900m-3050m]) [June, Aug.] (23; DHKa, MCZ), Grandaddy Lake (2; UMMZ), Mirror Lake (1; UMMZ); Sanpete Co., Ephraim Canyon (Ephraim Creek [2900m]) [Aug.] (1; USNM); Salt Lake Co., Alta [June-July] (32; ANSP, ICCM, USNM), Lambs Canyon ([3000m]) (4; MHNP), Silver Lake [July] (6; ANSP, CUIC); Sevier Co., Monroe Peak (8.6 mi. [2620m] and 12.4 mi. [2990m] se. of Monroe) [July] (35; DHKa); Summit Co., Lost Lake ([2990m]) [Aug.] (15; CAS, DHKa), Tryol Lake (5; UMMZ); Uintah Co.,(15; USNM); Utah Co., Aspen Grove ([2070m]) (1; PURC); Weber Co., Uintah [Aug.] (1; EMUS); County unknown, Wasatch ([2440m]) [July] (2; OSUC), Wasatch National Forest [Aug.] (2; BFCa). WASHINGTON: Okanogan Co., Mount Bonaparte ([2130m] and Top Cache [2190m])[July-Aug.] (70; ANSP, CAS, MCZ, UIMI, USNM, UWBM, WSU); Walla Walla Co., Walla Walla area [July] (14; CUIC). WYOMING: (2; MCZ); Fremont Co., Union Pass [Aug.] (1; USNM), Wind River Rest Area ([2740m]) [June] (2; USNM); Grand Teton National Park [July] (8; CAS), Alaska Basin (Sunset Lake [2940m]) [July] (2; SJSC), Lake of Crags ([2900m]) [July] (1; SJSC), Mica Lake ([2970m]) [July] (15; DHKa, SJSC, USNM), Petersen Glacier ([2990m]) [July] (3; DHKa, SJSC, USNM), South Fork Cascade Canyon ([3020m-3110m]) (4; SJSC, USNM), Spalding Falls ([3230m]) [Aug.] (1; SJSC), Timberline Lake [July] (9; SJSC, USNM), Upper Cascade Canyon ([3050m]) [July] (1; SJSC); Park Co., Beartooth Plateau [Aug.] (1; SJSC); Sublette Co., Fremont Lake [July] (40; CAS), Green River

Lakes (west shores [2440m-2590m]) [July] (3; DHKa); Teton Co., Blackrock Creek (3.7 mi. wnw. of Togwotee Pass [2770m]) [Aug.] (1; DHKa), Jackson area [June] (1; UWLW), Sheep Mountain ([2900m]) [Aug.] (1; ANSP), Teton Pass area ([2650m]) [June] (1; SJSC); Togwotee Pass ([2960m]) [July-Aug.] (137; DHKa, KUSM, SJSC); Yellowstone National Park ([2130m-3050m]) [June, Sept.] (14; CAS, ICCM, MCZ, UCR, USNM), Hellroaring Divide [July] (2; DZEC), Mount Washburn [Aug.] (13; MCZ, USNM), Norris Junction [June] (1; CAS), Stinking Water Creek [Sept.] (7; ICCM, MCZ), Sylvan Pass [June] (1; USNM).

Doubtful Records. CANADA, ALBERTA: Edmonton [July] (15; UASM). UNITED STATES OF AMERICA, CALIFORNIA: (1; ICCM). OREGON: Jackson Co., Little Applegate River ([700m]) [Aug.] (5; FMNH, UWBM).

No Data. (4; ANSP, MCZ, ROM).

Nebria darlingtoni Kavanaugh, NEW SPECIES

Map: Figure 399

Specimens examined: 172 (106♂, 66♀)

UNITED STATES OF AMERICA

CALIFORNIA: El Dorado Co., [Aug.] (9; CAS, ICCM, KSUC, MCZ, USNM), Kyburz (2 mi. e. on South Fork American River [1340m]) [July] (5; CAS, DHKa), Pacific House [Sept.] (5; CAS), Riverton (South Fork American River [980m], 3 mi. w. at Bridal Falls Picnic Area [910m]) [July-Aug.] (151; AMNH, CAS, DHKa, KUSM), White Hall [June] (2; UASM).

Nebria desolata Kavanaugh

Map: Figure 400

Specimens examined: 258 (125♂, 133♀)

UNITED STATES OF AMERICA

UTAH: Garfield Co., Boulder (11 mi. se. at The Gulch [1710m-1830m]) [June-July] (207; CAS, DHKa, MCZ, MHNP, SJSC, UASM, USNM); Dry Creek (23.1 mi. sw. of Escalante [2130m]) [June] (29; DHKa), Escalante River (15 mi. e. of Escalante [1710m]) [June] (15; DHKa); Kane Co., Garfield (East Fork Virgin River) (4; MHNP), Orderville (East Fork Virgin River) [Apr.] (3; USNM).

Nebria diversa LeConte

Map: Figure 401

Specimens examined: 1797 (946♂, 851♀)

CANADA

BRITISH COLUMBIA: Vancouver area [June] (1; UAFA); Queen Charlotte Islands, Graham Island (Massett, North Beach, Rose Point, Tllel, 10 mi. s. and 25 mi. n. of Tllel, Tow Hill and on Tow Hill Road) [May-Aug.] (243; CNC, CUIC, DHKa, FMNH, ICCM, MCZ, UASM, UBC, UMMZ, UWBM); Vancouver Island, Tofino (and 6 mi. s. at Chesterman Beach, 12 mi. s. at Long Beach) [May-June, Aug.-Oct.] (119; ALar, CNC, DBUM, DHKa, UBC, UWBM); Victoria (and Albert Head) [Aug.] (6; CNC, UASM); Location unknown, Puget Sound (1; AMNH).

UNITED STATES OF AMERICA

CALIFORNIA: Del Norte Co., (1; FMNH), Crescent City [May, July] (5; CAS). OREGON: (34; ANSP, ICCM, INHS, KSUC, KUSM, MCZ, USNM, WSU); Clatsop Co., (2; OSUO), Astoria [July] (5; OSUC), Cannon Beach [June-Aug.] (14; JSch, MCZ, UASM, UWBM), Fort Stevens (at Fort Stevens State Park, at South Jetty) [Aug.-Sept.] (9; OSUO, UIMI, UWBM), Gearhart [Apr., June] (22; ALar, LRus, UCR, USNM, UWBM), Seaside [July, Sept.] (23; CAS, CUIC, FMNH, MCZ, UIMI, UWBM, WSU), Warrenton (1; UWBM); Coos Co., Bandon (and 2 mi. n.) [July, Sept.] (11; BFCa, CAS), Cape Arago [May] (1; FMNH), Charleston (and 1 mi. w.) [May-Sept.] (23; CNC, DHKa, FMNH, JSch, NMDo, OSUO, UIMI, UWBM), Coos Bay [May] (1; UWBM), Coos Head [May, Aug.] (9; CAS, FMNH), Hauser [May, Oct.] (21; MCZ, OSUO, UCD, USNM, UWBM), Seven Devils Beach [Aug.] (1; LRus), Sunset Beach [June] (5; JSch, NMDo); Curry Co., Gold Beach [Apr., June-July] (19; CAS, OSUO, USNM, UWBM), Hubbard Creek (near Port Orford) [Dec.] (1; USNM), Humbug Mountain State Park [May-June] (9; CAS, FMNH, ODA, OSUO, UCD, UWBM), Pistol River [July, Sept.] (23; CAS, FMNH, INHS, UWBM); Douglas Co., Carter Lake Campground (10 mi. s. of Dunes City) [June] (1; ROM), Gardiner [June] (2; CAS), Tahkenitch Lake [June] (2; UWBM), Winchester Bay [May] (4; FMNH, UWBM); Lane Co., Carl G. Washburne Memorial State Park [June] (3; USNM), Florence (and at Munsel Lake) [May-June, Sept.] (13; FMNH, JSch, OSUO, UMMZ, UWBM), Glenada [June-Sept.] (22; CAS, FMNH, INHS), Heceta Beach [July] (1; BFCa), Siltcoos area (Siltcoos Camp, Siltcoos Outlet) [Mar., June, Sept., Nov.] (20; FMNH, LRus, PUCA, UWBM); Lincoln Co.,[June] (7; FMNH), Boiler Bay [Apr.-May] (6; CAS, OSUO), Burntwood Beach [Aug.] (2; OSUO), Delake [June] (1; JSch), Depoe Bay [Apr.] (1; UWBM), Devils Lake [Apr., June] (2; UWBM), Fogarty Creek State Park [Oct.]

(1; OSUO), Governor Patterson Memorial State Park [July] (5; BFCa), Lincoln Beach [Mar.] (1; UWBM), Newport [Apr.-Aug., Dec.] (74; AMNH, ANSP, CAS, DBUM, DEUC, FMNH, KSUC, LACM, MCZ, OSUO, UMRM, USNM, UWBM, UWEM), Ocean Lake [May] (1; UWBM), Taft [July] (3; UIMI, UWBM), Waldport (and 2.5 mi. n.) [Mar.-July] (197; CAS, DHKa, FMNH, ICCM, MCZ, OSUO, UASM, UMMZ, USNM), Yachats [Aug.] (5; JSch, NMDo), Yaquina Bay [Sept.] (2; CAS); Tillamook Co., Barview Jetty [Aug.] (1; LRus), Cape Lookout State Park [Sept.] (1; OSUO), Island Camp (2 mi. s. of Sand Lake) [July, Sept.] (31; ODA, OSUO), Netarts [Aug.] (2; USNM), Pacific City [Feb., May, July-Aug.] (14; CAS DHKa, FMNH, NMDo, UCR, UWBM), Rockaway [Sept.] (1; UWBM), Sand Lake [June-July] (65; CDA, MSU), Tierra Del Mar [Sept.] (3; DHKa), Tillamook [Aug.] (1; UWBM). WASHINGTON: Clallam Co., Cape Flattery (2; MCZ), Mora area [May, Sept.] (7; UWBM), Mukkaw Bay [May] (3; UWBM), Neah Bay (and 1.8 mi. nw.) [May, Aug., Oct.] (22; FMNH,UWBM), Sequim Bay [May] (1; LRus); Grays Harbor Co., Copalis Beach [May, Aug.] (6; LRus, UWBM), Moclips [Apr., June, Sept.] (8; ANSP, CAS, UWBM), Ocean City State Park [May] (1; UWBM), Ocean Shores [May, Aug.] (399; DHKa, UWBM), Pacific Beach [Sept.] (1; UWBM), Twin Harbors State Park [July] (2; UWBM), Westport [Apr.-May, July-Aug.] (7; NMDo, OSUO, UWBM); Island Co., Whidbey Island (Coupeville, Deception Pass) [Apr.-May, July] (4; CAS, UWBM, WSU); Jefferson Co., Port Townsend (and at Fort Worden) [June] (52; CAS, CDA, UWBM, WSU); King Co., Seattle (and at West Point) [July] (10; FMNH, UWBM); Pacific Co., Bay Center [July] (1; UWBM), Chinook [Sept.] (1; UWBM), Fort Canby State Park [Aug.] (1; UWBM), Ilwaco (and at North Jetty Beach) [May, July-Aug.] (36; LRus, MCZ, USNM, UWBM, WSU), Leadbetter Point [Aug.] (1; UWBM), Long Beach [May-Aug.]

(60; CAS, DHKa, GRNo, UWBM), Long Island (Willapa Bay) [Aug.] (1; UWBM), Nahcotta [May, July-Aug.] (3; UWBM), Naselle (8 mi. s.) [May] (1; ODA), Ocean Park [Aug.-Sept.] (10; UWBM, WSU), Oysterville [Aug.] (1; UWBM), Seaview [July-Aug.] (5; USNM, UWBM), Tokeland [June] (6; USNM, UWBM); San Juan Co., San Juan Island (Friday Harbor) [July] (1; UWBM); Thurston Co., Tumwater area (Black Lake) [May] (3; UWBM); County unknown, Stackpole Harbor [Aug.] (1; UWBM).

Doubtful Records. UNITED STATES OF AMERICA, CALIFORNIA: Sierra Co., [June] (5; FMNH). NEBRASKA: (1; AMNH). OREGON: Baker Co., Pine Creek [June] (1; MCZ); Klamath Co., Lake of the Woods [July] (8; DHKa, USNM); Marion Co., Pratum [Aug.] (1; OSUO); Multnomah Co., Portland (6; UAFA, USNM); Yamhill Co., (1; CAS). WASHINGTON: Pierce Co., Puyallup [Mar.] (2; ODA, PURC).

No Data. (8; MCZ, OSUO, USNM).

Nebria eschscholtzii Ménétriés

Map: Figure 400

Specimens examined: 6169 (2940♂, 3229♀)

UNITED STATES OF AMERICA

CALIFORNIA: [Feb.] (65; AMNH, ANSP, DBUM, DEUN, FMNH, ICCM, INHS, MCZ, UASM, UMMZ, UMRM, USNM, WSU); Alameda Co., (3; CAS, USNM), Arroyo Mocho Canyon [Jan.] (1; DHKa), Berkeley [Jan., May-June, Aug., Oct.-Dec.] (15; AMNH, CAS, CUIC, MCZ, USNM), Niles Canyon [Jan., Apr., June, Nov.-Dec.] (23; CAS, MCZ, UCB, UCD, USNM), San Leandro [May] (6; UCB, UCD), Sunol [Apr.-May, Sept.] (37; ANSP, CAS, UCB), Sunol Valley Regional

Park [Feb.] (8; GRNo); Amador Co., Sutter Creek [Aug.] (15; CAS), Volcano [June] (1; USNM); Butte Co., Oroville [Feb.] (1; UCB); Calaveras Co., [July] (3; CUIC), Mokelumne Hill [June-Aug.] (11; CAS, PADA, USNM, WSU); Contra Costa Co., [May] (4; CAS), Antioch (and 2 mi. e., [Mar.-May, Dec.] (16; CAS, UCB), Moraga [Oct.] (2; CAS), Mount Diablo [Oct.] (1; CAS), Orinda [Mar.] (1; UCB), San Pablo (San Pablo Canyon) [Apr., Nov.] (4; UCB, UCD); Del Norte Co., [May] (1; FMNH), Crescent City [Mar.] (4; CNC, UBC), Elk Valley (3.6 mi. ssw. on Griffin Creek [550m]) [Sept.] (2; CAS, DHKa); El Dorado Co., [June, Aug.] (13; FMNH, KSUC), Camino (3 mi. s.) [June] (1; UCB), Coloma [Apr.-May] (29; GRNo, USNM), Kyburz (2 mi. e. on South Fork American River [1340m]) (1; CAS), Lake Tahoe [July] (1; CAS), Riverton ([980m] and 3 mi. w. on South Fork American River [910m]) [July] (78; CAS, DHKa); Fresno Co., Fresno [July] (2; UMRM), Trimmer [May] (6; CAS, UBC); Glenn Co., Estell Creek (Logan Basin [1050m]) [July] (3; CAS), Orland (1.5 mi. n. at Stony Creek [110m]) [May] (25; DHKa); Humboldt Co., (10; AMNH, OSUC, USNM), Alton [May] (18; CDA, UCD), Arcata [June] (1; ANSP), Blocksburg [May-June] (13; CAS, UCB), Blue Lake (1 mi. s.) [Sept.] (1; CDA), Bridgeville (Van Duzen River) [June] (5; UASM, UCB), Capetown [Mar.] (3; JSch), Carlotta (Van Duzen River, and 6 mi. e.) [June] (49; RTBe, UASM, UCB, USNM), Dyerville [May-July] (4; RTBe, UCB, UCD), Eel River (11 mi. s. of Weott) [Mar.] (1; JSch), Fernbridge (Eel River) [June] (1; UASM), Fort Seward [May-June] (31; CAS, CUIC, RTBe, UCB, UIMI), Garberville [Mar., Sept.] (3; UIMI), Green Point [June] (4; CAS), Hoopa [June] (10; UASM), HumboldtGrove [July] (5; MSU), Orick [May, July-Aug.] (12; BFCa, CAS, CDA, DBUM), Patricks Point [Aug.] (1; MSU), Prairie Creek [July] (1; USNM), Redwood Creek

(3 mi. n. of road to Hoopa [200m], e. of Blue Lake on Highway 299, 17 mi. w. of Willow Creek [290m]) [June, Aug.] (5; CAS, UASM), Shively (2; CDA); Kings Canyon National Park, Cedar Grove [June] (5; CAS, UASM, UBC), Kings River Canyon [June] (10; KSUC, OSUC, UASM); Lake Co., Adams Springs [June] (1; CAS), Lower Lake [Sept.] (1; CAS); Lassen Co., Hallelujah Junction [July-Sept.] (5; CAS, CDA), Susanville (0.1 mi. w. at Susan River [1300m]) [May] (18; DHKa); Los Angeles Co., Coldbrook Ranger Station [June] (2; UCB), East Fork San Gabriel River (2.5 mi. e. of Highway 39 [530m]) [May] (1; DHKa), Mount Wil[illegible] [May] (2; UCR), Pasadena [May] (1; CAS), San Antonio Canyon [May] (2; GRNo), Switzers Camp [Aug.] (1; CDA), Trail Canyon (1; SFVS); Marin Co., [Mar.-Apr.] (4; CAS, USNM), Bon Tempe Lake [June] (1; CAS), Fairfax [Apr., June] (2; CAS), Lagunitas (Lagunitas Creek) [Mar.-June, Nov.] (11; AMNH, ANSP, CAS, CNC, MCZ, PADA), Mount Tamalpais [Sept.] (1; CAS), Muir Woods [May] (2; USNM), Nicasio Reservoir (0.5 mi. sw. at Lagunitas Creek) [Mar., June] (66; DHKa, PMCh), Taylorville [Dec.] (3; CUIC), Tocaloma (Lagunitas Creek) [May] (2; CAS); Mariposa Co., [July] (4; FMNH); Mendocino Co., [Aug., Oct.] (6; FMNH), Branscomb [July] (2; BFCa), Cummings (Rattlesnake Creek) [Sept.] (2; CAS), Fort Bragg [July] (1; DHKa), H[illegible]ndy State Park (Navarro River) [June] (20; CDA), Howard Lake ([1200m]) [June] (1; UCB), Long Valley (n. of Willits) [Sept.] (2; CAS), Manchester area (Irish Beach) [Apr.] (1; JSch), McGoy Creek (s. of Piercy) [Sept.] (14; CAS), Ukiah [Mar.] (1; PURC), Westport [July] (3; BFCa), Willits (and 3 mi. w. at Baechtel Creek) [June, Aug.] (2; MSU, USNM); Merced Co., Dos Palos [Sept.] (2; UASM), Snelling [Nov.] (1; USNM); Modoc Co., Adin (0.5 mi. n. at Rush Creek [1360m]) [May] (16; DHKa); Mono Co., Hot Creek [July] (2; UCD), Topaz Lake

(south end) [May] (1; DHKa); Monterey Co., Arroyo Seco Camp (Arroyo Seco Creek [520m]) [May] (15; DHKa, USNM), Big Sur (Big Sur River [90m], and 2 mi. e. at Ventana Campground) [Jan., May, July, Sept.] (55; CAS, DHKa, USNM), Carmel [Oct.-Nov.] (6; CAS, CUIC), Escondido Camp (2.4 mi. se. on Arroyo Seco Creek [620m]) [May] (2; DHKa), San Antonio River (10.6 mi. se. of Escondido Camp [400m]) [May] (8; DHKa), Tassajara Hot Springs [May, Sept.] (23; CAS, MCZ, UASM); Napa Co., Conn Lake [= Lake Hennessey] [Apr.] (1; UCB), St. Helena [July] (3; AMNH, ROM); Placer Co., (2; MCZ, USNM), Dutch Flat [Nov.] (5; CAS, CUIC), Foresthill [Oct.] (1; USNM); Plumas Co., [June] (1; FMNH), Highway 70 (21 mi. w. of Highway 395 [1370m]) [June] (1; UASM), Lake Almanor [July] (2; UCB), Massack (Greenhorn Creek at Massack Rest Area [1140m]) [July-Aug.] (5; CAS, MSU, UBC), North Fork Feather River [July] (1; MCZ), Quincy ([1040m]) [Aug.] (3; CAS); Sacramento Co., Carmichael [Mar.] (2; USNM), Sacramento (and at Sycamore Park) [July, Sept.-Oct.] (20; CAS, FMNH, INHS, MSU); San Bernardino Co., Baldwin Lake area ([2620m]) [Aug.] (3; UASM), Barton Flats (3 mi.e. at Santa Ana River headwaters [1940m]) [May] (37; DHKa), Bear Lake [Oct.] (2; CAS), Beaumont (8.6 mi. n. at Little San Gorgonio Creek [1340m]) [May] (29; DHKa), Big Pine Flat Campground (5.5 mi.sw.) [July] (1; GRNo), Colton [Oct.] (2; UMMZ), Forest Home [June, Sept.] (20; UCR), Lytle Creek [June] (6; CAS), Mill Creek (and 0.1 mi. e. of Forest Falls [1650m], 1.0 mi. ne. of Mill Creek Ranger Station [910m]) [May, Sept.-Oct.] (28; CAS, DHKa, GRNo), San Gorgonio Mountain ([2130m]) [Sept.] (5; CAS), South Fork Campground (1; GRNo); San Francisco Co., San Francisco [Apr.] (1; JSch); San Joaquin Co., [May] (2; FMNH), Banta [Nov.] (2; ICCM, USNM); San Mateo Co., (1; UWEM), Corte Madera Creek

(and near Portola Valley) [June, Aug., Oct.] (35; CAS, USNM), Gazos Creek (2 mi. e. of Cloverdale Road [15m]) [May] (5; DHKa), Jasper Ridge [May, Oct.] (3; CAS), La Cañada [Apr.] (1; CAS), La Honda (and 0.3 mi. n. at La Honda Creek [110m], 1.9 mi. w. at San Gregorio Creek [60m]) [May, July-Aug.] (81; CAS, DHKa, JSch), Loma Mar (Pescadero Creek [15m]) [May] (25; DHKa), Mindego Creek (at Alpine Road [120m]) [May] (11; DHKa), Pescadero (4.5 mi. e.) [Sept.] (4; USNM), Pescadero Creek [Aug.] (13; RFre), San Gregorio [June] (4; CAS), Searsville Lake (2; CAS), West Ridge [May] (1; CAS), Woodside (5 mi. w. on Highway 84) [June] (35; PMCh); Santa Clara Co., (12; FMNH, ICCM, UMRM, USNM), Alma [Oct.] (5; CAS, CUIC), Almaden [Apr.] (3; UCD), Anderson Reservoir (south end) [Jan.-Feb., May, Sept.] (39; DHKa, USNM), Arroyo Bayo [Apr.] (1; DHKa), Arroyo Mocho [Feb.] (1; DJLa), Corte Madera Creek [Apr.] (13; CAS), Gilroy (7 mi. e. at Coyote Creek) [Mar.] (3; DJLa, USNM), Gilroy Hot Springs (and 0.5 mi. w., 1.0 and 7.0 mi. s. on Coyote Creek) [May, July-Aug., Nov.] (17; CAS, DJLa, USNM), Isabelle Creek [Oct.] (2; UCB), Los Gatos [June] (2; CDA, USNM), Mount Hamilton [Apr., June] (11; UIMI, USNM), Pacheco Creek (and 7.9 mi. w. of Pacheco Pass [140m]) [May, July] (32; CAS, DHKa), Palo Alto [Oct.] (1; USNM), San Jose (and Alum Rock Park at Penitencia Creek [200m]) [Feb., Apr.-June, Oct.] (54; AMNH, CAS, CUIC, DHKa, MCZ, USNM), Saratoga (0.5 and 1.0 mi. w. on Saratoga Creek [170m]) [May, Sept.] (14 M), Stanford University campus [May, Sept., Nov.-Dec.] (9; USNM), Stevens Creek (at Stevens Creek County Park [170m], June] (7; DHKa, USNM), Stow Creek Canyon [Nov.] (1; USNM), Sveadal [Feb., Oct.] (7; DHKa, USNM), Uvas Creek (at Croy Road) [Feb.] (2; DJLa, USNM); Santa Cruz Co., [June, Aug.] (2; CAS, USNM), Aptos Creek

[May] (1; UCB), Ben Lomond [May, July, Sept.] (30; AMNH, CAS, LACM, MCZ, UASM, UBC), Big Basin Redwoods State Park [May] (1; USNM), Brookdale [Oct.] (4; CUIC), Corralitos [May] (9; CAS, KSUC), Felton [Sept.] (3; CUIC), Glenwood [May, Oct.] (3; CAS, CUIC), Hinckley Creek [May] (2; USNM), Mount Herman [July] (18; CAS, LACM), Santa Cruz [Apr., June, Sept.] (37; CAS, CDA), Scotts Valley (2 mi. n. on Glenwood Road at Bear Creek) [Apr.] (1; USNM), Zayante [May] (2; UIMI); Sequoia National Park, Giant Forest [Aug.] (4; CAS); Shasta Co., (16; AMNH, CUIC, USNM), Anderson (2 mi. n. at Sacramento River [170m]) [May] (10; DHKa), Castella [July] (1; UMMZ), Dakkas Rock Picnic Area [Aug.] (1; GRNo), Hat Creek [June-July] (2; UCB, UCD), Hazel Creek [July] (1; AMNH), Old Station (Hat Creek [1400m]) [Aug.] (5; CAS, DHKa), Silverthorne [Feb.-June] (119; CDA); Sierra Co., Downieville [July] (3; AMNH); Siskiyou Co., [Sept.] (14; ANSP, KSUC, MCZ, PADA, USNM), Dunsmuir (4; ANSP, MCZ, USNM), Gottville (Klamath River) [June] (1; UASM), Klamath River (11 mi. w. of Klamath River Lodge) [May] (1; JSch), Pickawish Campground (84 mi. ne. of Willow Creek on Klamath River) [June] (9; UASM), Shasta Springs (Shasta Retreat [730m]) [June-July, Sept.] (12; ANSP, CAS, MCZ), Walker [June] (1; CAS); Solano Co., Rio Vista [June] (1; UIMI), Ryer Island [Jan.] (1; UCD), Winters (8 mi. w.) [Feb.] (6; USNM); Sonoma Co., [May, Aug.] (7; CAS, LACM, SDSU), Duncan Mills [July] (1; CAS), Forestville [Oct.] (2; CAS), Fort Ross [Nov.] (1; CAS), Guerneville [July-Aug.] (3; CAS), Guernewood Park [May] (3; UASM, USNM), Monte Rio (3 mi. n.) [Sept.] (1; CAS), Santa Rosa [Apr.] (6; OSUC, PURC, UMRM); Stanislaus Co., Knights Ferry [Apr.] (1; UCB); Sutter Co., Nicholaus [Apr.] (1; CDA); Tehama Co., Child's Meadow (0.5 mi. w. at Mill Creek [1460m]) [May] (2; DHKa), Corning

[Oct.] (1; CAS), Cottonwood (0.1 mi. s. at Cottonwood Creek [170m]) [May] (31; DHKa), Dales (1.3 mi. sw. at Paynes Creek [260m]) [May] (17; DHKa), Mineral ([1520m], and 1.4 mi. w. at Battle Creek [1460m]) [May] (14; CAS, DHKa), South Fork Battle Creek ([300m]) [Apr.] (1; DHKa), Thomas Creek (2.5 mi. s. of Tehama exit on Interstate Highway 5 [120m]) [May] (50; DHKa); Trinity Co., [Sept.] (1; CAS), Burnt Ranch [Sept.] (40; CAS), Coffee Creek (at Coffee Creek Ranch [1070m]) [July] (17; CAS, DHKa), Hayfork (6 mi. ne. [790m]) [May] (6; UCB), Mad River (at Mad River Post Office) [May, Aug.] (8; DJLa, USNM), Ruth Reservoir (and 5.5 mi. se. of Ruth Dam) [Feb., Apr.] (4; DJLa, GRNo, USNM), Slate Creek (18.5 mi. sw. of Trinity Center on Highway 3 [730m]) [July] (4; CAS, DHKa), South Fork Salmon River (at Big Flat Campground [1490m]) [June-Aug.] (8; CAS, DHKa), Weaverville ([610m]) [Sept.] (2; CAS), Willow Creek (20 mi. e.) [Sept.] (2; MSU); Tulare Co., Kaweah (2; MCZ), Three Rivers (0.2 mi. sw. at South Fork Kaweah River [240m]) [June] (85; DHKa); Tuolumne Co., [May] (7; CAS, FMNH), Lyons Dam [June] (4; UIMI); Yolo Co., Cache Creek Canyon [Apr.] (1; USNM), Davis [Mar., Oct.] (2; PURC, USNM), Esparto (5 mi. w. at Salt Canyon) [May] (1; CDA), Putah Canyon [Feb., Apr.] (2; DHKa, USNM), Rumsey (26 mi. n.) [Apr.] (10; CDA), Winters (7 mi. e.) [Mar.] (2; USNM); Yosemite National Park, Yosemite Valley ([1220m]) [June, Aug.-Sept.] (15; FMNH, RTBe, SFVS, UWBM); County unknown, San Francisco Bay area (1; CAS), Santa Cruz Mountains [May] (2; USNM), Sylvania [Aug.] (2; MCZ). IDAHO: Clearwater Co., Orofino [Oct.] (6; WSU); Latah Co., Central Grade [Apr.] (1; UIMI), Juliaetta (and 4 mi. s.) [Apr., Nov.] (3; MSU, UIMI), Kendrick [May, Sept.] (6; UIMI), Meadow Creek Reservoir [Oct.] (1; UIMI), Moscow (3; UIMI), Moscow Mountain ([910m]) [Apr.] (5; UIMI),

Robinson Lake [Oct.] (1; UIMI), Troy [May] (5; UIMI, USNM, UWBM); Nez Perce Co., Clearwater River (3 mi. e. of Highway 95 on Highway 12 [380m]) [May] (2; DHKa), Lapwai [Apr., Oct.] (5; UIMI), Lenore ([300m], and 6 mi. w. on Clearwater River) [May, July] (6; DHKa, UIMI, UWBM), Lewiston ([170m], and 2 mi. e. on Clearwater River [300m]) [Mar.-May, Aug.] (30; DHKa, GRNo, UIMI, UWBM), Myrtle [Apr.] (3; UIMI), Spalding [May] (1; OSUC), Webb [Oct.] (2; UIMI). NEVADA: (2; ANSP, INHS); Washoe Co., Franktown (3; MCZ, USNM), Lockwood (0.8 mi. w. on Truckee River [1430m]) [July] (22; DHKa), Pyramid Lake [Aug.] (4; ILar), Reno [Aug.] (1; ILar), Verdi [June] (8; UIMI, USNM), Wadsworth (Truckee River [1340m]) [July] (2; DHKa). OREGON: (51; AMNH, CAS, FMNH, INHS, KUSM, MCZ, PURC, USNM); Baker Co., East Eagle Creek [July] (1; UWBM), Robinette [June] (27; UWBM); Benton Co., Alsea [Mar.] (1; OSUO), Blodgett [June] (2; CUIC, MCZ), Coffin Butte [Sept.] (3; OSUO), Corvallis (and 5 mi. w.) [Mar.-June, Sept.] (43; CAS, CUIC, LRus, MCZ, MSU, OSUO, UBC, USNM, UWBM), Marys Peak [June] (1; OSUO), Philomath (and 3 mi. nw. on Marys River) [Apr., July] (8; OSUC, OSUO, UWBM), William Finley Memorial Wildlife Refuge [June] (1; LRus); Clackamas Co., (4; USNM), Brightwood (Salmon River [320m]) [July] (43; DHKa), Bull Run [Aug.] (1; OSUO), Clackamas River [May] (1; DHKa), Colton [Jan., Apr.] (3; CAS), Mollala (9.4 mi. sw. at Butte Creek [60m]) [July] (9; DHKa), Mollala River (at Highway 211 [80m]) [July] (84; DHKa), Sandy River [May] (4; JSch, MSU); Clatsop Co., Big Creek [July] (7; UWBM), Cannon Beach [June] (4; CAS); Columbia Co., Mist [July] (1; CAS); Coos Co., Allegany [Oct.] (3; DHKa), Upper Cherry Creek (15 mi. sw. of Powers) [July] (2; OSUO); Crook Co., Prineville (Crooked River [910m]) [May] (2; DHKa); Curry Co., Brookings (and 7 mi. e. at Myrtle Grove on Chetco

River) [May, Sept.] (14; CAS, FMNH, OSUO, UWBM), Brush Creek (at Highway 101) [July] (1; MSU), Chetco River [Aug.] (24; LRus), Gold Beach [June] (1; CAS), Humbug Mountain State Park [May, Sept.] (8; FMNH, OSUO, UWBM), Loeb State Park [May] (6; UWBM), McGribble Campground [Aug.] (8; UWBM), Pistol River [May, July, Sept.] (13; FMNH, UWBM), Port Orford [July] (1; UWBM); Deschutes Co., Upper Deschutes River [May] (1; UWBM); Douglas Co., [June] (1; FMNH), Canyonville [Aug.] (4; UIMI, UWBM), Gardiner (5 mi. e.) [Apr., June] (4; JSch), Glide (7 mi. e.) [May] (2; OSUO), Myrtle Creek [June] (1; UWBM), North Umpqua River (at Toketee Lake [730m]) [July] (33; DHKa), Reedsport [July-Aug.] (7; JSch, RTBe), Roseburg (and 7 mi. nw.) [Apr.-May, Sept.] (9; FMNH, INHS, JSch, MCZ), Scottsburg (6 mi. e. at Weatherley Creek) [June] (1; JSch), Steamboat Creek (at North Umpqua River [320m], at Steamboat Falls [320m]) [July] (37; DHKa), Tiller (and 2 mi. e. at Tilson Creek) [May] (4; DHKa, JSch), Winchester (North Umpqua River) [Mar.] (1; JSch); Gilliam Co., Arlington (5 mi. w. on Columbia River) [Apr.] (1; JSch); Grant Co., Beech Creek (11.4 mi. n. of Mount Vernon [1230m]) [May] (1; DHKa), Monument (North Fork John Day River [690m]) [May] (72; DHKa), Mount Vernon (1.5 mi. e. at John Day River [940m]) [May] (17; DHKa), Picture Gorge (John Day River) [Aug.] (3; UWBM); Hood River Co., Hood River (and 0.2 mi. s. on Hood River [60m]) [May-July, Sept.] (162; CAS, DHKa, MCZ, OSUO, USNM); Jackson Co., Applegate (2 mi. w. on Applegate River [410m]) [May] (17; DHKa), Brownsboro [May] (7; DHKa), Buckhorn Mineral Spring [May] (2; JSch), Butte Falls (0.3 mi. e. at South Fork Butte Creek [730m]) [July] (19; DHKa), Dead Indian Soda Springs ([760m], and 3 mi. w.) [May, Oct.] (15; JSch, OSUO), Eagle Point [May] (2; UCD, UWBM), Gold Hill (Rogue River) [Oct.] (4; OSUO, UWBM), Jacksonville

[May] (5; JSch, NMDo), Klamath Junction (2.8 mi. e. at Emigrant Creek [730m]) [May] (46; DHKa), Little Applegate River ([700m]) [Aug.] (1; FMNH), Medford [May-June] (37; UCD, UWBM), Rogue River (11.9 mi. sw. of Union Creek [760m]) [July] (71; DHKa), Rogue River City (2 mi. e. on Rogue River [300m]) [Sept.] (96; DHKa), Ruch (4 mi. s., 4.5 mi. s. at Little Applegate River [520m], 10 mi. s. at Applegate River [520m]) [May] (42; DHKa, LRus, ODA, OSUO), Shady Cove (6.3 mi. nw. at Elk Creek [410m], at Rogue River) [May, July] (109; DHKa, JSch), Star Ranger Station [Mar.] (2; UCD), Tou Velle State Park (Rogue River [380m]) [May] (62; DHKa, LRus), Trail [May] (1; JSch), White City (1.5 mi. n. on Agate Road at Little Creek [400m]) [May] (71; DHKa), Wimer [May] (3; UWBM); Josephine Co., [June-July] (9; FMNH), Applegate River (at Highway 199) [May] (1; DHKa), Cave Junction (1 mi. s. at East Fork Illinois River [440m]) [May] (106; DHKa), Golden (12; UWBM), Grants Pass (and 7 mi. w. at Applegate River) [May, July-Aug.] (20; AMNH, LRus, OSUO), Grave Creek [May] (7; FMNH, UWBM), Grayback Creek (w. of Oregon Caves [580m]) [June] (2; UWBM), Illinois River (headwaters) [May] (9; CAS, JSch, UBC), Selma (and 3 mi. n. [470m], 0.5 [440m] and 1.0 mi. s. at Deer Creek) [May] (22; DHKa, JSch, OSUO), Wolf Creek (4 mi. s.) [Mar.] (1; JSch); Klamath Co., Keno (7 mi. w.) [May] (2; JSch); Lane Co., Cottage Grove [June] (8; UWBM), Eugene [May-July, Sept.-Oct.] (17; CAS, FMNH), Nimrod (0.9 mi. w. at McKenzie River [270m]) [July] (42; DHKa), North Fork McKenzie River (at Boulder Creek [520m]) [July] (5; DHKa), Oakridge (Salmon Creek [350m], 4.6 mi. nw. at Willamette River, and 9.5 mi. se. at Salt Creek [610m]) [June-July] (164; DHKa, USNM), Salmon Creek (10.6 mi. e. of Oakridge at Blue Pool Campground [610m]) [June] (2; USNM), Vida [Sept.] (7; UIMI); Lincoln

Co., Nashville [June] (22; ICCM, LACM, MCZ, UASM), Otis [July] (1; BFCa), Tidewater (7 mi. e. at Mike Bauer Campground) [Aug.] (1; RTBe); Linn Co., [Oct.] (2; OSUO), Albany [June] (5; CAS), Foster [July] (9; OSUO), North Santiam River (1; ICCM); Marion Co., Detroit (and 2.5 mi. e. on North Santiam River [490m]) [June-July, Sept.] (36; CAS, DHKa), Mill City (7.4 mi. w. at Little North Santiam River [200m]) [July] (11; DHKa), Silver Creek Falls [July-Aug.] (3; UWBM); Morrow Co., Heppner Junction (5 mi. e. at Columbia River [180m]) [May] (2; DHKa); Multnomah Co., Horsetail Falls [June] (1; DHKa), Multnomah Falls [May] (1; UWBM), Portland [Apr., June-July, Sept.] (36; ANSP, CAS, DEUN, FMNH, ISUI, MCZ, OSUO, PADA, USNM, UWBM, WSU), Rooster Rock State Park (2 mi. e. of Corbett) [May] (7; DHKa, OSUO), Wahkeena Falls ([90m]) [July] (1; DHKa); Polk Co., Rickreall [Apr.] (12; UWBM); Sherman Co., John Day River (at Highway 30) [May] (1; JSch); Tillamook Co., Beaver [July] (2; MSU), Garibaldi (2 mi. e. at Miami River) [Apr.] (2; JSch), Lee's Camp (Wilson River) [Apr.] (2; MSU), Nehalem Creek [June] (6; UWBM), Tillamook [Sept.-Oct.] (6; UWBM); Umatilla Co., Cottonwood Creek [June] (1; USNM), Echo (Umatilla River [290m]) [May] (5; DHKa), Freewater [Sept.] (7; OSUO, USNM), Meachem (2 mi. sw. at Meachem Lake [1190m]) [Aug.] (3; UASM), Milton (and 7 mi. e., Walla Walla River) [Apr.-June, Sept.] (7; CAS, JSch, UIMI, UWBM), Rieth (5.9 mi. w. at Umatilla River [370m]) [May] (11; DHKa), south of Kooskooskie (Washington) [Oct.] (3; UWBM), Umatilla [June, Aug.] (8; MCZ, UWBM); Union Co., Elgin (0.1 mi. s. at Grande Ronde River [1130m], 3.1 mi. nw. at Little Phillips Creek [1020m]) [May] (14; DHKa), La Grande (and 1 mi. ne. at Grande Ronde River [1070m]) [May, Aug.] (18; DHKa, UWBM), Morgan Lake [June] (1; UIMI); Wasco

Co., The Dalles (and 5 mi. s. at Eightmile Creek) [Apr.-May] (17; CAS, FMNH, JSch, PURC, USNM), Tygh Creek (at Highway 197) [June] (7; JSch), Tygh Valley (2 mi. n. [410m]) [May] (4; OSUO), Warm Springs Indian Reservation (Hot Springs) [May] (8; JSch, MSU); Washington Co., Dilley (1; FMNH), Gales Creek [Apr.] (1; MSU); Wheeler Co., John Day River (0.4 mi. s. of west junction of Highways 19 and 207 [560m]) [May] (72; DHKa), Spray (John Day River [580m]) [May] (7; DHKa), West Branch Bridge Creek (16.0 mi. sw. of Mitchell [1070m]) [May] (47; DHKa); Yamhill Co., [Sept.] (1; CAS), Dayton (Dorsey Gravel Bar, Willamette River) [Apr.-May, July] (8; DHKa, UWBM), McMinnville (and 3 mi. nw.) [Feb., June-Aug.] (15; UCR, USNM, UWBM), Newberg [Oct.] (1; UWBM); County unknown, Farmers River [June] (1; UWBM). WASHINGTON: (58; AMNH, ANSP, CAS, FMNH, ICCM, INHS, MCZ, OSUC, ROM, USNM); Adams Co., Washtucna [May] (1; LRus); Asotin Co., Asotin (Asotin Creek [370m], Snake River) [May-June] (12; CAS, DHKa, OSUO), Buford Creek (3.6 mi. s. of Grande Ronde [760m]) [May] (118; DHKa), Clarkston [May, Aug.] (18; UIMI, UWBM), Grande Ronde River (at Highway 129 [550m]) [May, Sept.] (26; DHKa, SJSC); Benton Co., Kennewick [Sept.] (1; UWBM), Plymouth [Sept.] (4; UWBM), Richland [Apr.-May] (11; FMNH, UWBM); Clallam Co., Forks [July] (31; CAS), Klahowya State Park (Soleduck River) [June] (4; CAS), La Push [May] (6; CNC), Mora [Sept.] (1; UWBM); Clark Co., Battle Ground (1 mi. s. at Eas Fork Lewis River [80m]) [May] (10; DHKa), Lewisville Park [June] (1; MSU), Vancouver (2; CAS), Washougal [May, Sept.] (4; UWBM); Columbia Co., Central Ferry [Sept.] (14; UWBM), Dayton (and at Petit Creek [580m], Touchet River [580m]) [May, July, Sept.] (30; CUIC, DHKa, WSU), Tucannon River (at Highway 12 [370m])[May] (2; DHKa); Cowlitz Co., Ariel [May] (3; UWBM), Castle Rock

[Sept.] (1; UWBM), Longview (5 mi. se. at Carrols Hill, 9 mi. w. at Columbia River) [Mar., Aug.] (2; DHKa), North Fork Toutle River (14 mi. e. of Toutle [300m]) [Aug.] (11; CAS, DHKa), South Fork Toutle River [July] (1; UWBM), Toutle [May, Sept.] (3; CNC, USNM), Toutle River [May] (7; UWBM); Franklin Co., Palouse Falls State Park [May] (6; LRus), Pasco [May] (82; MCZ, UWBM, WSU), Perry [May] (1; ICCM); Grays Harbor Co., Lake Quinault [May] (2; CAS), Melbourne [July] (1; CAS), Schafer State Park [Aug.] (2; RTBe); Island Co., Whidbey Island (Coupeville, Saratoga Beach) [June-July] (2; UWBM); Jefferson Co., Clearwater (1 mi. s.) [June] (3; CDA), Port Townsend [July] (1; MCZ); King Co., Auburn [Aug.] (4; UWBM), Bellevue [July] (1; UWBM), Carnation (and at Snoqualmie River) [May] (29; LRus, UWBM), Cedar Mountain [May, July] (69; UWBM), Cedar River [Mar., May] (3; UWBM), Fall City (Snoqualmie River) [Sept.] (10; UWBM), Green River (and at Green River Gorge) [Apr.-May, Aug.] (11; UWBM), Issaquah (and 6 mi. e.) [June] (4; ALar, LRus), Maple Valley (Cedar River) [May] (5; UWBM), North Bend (and Snoqualmie River at Maloney's Grove) [May-Sept.] (36; FMNH, ICCM, MCZ, SDSU, UIMI, UWBM), Renton (Cedar River) [May-June, Sept.] (74; UWBM), Seattle (and Carkeet Park, Golden Gardens, Woodland Park) [Apr.-Aug., Oct.] (63; CAS, DHKa, FMNH, KSUC, USNM, UWBM, UWEM, WSU), Snoqualmie [May] (1; UWBM), Snoqualmie River Snoqualmie Falls) [Apr.-May, July-Sept.] (17; SDSU, UWBM), Tokul [Aug.] (1; UWBM); Kitsap Co., Bainbridge Island [Oct.] (2; CAS), Gilberton [June] (1; UWBM); Kittitas Co., Ellensburg [May] (2; UWBM); Klickitat Co., Rock Creek (15.6 mi. e. of Goldendale [430m]) [May] (93; DHKa), Spearfish [June] (2; FMNH), Spring Creek (10 mi. sw. of Bickelton [1010m]) [May] (108; DHKa), White Salmon [June] (1; UWBM); Lewis Co., Carlson (8.4 mi. s.

at East Fork Tilton [350m]) [July] (31; DHKa), Chehalis [May, Aug.] (5; CAS, UWBM), Cinebar [June] (1; CDA), Curtis (1 mi. n. at Chehalis River [140m]) [May] (5; DHKa), Newaukum River [Aug.] (2; UWBM), Pe Ell (Chehalis River [180m]) [May] (6; DHKa), Packwood (3.0 mi. ne. at Lake Creek [370m]) [July] (1; DHKa), Rainbow Falls State Park [Aug.] (6; CAS), Toledo (1 mi. s. at Salmon Creek [90m]) [May] (7; DHKa); Mason Co., Harstine Island [Sept.] (1; MSU), Skokomish River [May] (1; USNM); Olympic National Park, Hoh River (at Hoh River Campground, at Jackson Campground) [July-Aug.] (4; FMNH, ROM); Pacific Co., Bay Center [Aug.] (6; UWBM), Long Beach [July] (1; UWBM), Nasel River [June] (4; UWBM), Seaview [July] (1; UWBM), Trap Creek [July] (1; CAS); Pierce Co., Ashford (4 mi. e. on Nisqually River at Goat Creek [590m]) [July] (2; DHKa), Elbe (Nisqually River [400m]) [July-Aug.] (137; DHKa), Electron [May] (2; UWBM), Nisqually River [Mar.] (7; GRNo, LACM), South Prairie [Oct.] (5; FMNH); Skamania Co., Carson (8 mi. n. at Wind River [340m]) [May] (1; DHKa), Columbia River (15 mi. w. of Underwood [10m]) [May] (13; DHKa), North Bonneville (1 mi. w. at Hamilton Creek [50m]) [May] (29; DHKa); Snohomish Co., Arlington (North Fork Stillaguamish River) [Aug.] (12; UWBM, WSU), Cicero (North Fork Stillaguamish River) [Aug.] (1; UWBM), Lake Stevens [May] (1; UWBM), Monroe [July] (2; CAS), North Fork Stillaguamish River [May] (1; UWBM), Stillaguamish River [Mar.] (1; UWBM), Sultan [Apr.] (2; UWBM); Spokane Co., Spokane [Aug.] (2; LACM); Thurston Co., Deschutes River [May] (3; UWBM), Olympia (and Madrona Beach) [May-July] (12; MCZ, UWBM), Tenino (6; USNM); Walla Walla Co., Coppei [May] (7; ICCM, MCZ, UIMI), Kooskooskie [Apr., June, Aug.] (19; JSch, PUCA, UCD, UWBM), Snake River (at Columbia River) [Aug.] (2; CAS), Touchet

River (near Waitsburg) [July] (5; DJLa), Walla Walla (and Mill Creek, 2 mi. s. at Walla Walla River [320m]) [Apr.-Sept.] (81; CAS, DHKa, MCZ, NMDo, OSUO, PURC, UIMI, USNM, UWBM, WSU), Wallula [Apr.] (1; UIMI); Whatcom Co., Lynden [Mar.-Apr., June, Sept.] (13; LRus); Whitman Co., Almota (and Smockle Creek) [Mar.-May, Aug.] (40; CAS, MCZ, UIMI, UWBM, WSU), Palouse [Aug.-Sept.] (5; UWBM, WSU), Pullman [Apr.-July, Sept.-Oct.] (58; CAS, FMNH, ICCM, NMDo, UWBM, WSU), Snake River [June] (2; UWBM), Wawawai (and 0.2 mi. ne. in Wawawai Canyon [340m], 2.8 mi. nw. on Snake River [300m]) [Mar.-May, July-Aug., Sept.] (97; CAS, DHKa, DJLa, FMNH, MCZ, PURC, USNM, UWBM, WSU), Wilma [Apr.-May] (4; FMNH, PURC, UWBM).

State Unknown. Service Creek [Aug.] (1; CAS), Shadow Lake [May] (2; UWBM), Snake River [Oct.] (1; WSU).

Doubtful Records. UNITED STATES OF AMERICA, COLORADO: Garfield Co., Glenwood Springs [July] (2; ALar, DBUM).

No Data. (5; INHS, MCZ, USNM).

Nebria fragilis Casey

Map: Figure 394

Nebria fragilis fragilis Casey

Specimens examined: 390 (251♂, 139♀)

UNITED STATES OF AMERICA

UTAH: (1; ANSP); Salt Lake Co., Alta [June] (9; ANSP, USNM); Sanpete Co., Ephraim Creek ([2900m]) [Aug.] (1; USNM); Utah Co., American Fork Canyon ([2900m], 5.1 mi. e. of Highway 146 [1860m], American Fork River

at Little Mill Campground [1830m]) [June ug.] (151; ANSP, DHKa, MCZ, USNM), Aspen Grove [Aug.] (1; CAS), Mount Timpanogos [July] (37; CAS), North Fork Provo Canyon (1.5 mi. n. of Highway 189 on North Fork Provo River [1680m], Sundance Ski Area [1890m]) [Aug.] (115; DHKa, FMNH, USNM), Provo Canyon [July] (1; CAS), South Fork American Fork Canyon (6.4 mi. e. of Highway 146 [1980m]) [Aug.] (76; DHKa).

Nebria fragilis teewinot Kavanaugh, NEW SUBSPECIES

Specimens examined: 379 (220♂, 159♀)

UNITED STATES OF AMERICA

WYOMING: Grand Teton National Park, Mica Lake ([2970m]) [July] (1; DHKa), Mount Teewinot (southeast slope [2160m-2740m]) [Aug.] (79; DHKa), South Fork Cascade Canyon ([3080m]) [July] (1; SJSC), South Fork Garnet Canyon ([2820m]) [July] (1; SJSC), Timberline Lake area [July] (1; DHKa); Lincoln Co., White Creek (20 mi. se. of Alpine Junction [1950m-2190m]) [Aug.] (40; DHKa), Wolf Creek (16.1 mi. sw. of Hoback Junction [1770m-1780m]) [July-Aug.] (137; DHKa); Sublette Co., Green River Lakes (west shores [2440m-2590m]) [July] (53; DHKa), Hoback River (14 mi. sw. of Highway 187/189 [2440m]) [July] (11; DHKa); Teton Co., Alaska Basin (near Sunset Lake [2940m]) [July] (1; SJSC), Gran e Creek (at Granite Falls [2160m]) [July] (37; DHKa), Togwotee Pass ([2960m] and 3.7 mi. wnw. at Blackrock Creek [2770m]) [Aug.] (2 DHKa, KUSM).

Nebria frigida R. F. Sahlberg

Map: Figure 389

Specimens examined: 295 (173♂, 122♀)

CANADA

BRITISH COLUMBIA: Sikanni Chief River (Alaska Highway mi. 160) [June] (2; UASM), Swift River (Alaska Highway mi. 733.3) [June] (3; UASM). NORTHWEST TERRITORIES: Aklavik [June-Aug.] (17; CAS, DHKa), Anderson River Delta (Eagle Perch Island) [July] (2; UASM), Fort McPherson [June-July, Sept.] (3; CNC, DHKa), Kittigazuit [July] (1; CNC), Mackenzie River Delta [June] (1; AMNH), Norman Wells [Aug.] (1; DHKa), Reindeer Depot [July] (2; CNC). YUKON TERRITORY: District of McKenzie, Dawson [June] (1; CAS), Dempster Highway (mi. 35 [880m]) [July] (14; CNC), Firth River [Aug.] (1; CNC), Morley River (Alaska Highway mi. 777) [Aug.] (1; DHKa), North Fork Crossing ([1070m]) [June-July] (4; CNC), North Fork Klondike River (1; CNC), Rampart House [May-June] (3; CNC, USNM), Snag [July] (1; CNC), Swift River (Alaska Highway mi. 733) [Aug.] (1; DHKa).

UNITED STATES OF AMERICA

ALASKA: [July] (19; CAS, DHKa, USNM, UWBM); Mount McKinley National Park [July-Aug.] (4; CUIC, MCZ, USNM, UWBM), Savage River (1.2 mi. n. of Denali Highway [730m-760m]) [July] (9; DHKa); Other localities, Anvik (Yukon River) (1; USNM), Big Gerstle River (Alaska Highway mi. 1393) [June] (1; MCZ), Black Rapids Glacier (Richardson Highway mi. 227) [July] (5; USNM), Chatanika River (at Chatanika River Campground [240m]) [July] (20; DHKa), Chena River (2 mi. w. of Fairbanks at Chena River Campground [140m]) [July] (6; DHKa), Chitina Glacier (30 mi. n. of Mount St. Elias) [May-June] (1; USNM), Deering [Aug.-Sept.] (2; JVMa), Delta River [Aug.] (1; JVMa), Eagle Summit (Steese Highway mi.

108 to 109 [1100m-1190m]) [July] (28; DHKa, MCZ, UASM), Fairbanks (6; UASM), Fort Yukon (1; UWBM), Holy Cross (8 mi. n. at Yukon River) [July] (1; USNM), King Salmon (Naknek River) [July] (8; CNC), Knik River (at Glenn Highway) [July] (1; UASM), Kugruk River (90 mi. n. of Nome) [July] (2; CAS), Kuzitrin River (at Copper Creek) [July] (2; JVMa), Little Nelchina River (Glenn Highway mi. 138) [July] (2; MCZ, UASM), Pavlof Volcano [Sept.] (6; CAS), Nome [June-Aug.] (60; CAS, ICCM, INHS, JVMa, MCZ, USNM, UWBM), Nunivak Island [Aug.] (1; USNM), Paimuit (30 mi. wsw. at Yukon River) [July] (1; USNM), Point Barrow [June] (3; UMMZ), Ptarmigan Creek (Steese Highway mi. 101.1 [730m]) [July] (4; DHKa), St. Michael [July] (4; CAS, MCZ), Security Cove (Kuskokwim River) [July] (1; USNM), Seward [June] (1; ICCM), Solomon River (37 mi. e. of Nome) [Aug.] (1; MCZ), Teller [June, Aug.] (6; CAS, USNM), Tolstoi [July] (1; USNM), Ukak [July] (1; PURC); Aleutian Islands, Unalaska Island (Unalaska) [July] (2; ICCM); Pribilof Islands, St. George Island [Ju] (1; ICCM).

Nebria gebleri Dejean

Map: Figure 402

Nebria gebleri gebleri Dejean

Specimens examined: 2277 (1179♂, 10 ♀

CANADA

ALBERTA: [July] (2: BFCa, UASM); Banff National Park, Banff [May-Sept.] (107; AMNH, BFCa, CAS, CNC, CUIC, DBUM, DHKa, KSUC, KUSM, MCZ, UASM, UCD, USNM, UWBM), Bow River ([1830m]) [July] (5; CNC), Cascade

River (near Banff) [Aug.] (2; CAS, MCZ), Eisenhower Junction ([1430m]) [July] (1; CNC), Johnson Creek Trail (at Johnson Creek Campground) [July 9; ROM), Lake Agnes [Aug.] (1; CUIC), Lake Louise [June-Sept.] (40; AMNH, CAS, CUIC, MCZ, SJSC, UASM, UBC, USNM), Lake Minnewanka [Aug.-Sept.] (6; AMNH, DJLa, UASM), Moraine Lake [July-Aug.] (12; CAS, CNC, UASM), Ptarmigan Lake ([2290m]) [July] (2; CNC), Waterfowl Lake Campground [Aug.] (1; SJSC); Jasper National Park, Amethyst Lake Trail ([1710m]) [July] (5; DHKa), Astoria River ([1770m]) [Aug.] (7; DJLa, GRNo, USNM), Geikie Road (Miette River) [Aug.] (1; CNC), Geraldine Lakes [July] (7; USNM), Jasper [Aug.-Sept.] (3; MCZ, UBC), Miette Hot Springs (Sulphur Creek) [July-Aug.] (26; DHKa, MCZ), Miette River (at Meadow Creek [1100m]) [July] (28; DHKa), Mount Edith Cavell ([1370m-1770m]) [Sept.] (13; DHKa, UAFA), Portal Creek ([1190m]) [Aug.] (1; DJLa), Pyramid Lake [Sept.] (2; RTBe); Waterton Lakes National Park, Cameron Lake area ([1660m-1980m]) [July] (6; UASM), Red Rock Canyon [July-Aug.] (11; CAS, DJLa, UWBM), Twin Lakes ([1120m]) [July] (4; DJLa), Waterton Park [July-Aug.] (34; CAS, CDA, CNC, LACM, LEMC, MCZ, UASM, UBC, UCD); Other localities, Bellevue (2 mi. w. at Gold Creek [1370m]) [July] (4; DHKa), Belly River [July] (1; CAS), Blakiston Creek [July] (21; UASM), Cadomin [June] (1; UASM), Calgary [June] (3; BFCa), Cardinal River [May] (2; DHKa), Cline River (at Highway 11) [Aug.] (2; DHKa), Crowsnest Pass [Aug.] (3; CNC, UASM), Entrance (20 mi. nnw. on Grande Cache Road at Wildhay River [1310m]) [June] (10; DHKa), Fort Macleod [Aug.] (1; USNM), Gap [Aug.] (1; CAS), Gorge Creek [July] (7; UASM), Happy Valley [May, Aug.] (4; AMNH, UASM, USNM), Highwood Pass ([2380m]) [July] (6; CNC), Jumpingpound Creek (20 mi. sw. of Highway 1) [June] (7; DHKa), Lusk Creek [July] (15; CNC), Marmot

Creek Basin ([1980m]) [July] (7; CNC), Mill Creek Ranger Station [Aug.] (2; CAS, UBC), Nordegg (South Creek Bridge) [July] (8; DJLa, UASM), North Saskatchewan River (near Nordegg) [July] (3; RFre), Pincher Creek ([1620m]) [July] (5; DJLa), Sheep River (4.5 mi. above Gorge Creek) [Aug.] (8; DHKa), Spionkop Creek ([1740m]) [July] (3; DJLa), Spray Lakes [July] (3; JVMa), West Branch Castle River ([1340m]) [Aug.] (5; DJLa), Willow Creek [Aug.] (1; CAS). BRITISH COLUMBIA: (1; MCZ); Glacier National Park [July] (8; ROM), Glacier [June-Aug.] (25; ANSP, BFCa, CAS, USNM), Illecillewaet Campground [July] (12; DHKa, GRNo, USNM), Loop Creek [June] (1; UASM), Rogers Pass ([1370m]) [Aug.] (2; CUIC); Kootenay National Park [July-Aug.] (9; CAS, CNC, UBC), Kimpton Creek ([1220m]) [July] (2; CNC), Kindersley Pass ([2130m]) [July] (2; CNC), Marble Canyon [July-Aug.] (2; CAS), McLeod Meadows [July] (1; CNC), Sinclair Creek ([1830m]) [June-Aug.] (59; CAS, CNC, ISUI, KSUC, MCZ, ROM, UASM, UBC), Vermillion Creek [July] (1; CNC); Mount Revelstoke National Park ([1370m]) [July-Aug.] (9; BFCa, CNC); Yoho National Park [July-Aug.] (5; BFCa, UWBM), Amiskwi River (and at Amiskwi Falls [1830m]) [Aug.] (13; CNC), Field (Kicking Horse River) [July-Aug.] (5; CAS, UBC, USNM), Hector [June] (1; USNM), Kicking Horse Pass (1; ROM), Kicking Horse River (at Amiskwi River) [Aug.] (1; DHKa), Lake Oesa ([2130m]) [July] (6; CNC), Lake O'Hara [July] (2; CAS), Otterhead River ([1680m]) [Aug.-Sept.] (33; CNC, DHKa), Wapta Lake ([1580m]) [July] (1; CAS), Yoho River (4 to 12 mi. ne. of Field, at Takkakaw Falls [1520m]) [July-Aug.] (39; DHKa, MCZ, UASM); Other localities, Barkerville (Grouse Creek) [Aug.-Sept.] (8; UBC), Big Boulder Creek (e. of Pine Pass) [June] (4; CNC, UASM), Birch Creek [July] (1; CAS), Bridesville [May] (1; CAS), Cabin Creek ([1520m])

[July-Aug.] (24; CNC, UASM, UBC), Cherryville [July] (3; CAS, UBC), Cottonwood [July] (1; CAS), Couldrey Creek ([1520m]) [Aug.] (1; UBC), Creston (8 mi. w.) [June] (4; CNC), Crowsnest Pass (2 mi. w. [1280m], 5 mi. w. at Elk River [1220m]) [July] (21; DHKa), Duck Creek (near Wyndel) [June] (1; UASM), Elk Creek (east of Fernie) [July] (1; UASM), Erickson [Aug.] (3; UBC), Fernie (Coal Creek) [July-Aug.] (19; BFCa, CAS, CUIC, UBC), Flathead [June] (2; UBC), Glenora (1; USNM), Golden (9 mi. e. at Kicking Horse River [1160m]) [June, Aug.] (4; DHKa, USNM), Grave Creek (15 mi. n. of Michel [1740m]) [Aug.] (7; UBC), Invermere [July] (2; CNC), Kalum Lake (13 mi. n. of Terrace) [June] (1; UASM), Kaslo [June] (13; USNM), Kay Falls [July] (18; CAS, CNC, DBUM, ISUI, UBC), Kitchener [Aug.] (8; UBC), Kootenay River (at Highway 3) [Aug.] (4; UASM), Moberly Lake Provincial Park [July] (7; DHKa), Mount Robson Provincial Park (Mount Robson [1830m]) [July] (23; ANSP, UASM), Muncho Lake Provincial Park (Peterson Creek at Alaska Highway mi. 445) [July-Aug.] (21; CNC, UASM), Natal (at Hope Trail) [June] (1; RFre), Osoyoos (1; MCZ), Price Creek (near Kitwanga) [June] (1; UASM), Prince Rupert [July] (1; CUIC), Radium Hot Springs [July-Aug.] (7; CAS, CNC, UBC), Retallack [Aug.] (3; BFCa), Rock Creek [July] (5; CAS, MSU), Rossland (2 mi. w.) [May] (5; CNC, UASM), Sanca [Sept.] (3; UBC), Shuswap Falls [June] (1; DBUM), Slide Mountain (10 mi. e. of Barkerville [1370m]) [June] (2; CNC), Slocan [Aug.] (1; BFCa), Stanley [July] (23; CAS, CNC, FMNH, ISUI, MSU, UBC, UMMZ), Summit Creek (near Creston) [Aug.] (1; UASM), Summit Lake (Alaska Highway mi. 392 [1520m]) [June-July] (7; CNC), Swift River (Alaska Highway mi. 733.3) [Aug.] (1; LRus), Tetsa River (Alaska Highway mi. 376 and mi. 390) [Aug.] (3; LRus, MSU), Trinity Valley [June-July]

(6; ALar, DBUM, FMNH), Two Sisters Mountain (15 mi. e. of Barkerville [1680m]) [June] (3; CNC), Tyee (2.6 mi. nw.) [June] (1; UASM), Wyndel [July] (4; BFCa, CNC, UBC). YUKON TERRITORY: Rancheria (Swift River) [Aug.] (30; ALar, CNC, UASM), Swift River (Alaska Highway mi. 733) [June, Aug.] (6; CNC, DHKa).

UNITED STATES OF AMERICA

ALASKA: Baranof Island (Sitka) (1; MHNP), Haines (8 mi. nw., 13 to 14 mi. n.) [June-July] (5; CNC, MCZ), Thane [July] (1; UWBM). IDAHO: [May] (1; UIMI); Adams Co., Bear [July] (1; BFCa), Huntley Gulch (2 mi. nne. of Cuprum [1250m]) [Aug.] (3; DHKa), Indian Creek (1 mi. nne. of Cuprum [1370m]) [Aug.] (3; DHKa), New Meadows [June] (14; UIMI, USNM, UWBM); Blaine Co., Cherry Creek (0.1 mi. nw. of Highway 93 [2230m]) [Aug.] (9; DHKa), Dollarhide Summit (2 mi. e. at North Fork Warm Springs Creek [2350m-2410m]) [Aug.] (37; DHKa), Galena Summit (2.4 mi. ne. [2320m]) [Aug.] (15; DHKa), Hyndman Creek [July] (24; FMNH, UWBM), Ketchum (10 mi. w. at North Fork Warm Springs Creek) [Aug.] (4; DHKa), Petit Lake Creek (at Twin Lakes Trail [2130m-2440m]) [Aug.] (30; DHKa); Boise Co., Crouch (South Fork Payette River [910m]) [Aug.] (6; RTBe), Lowman [June-July] (3; BFCa, RTBe); Bonner Co., Sandpoint [July] (1; NMDo), Soldier Creek (at Priest Lake) [July] (4; CAS); Camas Co., Carrie Creek (32 mi. [2440m] and 36 mi. wsw. of Ketchum) [Aug.] (35; DHKa), Skeleton Creek (14 mi. e. of Featherville on South Fork Boise River [1550m]) [Aug.] (21; DHKa), South Fork Boise River (34 mi. e. of Featherville [1830m] at Bear Creek) [Aug.] (42; DHKa); Custer Co., Bayhorse Creek (7 mi. nw. of Highway 93 [2440m]) [Aug.] (18; DHKa), Fourth of July Creek (3 mi. e. of Highway 93 [2230m]) [Aug.] (67; DHKa), Lower Stanley

(Salmon River [1800m]) [Aug.] (1; DHKa), Trail Creek Summit (2 mi. e. at Summit Creek [2320m]) [Aug.] (17; DHKa); Elmore Co., Rocky Bar ([1830m]) [June] (4; UWBM); Idaho Co., Orogrande Creek [Aug.] (1; UWBM); Lemhi Co., Salmon [July] (1; EMUS); Shoshone Co., Burke [June, Aug.] (2; UIMI), Wardner (1; CAS); Valley Co., Dagger Falls [July] (2; BFCa), Middle Fork Salmon River (near Boundary Creek) [Aug.] (11; RTBe); County unknown, Twin Creek Forest Camp ([1520m])[July] (50; FMNH, UWBM). MONTANA: (2; CAS, FMNH); Cascade Co., Belt Creek (1 mi. [1400m] and 17 mi. [2100m] s. of Monarch) [July] (82; DHKa), Jefferson Creek (2 mi. e. of Highway 82 [1870m]) [July] (9; DHKa); Chouteau Co., Briggs Creek (at North Fork Highwood Creek [1370m]) [July] (32; DHKa), Highwood Creek (26 mi. ne. of Belt [1310m]) [July] (2; DHKa), South Fork Highwood Creek (at Big Coulee [1490m]) [July] (29; DHKa); Flathead Co., Hungry Horse Reservoir [July] (4; LRus); Glacier National Park [June-Aug.] (41; CAS, CUIC, DHKa, SJSC, USNM, UWBM), Baring Creek [Aug.] (9; UWBM), Canyon Creek (at Lake Sherburne) [July] (6; CAS), Fish Creek Campground ([1280m]) [July] (11; LRus), Going-to-the-Sun Chalet [Aug.] (24; UWBM), Grinnell Glacier [Aug.] (1; SJSC), Hidden Pass ([2130m]) [Aug.] (1; DHKa), Lake McDonald (and at Sprague Creek) [June-Aug.] (7; CAS, RTBe, SJSC, UWBM), Logan Pass (Granite Park [1520m]) [July] (2; LRus), Many Glacier ([1680m]) [July] (3; LRus), Mount Reynolds area ([2590m]) [Aug.] (1; SJSC), Piegan Pass ([2410m]) [Aug.] (2; SJSC), St. Mary Lake [July] (3; CAS, USNM), St. Mary River [Aug.] (1; CAS), Sperry Chalets [July] (1; SJSC), Swiftcurrent Creek [July] (13; CAS, SJSC), Swiftcurrent Pass ([2160m]) [Aug.] (6; SJSC), Two Medicine Lake [July] (4; CAS), Weeping Wall [Aug.] (2; DHKa, USNM), Wilbur Creek [July] (5; SJSC); Judith Basin Co., Arrow Creek ([1520m]) [July] (11; DHKa), Drywolf Creek (at

Drywolf Campground [1840m]) [July] (22; DHKa); Lewis and Clark Co., Wolf Creek area [June] (1; UASM); Meagher Co., White Sulphur Springs [Sept.] (3; CAS, CNC); Mineral Co., Lookout Pass ([1280m]) [July] (4; LRus); Missoula Co., Lolo Pass (east side [1580m]) [Aug.] (1; ROM), Seeley Lake (16 mi. w. [1070m]) [July] (2; LRus); Silver Bow Co., Butte (3; ICCM); Sweetgrass Co., Big Timber Creek ([1830m] and at Halfmoon Campground [2230m-2290m]) [July] (150; DHKa); County unknown, Bitterroot Mountains (22; AMNH, CAS, FMNH, KSUC, MCZ, USNM). OREGON: Baker Co., Anthony Lake ([2130m]) [May-June] (2; FMNH, UWBM), Antone Creek ([1910m-2100m]) [May] (26; DHKa), Baker [June] (1; NMDo), Cornucopia [June-July] (14; BFCa, UWBM), East Fork Eagle Creek [July] (3; UWBM), Pine Creek (10 mi. nw. of Baker [1120m]) [May-July, Sept.] (130; DHKa, FMNH, JSch, MSU, NMDo, ODA, UCD, UCR, UWBM), Spring Creek [July, Sept.] (3; JSch); Union Co., Elgin (and 9 mi. nw. at Little Phillips Creek [1300m]) [May, Aug.] (5; DHKa, UWBM), Langdon Lake area (southeast of summit) [Aug.] (1; UWBM); Wallowa Co., [Aug.] (2; JSch), Imnaha River (at Indian Crossing) [Aug.] (2; MSU, OSUO), Lostline River ([1310m] and at French Campground, Lake Creek Campground, 16 mi. s. of Lostline, Two Pan Campground [1710m-1980m]) [July-Aug.] (84; DHKa, UIMI, USNM, UWBM), Lost Lake [Aug.] (1; DHKa), Wallowa Lake ([1490m-1680m]) [May-Sept.] (110; CAS, DHKa, MSU, NMDo, OSUO, UCR, UIMI, UWBM), Wallowa River [Aug.] (1; UWBM). WASHINGTON: Columbia Co., Dayton [July] (9; CAS, JSch, WSU); Walla Walla Co., Walla Walla [May, July] (3; UIMI, USNM, UWBM); County unknown, Blue Mountains ([910m]) [July-Aug.] (9; CAS, MCZ, USNM, WSU).

Doubtful Records. CANADA, ALBERTA: Jenner (1; CAS). UNITED STATES OF AMERICA, IDAHO: Twin Falls [June] (1; UIMI). ILLINOIS: Alton

[July] (1; UMMZ). UTAH: Provo Canyon [July] (1; CDA).

Nebria gebleri cascadensis Kavanaugh, NEW SUBSPECIES

Specimens examined: 1690 (944♂, 746♀)

CANADA

BRITISH COLUMBIA: Copper Mountain [Aug.] (4; UCB), Cultus Lake Provincial Park (Entrance Bay Campground) [June] (4; ROM), Garibaldi Provincial Park (Diamond Head Trail [1070m]) [July] (3; CNC), Hope [June-July] (8; BFCa, INHS), Hunter Creek (at Restmore Lodge) [July] (3; CAS), Manning Provincial Park (Blackwell Peak [910m], Nicomen Ridge, Skagit River) [May-Sept.] (34; CAS, CNC, KUSM, MCZ, MSU, RTBe, UBC, UMMZ), Midday Valley (near Merritt) [Aug.] (1; INHS), Nicolum River (at Hope Trail) [July] (2; UBC), North Bend [July] (19; USNM), Skagit River (at Hope Trail [760m]) [July] (3; UBC), Snass Creek (at Warburton Trail [760m]) [July] (5; UBC), Spious Creek [May] (1; CAS), Vancouver (2; ANSP), Whipsaw Creek (at Hope Trail [1220m]) [May, July] (4; UASM, UBC), Vancouver Island, Port Alberni (Robertson Creek Spawning Channel) [June] (1; ROM).

UNITED STATES OF AMERICA

OREGON: Clackamas Co., Austin Hot Springs [July] (1; OSUO), Brightwood (Salmon River) [July] (8; DHKa), Mount Hood (south slope below Timberline Lodge [1190m]) [Aug.] (2; DHKa), Rhododendron ([490m] and 1 mi. se. at Zig Zag River [600m]) [July-Aug.] (55; CAS, DHKa, SJSC, UWBM); Deschutes Co., Elk Lake [July] (1; UWBM), Upper Deschutes River [May] (1; UWBM); Hood River Co., Hood River [May, July] (8; CAS, USNM), Mount Hood (Cloud Cap, Hood River Meadows Ski Area [1710m], Sand Creek,

Tillie Jane Creek, Umbrella Falls) [June-Sept.] (70; CAS, DHKa, MCZ, NMDo, ODA, UCR, UIMI, UWBM); Marion Co., Detroit ([460m] and 5 mi. n.) [July-Aug.] (3; LRus, UWBM); Multnomah Co., Horsetail Falls ([120m]) [May-July] (87; DHKa, JSch, ODA, OSUO). WASHINGTON: (32; ANSP, CAS, INHS, MCZ, OSUC, USNM); Chelan Co., Fish Lake [July] (1; UWBM), Leavenworth [July] (8; ANSP, KUSM, MCZ, SDSU, USNM), Tumwater Canyon ([610m]) [May] (1; LRus); Cowlitz Co., Ariel [May] (1; UWBM), Cougar [Sept.] (2; OSUO), Hoffstadt Creek (at Toutle River) [July] (2; MSU, OSUO), North Fork Toutle River (14 mi. e. of Toutle [300m]) [Aug.] (33; CAS, DHKa), Toutle River [July] (11; UWBM); King Co., Baring [July] (2; FMNH), Green River Gorge (Green River) [May, Aug.] (5; UWBM), Greenwater River (at Greenwater Campground) [June] (1; UWBM), North Bend [July] (17; CAS, CUIC, MCZ), Renton (Cedar River) [May] (1; UWBM), Skykomish [July, Sept.] (2; UASM, UWBM), Snoqualmie [June] (4; UIMI), Stevens Pass (and 4 mi. w.) [June, Aug.] (5; LRus, UASM), Wellington [July] (10; CAS, MCZ, USNM, UWBM), White River (5 mi. w. of Greenwater [1490m], Slippery Creek) [July-Aug.] (42; DHKa, UWBM); Kittitas Co., Blewett Pass (Niger Creek) [July] (2; USNM), Easton (22; CAS, INHS, MCZ, USNM), Snoqualmie Pass [July] (4; CAS), Teanaway Ridge ([910m]) [July] (10; LRus); Klickitat Co., Klickitat Valley [July] (1; MCZ); Lewis Co., Lake Creek (3 mi. ne. of Packwood [370m]) [July] (5; DHKa), White Pass (and 1.5 mi. w. at Millridge Creek [1280m]) [June-July] (42; DHKa, SJSC, USNM); Mount Rainier National Park ([760m-1830m]) [June-Sept.] (30; ANSP, CAS, CUIC, KSUC, MCZ, OSUO, SJSC, UIMI, UWBM), Bear Flat ([1520m-1830m]) [July] (1; CAS), Carbon River [June] (4; UWBM), Cayuse Pass [1400m] [June] (4; USNM), Fish Creek (at West End Road) [June] (1; ROM), Fryingpan Creek ([1160m-1190m]) [July-Aug.]

(38; CNC, DHKa, SJSC), Horse Creek (near Longmire) [July] (15; CAS), Ipsut Creek Campground [Aug.] (1; OSUO), Kautz Creek (at Nisqually River) [Sept.] (2; UWBM), Longmire ([760m]) [June-Aug.] (25; CAS, SJSC, USNM), Narada Falls ([1370m-1460m]) [July-Aug.] (118: DHKa, USNM, UWBM), Nisqually River (0.1 mi. above Paradise River [980m], toe of Nisqually Glacier [1220m-1520m]) [July-Aug.] (7; AMNH, CAS, CUIC, DHKa, MCZ), North Fork Puyallup River (below toe of Puyallup Glacier [1100m-1650m]) [July-Aug.] (22; CNC, DHKa, USNM), Ohanapecosh [June, Aug.] (18; DJLa, LRus, SJSC, UIMI, USNM), Paradise area (below Sluskin Falls, Paradise Park [1220m-1830m], Paradise River [1440m-1680m], Paradise Valley) [June-Sept.] (88; CAS, CUIC, DHKa, FMNH, MCZ, USNM, UWBM), St. Andrews Creek (at West End Road [1160m]) [Aug.] (5; DHKa), Silver Creek [Aug.] (10; UWBM), Sluskin Falls [July] (8; UWBM), Stevens Creek ([1190m-1220m]) [June-July] (4; DHKa, USNM), Sunbeam Falls ([1220m]) [May] (1; CNC), Sunrise area [July] (2; LRus), Tahoma Creek ([910m]) [July] (1; USNM), West End Road [July] (1; CAS), White River ([1190m] and at White River Campground [1520m]) [July-Aug.] (12; FMNH, SJSC, USNM, UWBM), Van Trump Creek (above Christine Falls [1220m-1280m]) [July-Aug.] (62; DHKa, UWBM); Pierce Co., Goat Creek (at Nisqually River [610m]) [July] (130; DHKa), Fairfax [Oct.] (1; FMNH), Poch Creek (at Carbon River) [Aug.] (5; UCB, UWBM), Tenas Creek (5 mi. e. of Ashford [610m]) [July] (1; DHKa), White River (at Silver Springs Campground [790m]) [June, Aug.] (15; DHKa, USNM); Skamania Co., Carson [Aug.] (6; UIMI), Mount St. Helens (Maratta Creek) [July] (3; DHKa), North Fork Cipsus River [June] (14; UWBM), North Fork Toutle River (at Spirit Lake Lodge [940m]) [Aug.] (31; CAS, DHKa), Spirit Lake [July, Sept.] (3; DHKa, UWBM), Stabler [June] (1; OSUO), Wind River

(8 mi. n. of Carson [340m]) [May, July] (14; DHKa); Snohomish Co., Darrington (Clear Creek Falls) [May] (5; UWBM), Glacier Peak [July-Aug.] (2; CAS, UWBM); Whatcom Co., Glacier (North Fork Nooksack River) [July] (13; CAS, LRus), Lookout Creek (4 mi. e. of Glacier [380m]) [Aug.] (18; CAS, DHKa), Mount Baker (Austin Pass [1520m], Bagley Creek [670m], Razor Hone Creek [1680m]) [July-Sept.] (124; CAS, DHKa, LRus, UCR, UWBM), North Fork Nooksack River (4 mi. e. of Glacier [380m], Silver Fir Campground [610m]) [Aug.] (3; CAS, DHKa), Shuksan ([760m]) [Aug.] (3; LRus), Shuksan Creek [Aug.] (12; UWBM), Skagit River (at Newhalem) [July] (2; UWBM); Yakima Co., American River (and at Hell's Crossing [1040m]) [July-Aug.] (17; DHKa, ICCM, KUSM, MCZ, UIMI, UMMZ, UWBM), Bumping River (0.8 mi. sw. of Highway 410 [1010m]) [July-Sept.] (92; CAS, DHKa, ICCM, MCZ, MSU, PURC, UAFA, USNM, WSU), Dog Lake ([1310m]) [July] (25; DHKa), Mount Adams (Bird Creek [910m-2440m], Chaparral Creek [880m], Klickitat River) [June-July, Sept.] (82; AMNH, ANSP, CAS, CUIC, FMNH, ICCM, MCZ, UASM, UIMI, USNM, UWBM, WSU), Naches River [July] (2; USNM), Tampico [July] (1; USNM), Tieton Dam [Aug.] (2; AMNH, WSU), Wildcat Creek (at Tieton River [880m]) [July] (3; DHKa, OSUO), Yakima (11; JSch, MCZ, USNM, WSU), Yakima Indian Reservation ([910m]) [July] (1; CAS).

Doubtful Records. UNITED STATES OF AMERICA, COLORADO: Leavenworth Valley (1; ANSP). WASHINGTON: Pullman (1; ICCM).

No Data. (4; CDA, MCZ, MSU, UWBM).

Ne[illegible]a gebleri rathvoni LeConte, NEW STATUS

Specimens examined: 954 (524♂, 430♀)

UNITED STATES OF AMERICA

CALIFORNIA: 2; KUSM); Alpine Co., Carson River [Apr.] (3; DJLa, USNM), East Fork Carson River (1.5 mi. se. of Markleeville [1680m]) [July] (6; DHKa), Loope Creek (5.4 mi. se. of Markleeville [1830m]) [July] (45; DHKa), Luther Pass [Aug.] (2; CAS), Markleeville (Markleeville Creek [1680m]) [July] (22; DHKa); El Dorado Co., (5; AMNH, CAS, USNM), Desolation Valley [Aug.] (8; CAS), Fallen Leaf Lake [July] (1; CAS), Kyburz (2 mi. e. on South Fork American River [1340m]) [July] (23; CAS, DHKa), Riverton (3 mi. w. on South Fork American River [910m]) [July] (6; CAS, DHKa), Strawberry Valley ([1830m]) [Aug.-Sept.] (76; ANSP, CAS, KSUC, MCZ, PADA, UMRM, USNM, UWBM), Tallac (5; CAS); Kings Canyon National Park, Bubbs Creek Canyon ([3200m]) [July] (10; CAS, UWBM), Rae Lake ([3200m]) [July] (3; CAS); Lassen Volcanic National Park [July] (1; CAS), Sulphur Works area (West Sulphur Creek [2130m]) [Aug.] (48; CAS, DHKa); Mariposa Co., [July] (2; FMNH); Mono Co., Robinson Creek Trail (above Twin Lakes [2286m]) [Aug.] (9; CAS), Twin Lakes [Aug.] (1; USNM); Nevada Co., [June] (59; ANSP, CAS, DBUM, DHKa, FMNH, MCZ, USNM), Donner Lake (2; CAS), Independence Lake ([2130m]) [Sept.] (4; CAS), Prosser Creek (1 mi. sw. of Hobart Mills [1770m]) [June-July] (10; CAS, CDA, DHKa, UCD), Truckee (Truckee River [1770m]) [July-Aug.] (19; CAS, DHKa, MCZ, USNM); Placer Co., Blackwood Creek [Aug.] (2; CAS), Deer Park Inn (Alpine Meadows Ski Area) [July] (1; UMRM), Tahoe City (3; KUSM, MCZ); Plumas Co., Greenhorn Creek (Highway 70/89 at Massack Rest Area[1140m]) [July] (45; CAS, DHKa), Harrison Flats [Aug.] (1; CDA); Sequoia National Park, Giant Forest ([2290m]) [June] (1; CAS), Marble Fork Kaweah River [Sept.] (1; KSUC), Rattlesnake Creek [Sept.] (2; CAS), Sillman Creek ([2130m]) [Sept.] (3;

CAS); Shasta Co., Hat Creek (Hat Creek [1400m]) [July] (2; CAS, UCD), Old Station (Hat Creek) [Aug.] (2; CAS, DHKa); Sierra Co., Yuba Pass (2 mi. e. on Big Canyon Creek [1830m]) [July] (3; CAS, DHKa); Tulare Co., ([2130m]) [Sept.] (1; OSUC), Franklin Creek ([2500m-2990m]) [July] (96; DHKa), Franklin Lakes ([3050m-3140m]) [July] (4; DHKa), Mineral King [Sept.] (10; CAS, CNC, INHS), Sawtooth ([3050m]) [Sept.] (4; MCZ, UMRM), Tar Gap Trail [Sept.] (5; CAS); Tuolumne Co., Clark Fork Stanislaus River [Aug.] (41; CAS); Yosemite National Park, Dana Fork Tuolumne River at John Muir Trail [2620m]) [Sept.] (1; DHKa), Illilouette Creek [July] (2; CAS), Merced River [June] (2; CAS); County unknown, Lake Tahoe [May, July] (21; USNM). NEVADA: (3; ANSP, MCZ); Washoe Co., Galena Creek (11 mi. w. of Highway 395 [1920m-2290m]) [July] (66; DHKa, NSDA), Mount Rose ([2440m]) [Aug.] (31; CAS), Third Creek (at Highway 267 [2210m]) [July] (218; DHKa).

No Data. (1; INHS).

Nebria gebleri siskiyouensis Kavanaugh, NEW SUBSPECIES

Specimens examined: 35 (20♂, 15♀).

UNITED STATES OF AMERICA

CALIFORNIA: Trinity Co., Boulder Creek (at Goldfield Campground [1070m]) [July] (2; CAS, DHKa), South Fork Salmon River (at Big Flat Campground [1490m]) [June-July] (30; CAS, DHKa, FMNH), Taylor Lake Road (branch of Taylor Creek [1750m]) [Aug.] (1; CAS). OREGON: Jackson Co., Little Applegate River ([700m]) [Aug.] (2; CAS, FMNH).

Nebria gebleri strawberriensis Kavanaugh, NEW SUBSPECIES

Specimens examined: 29 (22♂, 7♀)

UNITED STATES OF AMERICA

OREGON: Grant Co., Strawberry Creek ([17 m, May] (29; DHKa).

Nebria gouleti Kavanaugh, NEW SPECIES

Map: Figure 383

Specimens examined: 516 (228♂, 288♀)

UNITED STATES OF AMERICA

IDAHO: Adams Co., New Meadows ([1170m]) [June] (1; UIMI); Bonner Co., Sandpoint [Sept.] (1; CAS); Cl rwater Co., Canyon Ranger Station [Sept.] (1; UIMI); Custer Co., Lower Stanley (10 mi. e. on Salmon River [1800m]) [Aug.] (1; DHKa), Salmon River (at Bayhorse Creek [1620m]) [Aug.] (45; DHKa); Idaho Co., Fenn Ranger Station (Selway Fork Clearwater River) [Aug.] (3; UIMI), Lochsa River (at Canyon Creek [520m]) [July] (2; DHKa), Lowell (39 mi. ne. on Lochsa River [850m]) [July] (1; DHKa), Meadow Creek (1.5 mi. s. of Selway Falls) [Sept.] (1; CAS), Orogrande Creek [Aug.] (3; UWBM), Selway Falls [July] (1; UWBM); Kootenai Co., Coeur d'Alene [June-July] (5; CAS, MCZ, USNM), Hayden [Aug.] (9; AMNH, MCZ, UIMI, USNM); Latah Co., Kendrick [Sept.] (2; UIMI), Moscow (1; USNM); Lemhi Co., Salmon (and 21 mi. n.) [July-Aug.] (2; UASM, UIMI); Nez Perce Co., Lenore [May] (2; UIMI), Lewiston (and 2 mi. e. and 3 mi. e. on Clearwater River [300m-380m]) [May, Aug., Oct.] (52; DHKa, UIMI), Waha [Aug.] (5; CAS, MCZ, PURC, USNM), Waha Lake [July] (4; CAS, MCZ); Shoshone Co., Avery [Sept.] (2; UWBM), Clarkia

[June] (1; UIMI), St. Joe River (17 mi. e. of St. Maries) [July] (10; CAS); Valley Co., Dagger Falls [July] (2; BFCa), Middle Fork Salmon River (near Boundary Creek) [Aug.] (12; RTBe), Zena Creek [June] (1; UIMI); County unknown, Bungalow [Aug.] (15; UWBM). OREGON: Baker Co., East Fork Eagle Creek [July] (2; UWBM), Halfway [July] (1; BFCa); Hood River Co., Hood River [Sept.] (2; MCZ); Multnomah Co., Portland [July] (3; CUIC); Umatilla Co., Cottonwood Creek [June] (3; USNM, UWBM), Kamela [June] (1; CAS), Milton (Walla Walla River) [May-June] (4; UWBM), south of Kooskooskie (Washington) [June] (2; UWBM); Union Co., Elgin (and 0.1 mi. s. at GrandeRonde River [1130m]) [May, Aug.] (2; DHKa), Hilgard Junction State Park [Aug.] (3; RTBe), La Grande (1 mi. ne. on Grande Ronde River [1070m]) [May] (5; DHKa); Wallowa Co., Minam (0.2 mi. se. at junction of Minam River and Wallowa River [790m]) [May] (5; DHKa). WASHINGTON: Asotin Co., Anatone (10 mi. sw. at Rattlesnake Creek [910m]) [Aug.] (21; DHKa), Asotin (Asotin Creek [370m]) [May-June] (18; ANSP, CAS, DHKa), Buford Creek (3.6 mi. s. of Grande Ronde River [760m]) [May] (8; DHKa), Grande Ronde River (at Highway 129 [550m]) [May, Sept.] (2; DHKa, SJSC); Chelan Co., Leavenworth [July] (20; ANSP, CAS, MCZ, PURC, USNM, UWBM), Peshastin Creek [July] (1; UASM), Tumwater Canyon ([610m]) [May] (2; LRus); Columbia Co., Dayton (Touchet River [580m]) [May, July] (5; DHKa, WSU); Franklin Co., Palouse Falls State Park [May] (2; LRus); Klickitat Co., Trout Lake [July] (1; UWBM), White Salmon [Aug.] (2; UWBM); Skamania Co., Underwood (15 mi. w. on Columbia River [90m]) [May] (4; DHKa); Spokane Co., Spokane Falls (1; CAS); Walla Walla Co., Burbank [May] (1; ANSP), Coppei [May] (1; UAFA), Coppei Creek [May] (1; UIMI), Kooskooskie [June, Aug.] (3; UIMI, UWBM), Touchet River (near Waitsburg)

[July] (8; DJLa), Walla Walla (and 2 mi. s. [320m], Mill Creek) [May-Sept.] (139; CAS, CUIC, DHKa, MCZ, OSUO, PURC, UIMI, UMMZ, UWBM, WSU); Whitman Co., Almota [May] (2; MCZ, MSU), Wawawai (2.8 mi. nw. at Snake River [300m]) [May] (11; DHKa), Wilma [Apr.-May] (6; ANSP, UWBM).

Doubtful Records. CANADA, ALBERTA: Longview (Highwood River) [July] (7; CAS). UNITED STATES OF AMERICA, CALIFORNIA: (2; USNM).

Nebria gregaria Fischer

Map: Figure 393

Specimens examined: 2406 (1115♂, 1291♀)

UNITED STATES OF AMERICA

ALASKA: (60; AMNH, CAS, DHKa, INHS, KSUC, KUSM, MCZ, OSUC, UMMZ, UMRM, USNM); Aleutian Islands (1614; CAS, DHKa, KSUC, MCZ, MSU, USNM), Adak Island (Adak, Mount Moffett) [July-Sept.] (9; INHS, MCZ, MSU), Akutan Island [Aug.] (1; CAS), Amlia Island [Aug.] (2; CAS, USNM), Atka Island (Nazan Bay area) [July-Aug.] (37; CAS, USNM), Attu Island (Peaceful River) [July] (1; MCZ), Kiska Island [June, Oct.] (9; CUIC, USNM, UWBM), Little Kiska Island [June] (16; USNM, UWBM), Semisopochnoi Island [July] (2; USNM, UWBM), Unalaska Island (Captains Bay, Dutch Harbor [0m-30m], Makushin Bay [0m-460m], Mount Makushin, Unalaska and 3 to 6 mi. s.) [June-Sept.] (607; ALar, ANSP, CAS, CNC, CUIC, DBUM, DHKa, FMNH, ICCM, KUSM, MCZ, PADA, UASM, USNM, UWBM).

Doubtful Records. CANADA, "ALBERTA/BRITISH COLUMBIA": (1; ICCM). UNITED STATES OF AMERICA, ALASKA: Juneau [July] (1; FMNH), Nome (7; CAS), Pilot Cove [May, July] (6; ICCM, KUSM, WSU), Sitka (3; ICCM,

INHS), White Pass [July] (8; LACM), Wrangell Island (Wrangell) [June] (3; ICCM). OREGON: (4; CAS, UMRM, USNM).

No Data. (1 ANSP, INHS, MCZ, UMMZ, USNM).

Nebria gyllenhali Schönherr

Map: Figure 388

Nebria gyllenhali castanipes Kirby

Specimens examined: 4499 (2344♂, 2155♀)

CANADA

ALBERTA: Banff National Park, Banff [May-Aug.] (102; BFCa, CAS, CUIC, DHKa, MCZ, UASM, USNM), Bow River (and 1 mi. s. of Banff) [July, Sept.] (7; DHKa, RTBe), Eisenhower Junction ([1430m]) [July] (1; CNC), Lake Louise [July] (1; AMNH), Lake Minnewanka [Aug.-Sept.] (5; DJLa, UASM), Vermillion Lakes [Aug.] (1; CAS); Jasper National Park [July] (1; AMNH), Astoria River ([1770m]) [Aug.] (1; DJLa), Jasper [Aug.] (15; CNC, MCZ), Medicine Lake (on trail to Beaver Lake) [Aug.] (2; RTBe), Miette River (at Meadow Creek [1100m]) [July-Aug.] (39; DHKa, UASM), Mount Edith Cavell [Sept.] (1; DHKa), Sunwapta Pass [Aug.] (1; RTBe), Two Jack Lake [July] (1; USNM); Waterton Lakes National Park [May, July-Aug.] (36; BFCa, CNC, DJLa, UASM); Other localities, Aldersyde area [July] (1; BFCa), Athabasca (4; UASM), Athabasca River (at Calling Lake, 3 mi. ne. of Chain Lakes) [June, Sept.] (8; UASM), Beaver Creek [July] (10; UASM), Beaverdam Lake [May] (1; DJLa), Big Hill Springs Provincial Park [July] (8; ROM), Bilby [Apr., June-July] (8; CAS), Blackstone Gap [Aug.] (4; CAS, CNC), Blakiston Brook [July] (14; UASM), Calgary [May-June, Aug.]

(7; BFCa, DJLa, MCZ), Calling Lake (w. of Campbell's Beach [590m]) [June, Sept.] (89; DHKa, DRWh, UASM), Calling River (near Calling Lake) [June] (2; UASM), Canmore [June] (1; BFCa), Cline River (at Highway 11) [July-Aug.] (7; BFCa, DHKa), Crowsnest area (Crowsnest Lake and 1 mi. w.) [July-Aug.] (21; CNC, UASM, UWBM), Devon (6 mi. sw. at Conjuring Creek [700m]) [June] (3; DHKa), Edmonton (McKinnon Ravine, North Saskatchewan River at Emily Murphy Park and at Goat Bridge [670m]) [Apr.-Oct.] (243; CAS, CNC, DHKa, DJLa, DRWh, KUSM, MCZ, PURC, RFre, RTBe, UASM, UCD, UMMZ, USNM), Elk Creek area [Aug.] (1; BFCa), Entrance (34 mi. wnw. at Collie Creek [1460m], 40 mi. nw. at North Fork Wildhay River [1430m-1460m])(10; DHKa, UASM), Error Lake area [July] (2; BFCa), Exshaw [Oct.] (1; BFCa), Fawcett [June] (2; UASM), Foggy Mountain [July] (21; DHKa, UASM), Fort Fitzgerald [Sept.] (1; CAS), Fort Macleod [Aug.] (1; USNM) Fort McMurray [June, Aug.] (15; CAS, CNC), Fox Creek (11 mi. sse. on Highway 43) [June] (2; UASM), Gap [Aug.] (2; CAS), Freeman Lake (10 mi. s. of Swan Hills) [Aug.] (18; HGou), George Lake ([700m]) [June] (39; DHKa, DJLa), Gold Creek (2 mi. w. of Bellevue [1370m]) [July] (1; DHKa), Goose Mountain ([1400m]) [Aug.] (16; HGou), Gorge Creek [June-July] (3; UASM), Grande Prairie [June] (3; BFCa), Hailstone Butte area [Aug.] (1; BFCa), Happy Valley [May, Aug.] (4; UASM), Hay River (near Highway 35) [July] (1; UASM), High River [May] (3; CAS), Highwood River [May] (1; BFCa), Hummingbird Creek area [July] (2; BFCa), Kootenay Plains [June] (2; RFre), Lake Wabamun (near Sundance) [June, Aug.-Sept.] (20; UASM, USNM), Lundbreck [July-Aug.] (3; LEMC, MCZ, UASM), Lusk Creek (near Kananaskis Forest Experiment Station) [July] (1; CNC), Mercoal [July] (1; UASM), Morse River (near Fort Assiniboine) [July] (1; UASM), Nojack (Cold Creek) [Sept.] (1;

RFre), Nordegg (and 20 mi. s. on F[illegible]ry Trunk Road, South Creek Bridge) [July] (102; DHKa, UASM), North Saskatchewan River (27 mi. sw. of Nordegg) [June] (3; USNM), Notikewin Campground [July] (1; UASM), Peace River [Aug.] (5; UASM), Pembina River (w. of Flatbush) [June] (4; UASM), Pincher Creek (and 11 mi. s.) [July-Aug.] (9; UASM), Prairie Bluff Mountain [July] (1; UASM), R. B. Miller Station (Gorge Creek) [Aug.] (11; DHKa), St. Albert (Sturgeon River) [June] (1; UASM), Sheep River (4.5 mi. above Gorge Creek) [Aug.] (1; DHKa), Smoky River [June] (6; JVMa), South James River area [Aug.] (1; BFCa), Spring Creek Basin [June] (46; UASM), Sundance [July] (1; UASM), Ware Creek (5 mi. nw. of R. B. Miller Station) [Aug.] (60; DHKa), West Branch Castle River ([1340m]) [Aug.] (6; DJLa), Willow Creek [Aug.] (7; CAS). BRITISH COLUMBIA: (1; AMNH); Kootenay National Park, Simpson River [Aug.] (2; CNC, UASM); Yoho National Park, Field [July] (1; USNM); Other localities, Atbara [May, July-Sept.] (27; CNC, CUIC, UASM, UBC), Atlin ([1460m]) [July] (1; CNC), Blanchard River (Haines Highway mi. 93) [June] (9; CNC, UASM), Blue River (18 mi. n.) [June] (1; BFCa), Bowron Lake Provincial Park (Bowron Lake) [Aug.] (5; UBC), Buchley River (near Houston) [June] (4; UASM), Castlegar [June] (1; GRNo), Chilcotin [Apr.-May] (7; CAS, UBC), Chilkat Pass ([1070m]) [July] (7; CNC, UASM), Cinema (Cottonwood Creek) [June] (1; UASM), Contact Creek (Alaska Highway mi. 588.1) [Aug.] (4; DHKa), Copper Mountain [May] (1; UBC), Cottonwood [July] (4; CNC), Creston [May, July-Sept.] (15; CNC, MSU, UASM, UBC), Crowsnest Pass (2 mi. [1280m] and 5 mi. [1220m] w.) [July] (4; DHKa), Dutch Creek (at Windermere Road) [Aug.] (1; UBC), Endako (20 mi. w.) [June] (1; UASM), Fernie [Aug.] (1; CAS), Fort Nelson [Aug.] (1; UASM), Fort St. John [Aug.] (3; UBC), Fraser Lake (east end)

[June] (10; UASM), Glenora (10; ANSP, CAS, MCZ, USNM), Hat Creek [Aug.] (1; UBC), Hope Pass (summit [1830m]) [July] (1; UBC), Island Pond (35 mi. n. of Kimberley) [Aug.] (1; UASM), Kamloops [Sept.] (1; CAS), Le Moray [July] (1; BFCa), Liard River (Alaska Highway mi. 491, at Trout River) [June] (4; CNC, UASM), Lorna [June] (3; CAS, INHS, UBC), MacDonald River (Alaska Highway mi. 413 [1370m]) [July] (1; CNC), Manning Provincial Park (Pasayten River at park entrance) [May] (3; CNC, UASM), Mara Lake [Aug.] (1; BFCa), Michel [July-Aug.] (9; UASM), Midday Valley (Midday Creek) [June-Aug.] (10; CAS, CNC, INHS, UBC), Minnie Lake [July] (5; CNC), Moberly Lake [July] (2; BFCa), Muskwa River (Alaska Highway mi. 296) [June] (8; CNC, UASM), Parsnip River (8 mi. n. of McLeod Lake) [June] (13; CNC, UASM), Pavilion [June] (25; CNC, UASM), Peace River (at Alaska Highway, at Pine River) [June] (5; UASM, UBC), Pine Pass (Hart Highway) [Aug.] (3; UBC), Pouce Coupe [July] (1; BFCa), Prince George [Aug.] (2; UBC), Princeton [July] (2; BFCa, UBC), Quesnel [Sept.] (2; KUSM), Racing River (Alaska Highway mi. 418) [June] (1; CNC), Radium [June] (1; BFCa), Rock Creek [July] (12; CAS, MSU, UBC, UMMZ), St. Mary Lake [Aug.] (5; UASM), Salmon Valley [July] (1; BFCa), Skeena River (near Terrace) [June] (1; CNC), Sikhanni Chief River (Alaska Highway mi. 160) [June] (4; UASM), Spillimacheen [Aug.] (1; UBC), Stanley [July] (1; UBC), Summit Lake (Alaska Highway mi. 392 [1280m-1370m]) [June-July] (9; CNC, UASM), Swan Lake [June] (1; UBC), Terrace (7 mi. e.) [June] (1; CNC), Tetsa River (Alaska Highway mi. 376 and 378) [Aug.] (11; DHKa, LRus), Toad River (2; JVMa), Upper Elk River [June] (1; BFCa), Wardner (Kootenay River) [Sept.] (1; UBC), Whipsaw Creek (at Hope Trail [1220m]) [May, July] (5; MCZ, UASM, UBC), Whirlpool Canyon (Alaska Highway mi. 538.5 at Liard River) [July] (1; CNC).

MANITOBA: [July] (2; CAS, UASM); Riding Mountain National Park [June] (1; CNC); Other localities, Cedar Lake [July] (1; MCZ). NEWFOUNDLAND: Island of Newfoundland, Bay of Islands [July] (4; AMNH, CAS, DHKa), Hampden [July] (2; UWBM), Humber River (near Deer Lake) [July] (5; MCZ, USNM), Little Codroy River [July] (10; MCZ, USNM), Nicholsville [July] (8; MCZ), St. Anthony [June-Aug.] (94; BMNH, CNC, CPQC, CUIC, JSch, MCZ, UASM), St. George's Bay [July] (1; AMNH), South Branch (Grand Codroy River) [July] (2; MCZ), Spruce Brook [Aug.] (7; AMNH, CUIC, MCZ, USNM); Labrador, Barge Bay [July] (1; UWBM), Battle Harbour [June-Aug.] (26; AMNH, CAS, CNC, CUIC, DHKa, MCZ, USNM), Blanc Sablon (4; ANSP), Brig Harbour Island (Harrison Inlet) [Aug.] (1; USNM), Cabot Lake (1; CNC), Chateau Bay [July] (1; CAS), Forteau [July] (17; CNC), Hawke Harbour [Aug.] (2; MCZ), Hebron [July] (2; CNC), Henley Harbour [July] (9; CNC, UWBM), Inlet Bay [July] (1; CNC), L'Anse au Loup [July] (8; CNC), Nutak [July] (1; CNC), Pinware River [July] (5; CNC), Red Bay [July] (25; AMNH, ANSP, CNC, CUIC), Voiseys Bay (3; CNC), West St. Modeste [July] (86; AMNH, CAS, CNC, CUIC, DHKa, MCZ, PADA, UMMZ, USNM, UWBM); Location unknown, Cape Charles (Labrador) (1; CAS). NORTHWEST TERRITORIES: District of Mackenzie, Fort Simpson [June] (3; CNC), Fort Smith (and Slave River, 26 mi. w.) [June-Aug.] (37; CNC, CUIC, UASM, USNM), Great Slave Lake (at Hay River) [Aug.] (5; USNM), Kakisa River [June] (6; DHKa), Lady Evelyn Falls [Aug.] (17; USNM), Norman Wells [June-July] (2; CNC), Pointed Mountain [June] (1; JVMa), Providence [July] (1; CAS). ONTARIO: Algoma District, Michipicoten River [Aug.] (3; ANSP, USNM); Cochrane District, Ogoki [July] (9; CNC); Kenora District, Fort Severn [July] (4; ROM); Thunder Bay District, Lake Superior (4; MCZ), Michipicoten Island [July] (10; ANSP, USNM), Nipigon [June-July] (16;

CAS, CNC, ICCM, MCZ), Rossport Provincial Park (McLean Creek) [June] (5; ROM), Terrace Bay (and 16 mi. e.) [June-July] (2; CNC, ROM); Location unknown, Shriver's Bay [Aug.] (2; RTBe). QUÉBEC: [Aug.] (1; DBUM); Cté d'Abitibi, Joutel [June] (10; ALar, CNC, DBUM), Lac Chicobi [July] (11; ALar, CNC), Matagami [June] (26; ALar, CNC, DBUM), Rapide-des-Cèdres [July] (2; ALar), Senneterre [July] (5; ALar, CNC), Val-d'Or [July] (10; ALar, CNC, DBUM); Cté de Bonaventure, Cascapèdia [Aug.] (6; CNC), Escuminac [July-Aug.] (8; ALar); Cté de Charlevoix-Est, Baie Ste-Catherine [June] (121; ALar, CNC, DBUM); Cté de Chicoutimi, St-Ambroise [June] (5; ALar); Cté de Gaspé-Ouest, Parc de La Gaspésie (Mont Albert northeast slope [480m], summit [910m-1070m], Ruisseau du Diable [980m-1070m]) [June-Aug.] (147; ALar, CNC, CUIC, DBUM, DHKa), Rivière-à-Claude ([60m]) [July] (1; CNC), Riviere-la-Madeleine [July] (3; ALar); Cté de Lac-St-Jean-Ouest, Cheverry [June] (2; ALar), Dolbeau [June] (16; ALar), Mistassini [June] (6; ALar); Cté de Montmorency No 1, Parc des Laurentides (Lac Jacques-Cartier [790m]) [July] (32; ALar, CDA, CUIC, JSch, LRus, NMDo); Cté de Saguenay, Aguanish [June] (2; ALar), Île d'Anticosti (Ellis Bay, Fox Bay, Pointe de l'Est, Port-Menier, Rivière Jupiter) [June-July] (17; ALar, CPQC, MCZ), Blanc Sablon [July] (2; ALar), Bradore Bay [July-Aug.] (25; ALar, CNC, MCZ), Chute-aux-Outardes [June-July] (10; ALar, CPQC, DBUM), Forestville [June] (1; ALar), Godbout [Aug.] (1; ROM), Grandes-Bergeronnes [June-July] (89; ALar, CNC, DBUM, RTBe, UASM), Harrington (Harrington Harbor) [July] (9; ALar, CNC), Île aux Perroquets [July] (3; MCZ), Lourdes-de-Blanc-Sablon [July] (2; ALar), Magpie [June] (1; ALar), Middle Bay [July] (3; ALar, CPQC), Natashquan [July] (1; CNC), Sept-Îles [July] (1; ALar), Tadoussac [June] (3; ALar, CPQC); Territoire de Mistassini Lac Albanel [June-Sept.]

(24; DBUM), Lac Mistassini [July] (29; DBUM), Rupert House [=Fort Rupert] [June-July] (24; ALar, CNC), Rupert River (85 mi. e. of Rupert House) [July] (2; CNC), Territoire du Nouveau-Québec, Fort-Chimo [Aug.] (3; CNC), Fort George [July] (9; ALar, DBUM), Inoucdjouac [July] (22; ALar, DBUM), James Bay (east coast) [Nov.] (1; CAS), La Guillaume-Delisle [=Richmond Gulf] [Aug.] (1; MCZ), Port-Nouveau-Québec [=George River] [July-Aug.] (6; PURC, UASM), Poste-de-la-Baleine [=Great Whale River] [June-July] (21; ALar, CNC, DBUM), Povungnituk [July] (8; ALar, DBUM), Rivière Koroc [July] (1; DBUM), Schefferville [July] (2; ALar). SASKATCHEWAN: Meota [July] (1; USNM). YUKON TERRITORY: Big Creek (Alaska Highway mi. 674) [Aug.] (1; DHKa), Little Salmon Lake [Aug.] (1; CNC), Logjam Creek (Alaska Highway mi. 751.1) [Aug.] (2; DHKa), Lower Rancheria River (Alaska Highway mi. 687.1) [Aug.] (2; DHKa), Mason Creek [Aug.] (2; CNC), Thikanni River [June] (1; CNC), Upper Liard River (Alaska Highway mi. 642.6) [June] (1; UASM), Whitehorse [Aug.] (1; CNC), Yukon River (at Alaska Highway) [Aug.] (1; DHKa).

UNITED STATES OF AMERICA

ALASKA: Circle [July] (5; MCZ, UASM), Holy Cross (3 mi. nw. on Yukon River) [July] (2; USNM), Wrangell Island (Wrangell) (1; MCZ), Marshal (Yukon River) [Aug.] (6; USNM), Russian Mission (Yukon River) [Aug.] (2; USNM), Yukon River (between Holy Cross and Paimuit, between Marshal and Old Andreanofski) [July, Sept.] (6; USNM). IDAHO: Blaine Co., Alturas Lake (at Inlet Campground [2130m]) [July-Aug.] (5; DHKa, UWBM), Cherry Creek (0.1 mi. nw. of Highway 93 [2230m]) [Aug.] (3; DHKa), Hyndman Creek [July] (9; UWBM), North Fork Warm Springs Creek (10 mi. w. of Ketchum [1890m]) [Aug.] (2; DHKa), Petit Lake [July] (5; BFCa);

Camas Co., Carrie Creek (33 mi. [2440m] and 36 mi. [2100m] ese. of Ketchum) [Aug.] (2; DHKa), South Fork Boise River (34 mi. e. of Featherville at Bear Creek [1830m]) [Aug.] (12; DHKa); Custer Co., Bayhorse Creek (7 mi. nw. of Highway 93 [2440m]) [Aug.] (1; DHKa), Bayhorse Lake ([2590m]) [Aug.] (28; DHKa), Fourth of July Creek (3 mi. e. of Highway 93 [2230m]) [Aug.] (7; DHKa), Hellroaring Creek (at Salmon River [1620m]) [Aug.] (2; DHKa), Rothas (8 mi. nne. at Pass Creek [1980m]) [Aug.] (4; DHKa), Salmon River (at Bayhorse Creek [1620m]) [Aug.] (13; DHKa), Summit Creek (2 mi. ne. of Trail Creek Summit [2320m]) [Aug.] (7; DHKa), Wet Creek (2 mi. wsw. of Pass Creek Pass [2410m]) [Aug.] (16; DHKa); Kootenai Co., Coeur d'Alene [June] (11; ANSP, MCZ, USNM, UWBM), Coeur d'Alene Lake [July] (3; CAS); Shoshone Co., Clarkia [June] (1; UIMI), Enaville [July] (3; CAS), St. Joe River (17 mi. e. of St. Maries) [July] (1; CAS); Valley Co., Middle Fork Salmon River (near Boundary Creek) [Aug.] (1; RTBe); County unknown, Beaver Canyon [July] (1; USNM), Twin Creek Forest Camp ([1520m]) [July] (16; UWBM). MAINE: Piscataquis Co., Baxter State Park (Mount Katahdin [300m-1520m], at Chimney Pond [910m], top of Saddle Slide [1220m], summit area [1600m]) [June-Aug.] (72; ICCM, MCZ, USNM). MICHIGAN: Chippewa Co., Whitefish Point [July] (1; UMMZ); Isle Royale National Park, Isle Royale [July] (4; UMMZ, USNM). MINNESOTA: St. Louis Co., Duluth [Aug.] (2; ICCM). MONTANA: Beaverhead Co., Big Hole River (at Highway 91 [1550m]) [Sept.] (1; UASM); Blaine Co., Bear Paw Mountains [Sept.] (4; USNM); Carbon Co., East Rosebud Lake [June] (4; CUB), Rock Creek (at Red Lodge [1680m]) [July] (33; DHKa); Cascade Co., Jefferson Creek (2 mi. e. of Highway 89 [1870m]) [July] (5; DHKa); Chouteau Co., North Fork Highwood Creek (at Briggs Creek [1370m]) [July] (1; DHKa),

South Fork Highwood Creek (at Big Coulee [1490m]) [July] (7; DHKa); Fergus Co., Crystal Lake ([1870m]) [July] (36; DHKa), East Fork Rock Creek ([1710m]) [July] (13; DHKa); Flathead Co., Kalispell [June] (7; CAS, MCZ, USNM); Gallatin Co., Bozeman area (and Sourdough Canyon) [June-July] (3; DZEC, UWBM), Fairy Lakes [Aug.] (3; CUIC), Windy Pass [July] (1; CUIC); Glacier Co., St. Mary River [Aug.] (16; CAS); Glacier National Park [June-July] (7; CUIC), Grinnell Glacier ([1920m]) [Aug.] (1; SJSC), Swiftcurrent Creek (at Many Glacier [1480m]) [July-Aug.] (2; SJSC); Judith Basin Co., Arrow Creek ([1520m]) [July] (2; DHKa), Dry Wolf Creek (at Dry Wolf Campground [1840m]) [July] (21; DHKa); Lake Co., Arlee ([820m]) [July] (2; LRus); Lewis and Clark Co., Helena area [July-Aug.] (2; MCZ, USNM); Mineral Co., Alberton ([910m]) [Aug.] (1; LRus); Ravalli Co., Sula [July] (1; CAS); Silver Bow Co., Pipestone Pass ([1830m]) (1; LRus); County unknown, East Flathead ([1740m]) [July] (1; DZEC). NEVADA: Elko Co., Lamoille Creek (at Lower Lamoille Campground [1920m]) [Aug.] (86; DHKa), Thomas Creek (at Thomas Creek Campground [2320m]) [Aug.] (31; DHKa). NEW HAMPSHIRE: (41; ANSP, CAS, DEUN, DHKa, FMNH, ICCM, INHS, MCZ, PMNH, PSUC, RTBe, SDSU, UMRM, USNM); Coos Co., Ammonoosuc River (and at Fabyaus,[July] (3; ANSP, MCZ, UMMZ), Mount Adams [July] (2; AMNH), Mount Jefferson [July] (2; AMNH, PMCh), Mount Washington ([910m-1920m], Ammonoosuc River, Bigelow Lawn [1650m], Great Gulf, Hermit Lake, Lake of the Clouds [1520m], summit [1890m-1920m], Tuckerman Ravine) [May-Sept.] (630; ALar, AMNH, ANSP, CAS, CNC, CUIC, DBUM, DHKa, DEUN, FMNH, ICCM, INHS, KSUC, KUSM, LEMC, MCZ, MSU, NMDo, PADA, PMCh, RDav, RTBe, SJSC, UASM, UMMZ, USNM, WSU); Grafton Co., Franconia area (4; CAS, MCZ). NEW YORK: (2; CAS, MCZ); Essex Co., Mount Haystack [Aug.] (3; RTBe), Mount Marcy (Lake Tear, Plateau Camp,

Range Trail, summit [June-Aug.] (97; AMNH, CUIC, DHKa, MCZ, RTBe). OREGON: (1; INHS); Baker Co., Pine Creek [June] (3; UWBM); Union Co., Highway 204 (between Elgin and Tollgate) [June] (1; UWBM); Wallowa Co., Chief Joseph Mountain [Aug.] (2; MCZ), Lost Lake [Aug.] (1; DHKa), Lostine River (French Campground, Lake Creek Campground, above Two Pan Campground [1710m-1980m]) [Aug.] (68; DHKa, UWBM), Wallowa Lake (at inlet of Wallowa River [1940m]) [May-June, Aug.] (80; CAS, DHKa, JSch, MSU, OSUO, PURC, UCR, UWBM). SOUTH DAKOTA: Lawrence Co., East Fork Spearfish Creek (2.2 mi. se. of Cheyenne Crossing [1830m]) [July] (7; DHKa). WASHINGTON: Ferry Co., Keller (Sanpoil River) [July] (19; AMNH, CAS, ICCM, MCZ, USNM, UWBM); Okanogan Co., Tonasket (2 mi. e.) [June] (8; FMNH, UWBM); Yakima Co., (2; JSch, WSU), American River [July-Aug.] (4; UIMI, USNM, UWBM), Bumping River [Aug.] (7; ANSP, PURC, USNM, UWBM, WSU), Soda Springs Campground (at Bumping Lake Road) [May] (1; JSch), Tampico [July] (1; USNM), Yakima area (1; USNM). WISCONSIN: Bayfield Co., Bayfield (1; UWBM). WYOMING: Albany Co., Middle Crow Creek (2 mi. se. of Hidden Valley Picnic Area [2590m]) [July] (1; DHKa); Big Horn Co., Granite Creek (8 mi. sw. of Granite Pass [2380m]) [July] (12; DHKa), Meadowlark Lake ([2560m]) [Aug.] (16; FMNH, UWBM), Shell Creek (11 mi. sw. of Granite Pass [2130m]) [July] (2; DHKa), West Tensleep Creek ([2830m-3200m], 1 mi. n. of Tyrell Ranger Station [2560m]) [July] (40; DHKa), West Tensleep Lake ([2770m]) [July] (2; DHKa); Converse Co., La Prele Creek (at Camel Creek Campground [2530m]) [July] (61; DHKa); Grand Teton National Park, Colter Bay Campground [July] (11; CUIC), Emma Matilda Lake [July] (7; MCZ); Johnson Co., Clear Creek (5 mi. w. of Buffalo [1650m], 12 mi. w. of Buffalo [2190m]) [July] (30; DHKa), Powder River Pass [Aug.] (2; MSU), South Fork Clear

Creek (16 mi. w. of Buffalo [2350m]) [July] (6; DHKa); Park Co., Beartooth Plateau [Aug.] (3; DHKa, SJSC); Sheridan Co., Little Tongue River (13 mi. wsw. of Dayton [2380m]) [July] (74; DHKa); Sublette Co., Boulder Creek (15 mi. ne. of Boulder [2260m]) [July] (5; DHKa), Hoback River (8 mi. nw. of Bondurant [2100m], 14 mi. sw. of Highway 187/189 [2440m]) [July-Aug.] (8; DHKa), Pine Creek (at Pinedale [2180m]) [July] (24; DHKa); Teton Co., Blackrock Creek (3.7 mi. wnw. of Togwotee Pass [2770m]) [Aug.] (1; DHKa), Granite Creek (at Little Granite Creek [2150m]) [Aug.] (46; DHKa), Gros Ventre River (at Highway 89/187) [Aug.] (2; EAMa, USNM); Washakie Co., West Tensleep Creek (at East Tensleep Creek [2350m]) [July] (3; DHKa); Yellowstone National Park [July] (7; USNM); County unknown, "Bighorn Reserve" (1; MCZ), Medicine Bow Mountains [Aug.] (1; USNM).

Doubtful Records. CANADA, BRITISH COLUMBIA: Campbell River [July] (1; CAS). UNITED STATES OF AMERICA, ARIZONA: (2; AMNH, USNM). CALIFORNIA: (2; ICCM, MCZ). MASSACHUSETTS: (3; AMNH, MCZ); Middlesex Co., Sherborn (3; UMMZ). MISSOURI: (1; MCZ).

No Data. (2; CDA, MCZ).

Nebria gyllenhali lassenensis Kavanaugh, NEW SUBSPECIES

Specimens examined: 36 (19♂, 17♀)

UNITED STATES OF AMERICA

CALIFORNIA: Lassen Volcanic National Park, Emerald Lake ([2450m]) [Aug., Oct.] (6; CAS, DHKa, FMNH), Little Hot Springs Area (East Sulphur Creek [2440m-2530m]) [Aug.] (6; CAS, DHKa), Mount Lassen (3 mi. se.) [July] (1; USNM), Ridge Lake [Aug.] (16; CAS); Tuolumne Co., Sonora Pass

[Aug.] (3; CAS). OREGON: Deschutes Co., Todd Lake (and 1 mi. s.) [Aug.] (4; JSch).

Nebria gyllenhali lindrothi Kavanaugh, NEW SUBSPECIES

Specimens examined: 1393 (706♂, 687♀)

UNITED STATES OF AMERICA

COLORADO: (2; KUSM, PURC); Boulder Co., ([3810m]) [July] (1; CUB), Arapaho Pass ([2740m-3350m]) [Aug.] (1; RTBe), ArapahoePeak ([3510m]) [Aug.] (3; CArm), Beaver Creek ([2530m]) [July] (1; CArm), Fourth of July Mines ([3430m]) [Aug.] (2; CArm), Jenny Lake ([3200m]) [July] (2; CArm), Middle St. Vrain Creek ([3600m]) [July] (1; CArm), Niwot Ridge ([3050m]) [July] (5; CArm, CUB), Rainbow Lakes ([3350m]) [Aug.] (3; CNC), Rollins Pass ([3410m-3540m]) [Aug.] (2; CUB, DHKa), South Fork Middle Boulder Creek ([2900m-3960m]) [Aug.] (1; CArm); Clear Creek Co., Leavenworth Valley (Argentine Road [3660m-3960m]) (2; USNM), Loveland Pass ([3660m-3840m]) [July] (42; CAS, RTBe, UWBM), Mount Evans ([3600m-4330m], and Summit Lake [3900m-3960m]) [July-Aug.] (76; CAS, CNC, DHKa, FMNH, MCZ, PURC, RCGr, UASM); Conejos Co., Cumbres Pass ([3050m]) [June] (1; CAS); Custer Co., Ophir Creek (7.3 mi. sw. of Fairview [3140m]) [June] (9; DHKa), St. Charles River (1.9 mi. sw. of San Isabel [2710m-2830m] [June] (14; DHKa), Wet Mountains ([3470m]) [July] (2; USNM); Dolores Co., Lizard Head Pass ([3050m]) [Sept.] (1; CAS), Rico area ([2590m-3050m]) [July] (10; ANSP, MCZ, USNM); El Paso Co., Pikes Peak ([3960m]) [July] (8; AMNH, CAS), South Cheyenne Creek (at Gold Camp Road [2530m-2650m]) [June] (1; DHKa); Garfield Co., Trappers Lake ([2990m]) [Aug.] (49; DHKa); Gilpin Co., Central City ([2620m]) [July]

(1; CAS), Corona ([3350m]) [Sept.] (7; CAS, CUIC), South Boulder Creek (at Rollinsville and 2.5 mi. w. [2440m]) [July-Aug.] (5; CArm, DHKa, UAFA); Grand Co., Ptarmigan Peak (20; MCZ, ZMLS); Gunnison Co., Gothic ([2930m]) [July] (2; USNM), Mexican Cut Lakes (1 mi. nw. of Elko Park [3440m]) [Aug.] (1; PMNH); Huerfano Co., Apishapa Pass [June] (3; CUB), Bear Lake [June] (13; DHKa, EAMa), Blue Lake [June] (10; DHKa, EAMa), Cucharas Pass ([3050m] and 1.5 mi. n.) [June] (109; DHKa, EAMa), Cucharas River (near Blue Lake [3190m]) [June] (5; DHKa); Jackson Co., Cameron Pass ([3140m]) [Aug.] (1; UASM), Rabbit Ears Pass ([2740m]) [June-Aug.] (8; CAS, USNM); La Plata Co., Hermosa Creek Trail (nw. of Hermosa [2960m]) [Aug.] (9; UASM); Larimer Co., Browns Lake Trail [Aug.] (9; RTBe), Crown Point [July] (21; RTBe), Zimmerman Lake [Aug.] (3; RTBe); Los Animas Co., Apishapa Pass (2.1 mi. se. [3230m]) [June] (9; DHKa), Bear Creek (5 mi. s. of Cucharas Pass [2800m]) [June] (83; DHKa); Mesa Co., [Aug.] (5; PMCh, RDav), Grand Mesa ([3050m]) [July-Aug.] (6; CAS, CUB, USNM), Skyway ([3050m]) [June] (2; DHKa, FMNH); Mineral Co., Pagosa Springs (20 mi. n.) [June] (1; DRWh), Wolf Creek Pass ([3250m-3660m] and 2 mi. w.) [June-Aug.] (49; CAS, CNC, DHKa, EAMa, USNM); Ouray Co., American Flats ([3660m]) [July] (4; AMNH), Ouray area [June-July] (4; AMNH, CAS); Park Co., Middle Fork South Platte River (near Hoosier Pass [3540m]) [July] (1; DHKa), Mount Lincoln ([3350m]) [Aug.] (1; UASM); Rio Grande Co., Rio Grande River (1 mi. s. of South Fork [2400m]) [Aug.] (29; DHKa, EAMa), Summitville ([3050m-3350m]) [Aug.] (7; CNC, MCZ); Rocky Mountain National Park ([3200m-3510m]) [June-Aug.] (11; CAS, CNC, UASM), Fall River Pass ([3600m]) [July] (5; CUB), Longs Peak ([3840m] and at Chasm Lake [3810m]) [July-Aug.] (14; CArm), Milner Pass ([3280m]) [July] (1; AMNH), Ouzel Falls

([3050m]) [Aug.] (1; CArm), Sandbeach Lake ([3050m]) [June] (7; CArm), Trail Ridge Road ([3660m-3690m]) [Aug.] (2; CUB, USNM); Routt Co., Buffalo Pass (Summit Lake [3140m]) (4; CAS), Walton Creek (above Dumont Lake [2900m-2960m]) [Aug.] (5; DHKa); San Juan Co., Silverton ([3660m]) [July] (1; USNM); Summit Co., Quandary Peak (south slope [3410m-3960m]) [Aug.] (35; DHKa); Teller Co., ([3410m]) [June] (1; PADA), Phantom Canyon ([2960m]) [June] (. CAS); County unknown, "Hot Springs" (1; ICCM), King's Lake ([3350m]) [Aug.] (2; CArm), La Plata Mountains ([3200m-3660m]) [July-Aug.] (4; DHKa, USNM), "Laramie Co." (2; ICCM), Medicine Bow Range ([2440m-3660m]) [July] (3; MCZ), Mount Baldy (summit [3750m]) [J ly] (1; CArm), San Juan Mountains ([3660m]) [July] (1; USNM), "foothills of Rocky Mts." (1; PMNH). NEW MEXICO: (9; ANSP, ICCM, KUSM, MCZ, USNM); Rio Arriba Co., Gregorio Lake ([2790m]) [June] (5; DHKa), Rio Puerco (at Rio Puerco Campground [2350m-2440m]) [June] (3; DHKa); Santa Fe Co., Lake Katherine ([3600m]) [June] (30; DHKa), Nambe Divide ([3350m]) [July] (2; ANSP); San Miguel Co., Beaver Creek (sw. of Rincon Montoso [2620m]) [Aug.] (15; UASM), Crowles area ([2440m]) [June] (1; UASM), Las Vegas area ([2130m]) [July] (1; KUSM), Willow Creek (near Torrero [2740m]) [June] (8; UASM); Taos Co., Red River (2.2 mi. [2610m] and 4.1 mi. [2580m] w. of Red River, 8 mi. s. of Red River [2870m]) [June] (38; DHKa), Tres Ritos [July] (4; CAS), Wheeler Peak ([3050m-3640m], Middle Fork Lake [3340m], Middle Fork Red River [3260m-3690m]) [June] (153; DHKa). UTAH: Grand Co., Mill Creek (at Oowah Lake [2680m]) [Aug.] (12; DHKa); San Juan Co. ([2800m]) [Aug.] (1; FMNH), Geyser P s (at Blue Lake) [Aug.] (2; AMNH), Mill Creek Valley ([2900m]) [Aug.] (2; UASM). WYOMING: Albany Co., Brooklyn Lake ([3200m]) [July] (41; DHKa), Centennial area ([3050m]) [Aug.] (22; MSU, SDSU), Douglas

Creek (1 mi. sse. of Keystone [2680m]) [July] (32; DHKa), Little Brooklyn Lake ([3120m]) [July] (113; DHKa), Medicine Bow Peak ([3350m-3660m]) [July-Aug.] (3; FMNH, KSUC, UWL), Mirror Lake ([3290m]) [July] (37; USNM), Nash Fork Little Laramie River (7.5 mi. nw. of Centennial [2990m]) [July] (1; DHKa), Snowy Range Pass ([3200m]) [June, Aug.] (33; RTBe, UASM); Carbon Co., Elk Mountain (35.0 mi. ne. of Saratoga [3400m]) [July] (32; USNM), Hidden Treasure Gulch (11.5 mi. wsw. of Encampment [2870m]) [July] (2; DHKa), Lake Marie ([3230m] and 8 mi. sw. [2740m]) [July] (7; DHKa), North French Creek (4 mi. w. of Mirror Lake [3050m]) [July] (3; DHKa), Silver Lake ([3170m]) [July] (32; USNM).

Doubtful Records. UNITED STATES OF AMERICA, MASSACHUSETTS: (1; UMRM).

Nebria hudsonica LeConte

Map: Figure 384

Specimens examined: 2937 (1614♂, 1323♀)

CANADA

ALBERTA: [July-Aug.] (10; BFCa): Banff National Park, Banff (and 1 mi. s. on Bow River) [June-Oct.] (160; ANSP, CAS, CUIC, DHKa, ICCM, MCZ, UASM, USNM), Cascade Creek [Sept.] (6; DJLa, USNM, UWBM), Lake Louise [July] (2; AMNH), Lake Minnewanka [Aug.] (5; UASM), North Saskatchewan River (at Highway 93) [July] (1; DHKa); Jasper National Park, Amethyst Lakes Trail [Aug.] (2; DHKa), Jasper [Aug.] (6; CNC), Maligne Lake [July] (1; CUIC), Medicine Lake [July] (4; CUIC), Miette River (at Meadow Creek) [July-Aug.] (45; DHKa, UASM), Rortal Creek ([1190m]) [Aug.] (1; DJLa), Pyramid Lake [Aug.-Sept.] (2; RTBe); Waterton Lakes National Park, Waterton Park (Cameron Creek) [July] (18; CAS, CNC,

UASM); Other localities, Beaver Creek [Aug.] (3; UASM), Bellevue (2 mi. w. at Gold Creek [1370m]) [July] (8; DHKa), Blackstone Gap [Aug.] (8; CAS, CNC), Caroline (30 mi. w. at Elk Creek Campground) [Aug.] (1; MSU), Chain Lakes (3 mi. ne. at Athabasca River) [Sept.] (8; UASM), Cline River (at Highway 11) [Aug.] (4; DHKa), Crow's Nest Pass ([1340m-1360m] and Crow's Nest Lake) [July] (12; CNC, DHKa, UASM), Daisy Creek [Aug.] (11; CAS), Devon (0.2 mi. n. on North Saskatchewan River [700m]) [June] (8; DHKa), Edmonton (North Saskatchewan River) [May-Aug.] (17; CNC, DHKa, RTBe, UASM, USNM), Elbow Falls [July] (1; DRWh), Entrance (20 mi. nnw. at Wildhay River [1310m], 30 mi. wnw. at Wildhay River [1220m], 34 mi. wnw. at Collie Creek [1460m], 40 mi. wnw. at North Fork Wildhay River [1430m]) [June] (26; DHKa, UASM), Forestry Trunk Road (at North Saskatchewan River)[June] (1; DRWh), Fort Fitzgerald [Aug.] (1; UASM), Fort Macleod [Aug.] (3; UASM, USNM), Fort McMurray [June-July] (6; UASM), Fort Vermillion Ferry (Peace River) [July] (3; UASM), Freeman Lake (10 mi. s. of Swan Hills) [Aug.] (3; HGou), Gap [Aug.] (7; CAS, CNC), Gorge Creek [June-Aug.] (32; UASM, USNM), Grande Cache Road (at Athabasca River [1100m]) [June] (3; DHKa), Happy Valley [Aug.] (1; UASM), High River [July] (4; CAS, MCZ), Highwood River [Aug.] (2; CAS), Kananaskis Valley (Kananaskis Forest Experiment Station) [Aug.] (1; CNC), Kinuso (24 mi. n.) [Aug.] (1; UASM), Kootenay Plains [June] (1; RFre), Lethbridge [May, Sept.] (4; CNC, DJLa), Little Smoky (1 mi. w. at House Creek) [Aug.] (1; LRus), Longview (Highwood River) [July] (5; CAS), Lundbreck [July-Aug.] (12; CAS, LEMC, MCZ, UASM, UBC), Medicine Hat [May-Sept.] (104; ALar, AMNH, ANSP, CAS, GUIC, DBUM, KUSM, MCZ, MSU, OSUC, UASM, UCD, UMMZ, USNM), Nordegg (and 27 mi. sw.) [June-July] (19; UASM, USNM), Peace River [Aug.] (1; UASM), Pincher Creek [Aug.] (9; CNC,

UASM), Rocky Mountain House (North Saskatchewan River) [July] (3; UASM), Sheep River (4.5 mi. above Gorge Creek) [Aug.] (21; DHKa), Spray Lakes [July] (3; JVMa), Spring Creek Basin (Simonette River) [June] (5; UASM), Ware Creek (5 mi. nw. of R. B. Miller Research Station) [Aug.] (80; DHKa), West Branch Castle River ([1340m-1400m]) [July-Aug.] (12; DJLa), Willow Creek [Aug.] (1; CAS); Location unknown, Waterloo [July] (1; PURC). BRITISH COLUMBIA: [July, Sept.] (9; AMNH, FMNH, INHS, MCZ, NMDo); Kootenay National Park, Simpson River [Aug.] (10; CNC, UASM), Vermillion Creek [July] (1; CAS); Mount Revelstoke National Park [July] (8; CAS, UCB); Yoho National Park, Field [July-Aug.] (3; USNM); Other localities, Atbara [Aug.-Sept.] (7; CUIC, UASM, UBC), Atlin ([670m]) [Aug.] (1; CNC), Atlin Lake [July] (1; CUIC), Big Boulder Creek (east Pine Pass) [June] (9; CNC, UASM), Big Creek (Alaska Highway mi. [Aug.] (12; DHKa), Blanchard River (Haines Highway mi. 93) [June] ; UASM), Blind Bay [Oct.] (1; CAS), Boswell [Aug.] (21; UASM), Bowron Lake Provincial Park (Bowron Lake) [July] (1; BFCa), Buckinghorse River (at Alaska Highway) [July] (1; USNM), Bull River [Sept.] (1; UBC), Canim Lake [July] (1; BFCa), Christina Lake [May] (2; CNC, UASM), Contact Creek (Alaska Highway mi. 588.1) [Aug.] (11; DHKa), Creston (and 2 mi. w. at Kootenay River) [May, Aug.] (20; DHKa, UASM, UBC), Crow's Nest Pass (2 mi. w. at Elk Creek [1280m], 5 mi. w. at Elk River [1220m]) [June-July] (28; BFCa, DHKa), Edgewood [Aug.] (15; CAS, DBUM, KUSM), Elk Creek (e. of Fernie) [July] (6; UASM), Fernie (and 10.7 mi. w. on Elk River) [June-July] (38; CAS, CNC, FMNH, INHS, MSU, ROM, UWBM), Flathead [June] (1; CUIC), Fort Steele [Sept.] (1; UBC), Glenora (2; ANSP, USNM), Golden (9 mi. e. at Kicking Horse River [1160m]) [Aug.] (4; DHKa), Goodrich Creek (12 mi. w. of Little Prairie) [July] (5;

CNC, UASM), Greenwood [Aug.] (17; UASM), Hosmer (Elk River) [July] (4; CAS), Hyland River (Alaska Highway mi. 605) [Aug.] (4; DHKa), Iron Creek (Alaska Highway mi. 594.3) [Aug.] (5; DHKa), Kamloops [Sept.] (1; UBC), Keremeos (9 mi. w.) [June] (1; CNC), Kicking Horse Camp [July] (2; CAS), Kingsgate (Moyie River) [July, Oct.] (9; DJLa, UBC), Kimberley (17 mi. n. at Kootenay River) [Aug.] (14; UASM), Kuskonook [Sept.] (1; CUIC), Lake Windermere [Sept.] (2; CAS), Mable Lake [May, Aug.] (7; CAS, CNC), Marguerite [June] (2; CNC, UASM), Michel (and at Cabin Creek) [July-Aug.] (16; CNC, UASM), Midway (and 4 mi. w.) [June-July] (2; BFCa, CNC), Moberly Lake [July] (1; BFCa), Morrissey [July] (21; UWBM), Mount Robson Provincial Park (Robson, Robson Creek) [May-June, Sept.] (27; CNC, JVMa, RTBe, UWBM), Muncho Lake Provincial Park (Alaska Highway mi. 459) [July] (6; BFCa), Muskwa River (Alaska Highway mi. 296) [June] (4; CNC, UASM), Nation River [June] (8; DBUM, FMNH, PURC), Oliver (and 7 mi. n.) [May-June] (18; CNC, UASM), "115" Creek (Alaska Highway mi. 403.4) [Aug.] (1; DHKa), Peace River (at Alaska Highway) [June] (1; UBC), Penticton (and at Dog Lake, Skaha Lake) [Aug.-Sept.] (42; CAS, CNC, DHKa), Perow (McEvoy Creek) [June] (7; UASM), Princeton [May, July] (6; UBC, CNC), Prophet River (Alaska Highway mi. 233) [Aug.] (2; CNC, UASM), Quesnel [July] (2; UBC, UWBM), Quesnel Lake [Sept.] (3; CAS, KUSM), Racing River (Alaska Highway mi. 418.7) [June-July] (3; CNC, UASM), Revelstoke [July-Aug.] (2; BFCa, MCZ), Riondel [Aug.] (6; CAS, CNC), Rock Creek [May] (1; CNC), Salmon Arm [July] (3; CAS), Sheep Creek [June] (1; CAS), Shusway Falls [June] (1; CAS), Sikhanni Chief River (Alaska Highway mi. 160) [June] (10; CNC, UASM), Skookumchuk [Aug.] (6; UBC), Smithers (13 mi. n. at Trout Creek) [June] (3; UASM), Sugar Lake [July, Sept.] (3; CAS, CNC), Summit Lake

(Alaska Highway mi. 329.5 [1280m]) [June-July] (6; CNC, UASM), Swift River (Alaska Highway mi. 733.3) [June] (3; UASM), Tetsa River (Alaska Highway mi. 376 to 390) [June, Aug.] (11; CNC, LRus, MSU, UASM), Toad River (Alaska Highway mi. 422 [1370m] to 437.5) [Aug.] (9; CNC, DHKa, JVMa), Upper Collier Lake [July] (1; UWBM), Upper Liard River (Alaska Highway mi. 642.6) [June] (3; UASM), Vaseaux Lake [May] (1; CNC), Vernon [Aug.] (1; CAS), West Bank [June] (4; CAS). MANITOBA: Cedar Lake [July] (1; MCZ). ONTARIO: Thunder Bay (McIntyre River) [July] (2; JKus). SASKATCHEWAN: (1; MCZ); Saskatoon (South Saskatchewan River) [Sept.] (1; UASM). NORTHWEST TERRITORIES: District of Mackenzie, Fort Smith (Slave River) [June-Aug.] (35; CNC, CUIC, UASM, USNM). YUKON TERRITORY: Little Rancheria River (Alaska Highway mi. 670.2) [Aug.] (8; DHKa), Lower Rancheria River (Alaska Highway mi. 687.1) [Aug.] (9; DHKa), Morley River (Alaska Highway mi. 777) [Aug.] (7; DHKa), Nisutlin Bay (Alaska Highway mi. 803.4) [June] (1; UASM), Rancheria (Swift River) [Aug.] (28; CNC, UASM), Seagull Creek (Alaska Highway mi. 733) [Aug.] (2; DHKa), Swift River (Alaska Highway mi. 725.1 to 733) [June, Aug.] (28; CNC, DHKa, LRus), Upper Rancheria River (Alaska Highway mi. 721.6) [Aug.] (3; DHKa), Watson Lake [Aug.] (2; CNC), Whitehorse [June] (1; CUIC); Location unknown, Rock Creek [May] (1; CNC).

UNITED STATES OF AMERICA

COLORADO: (2; ANSP, INHS); Boulder Co., Boulder Creek (at junction with Fourmile Creek [1770m]) [Aug.] (1; DHKa), Eldora (South Fork Middle Boulder Creek [2530m-2900m]) [July-Aug.] (26; CArm), Lefthand Creek (near Boulder [1980m-2190m]) [July] (4; CArm), Middle St. Vrain

Creek ([2650m-2990m]) [July] (27; CArm, CUB), Nederland (Middle Boulder Creek in Boulder Canyon) [June] (1; CArm), Pinecliffe (and 3 mi. w. on South Boulder Creek [2380m-2440m]) [June-Aug.] (49; CArm, DHKa), Raymond (Middle St. Vrain Creek [2350m]) [Aug.] (2; CArm), South Boulder Creek (above El Dorado Springs [1980m-2100m], near Gross Dam [2130m]) [July] (24; CArm), South St. Vrain Creek ([2350m]) [July] (4; CArm), Ward ([2500m] and 5 mi. e. on Lefthand Creek [2440m]) [July-Aug.] (174; CArm, DHKa, USNM); Clear Creek Co., Empire (Clear Creek) [Sept.] (1; LRus), Graymont (Clear Creek [2740m]) [July] (3; DHKa), Idaho Springs ([2290m]) [July] (6; CAS), Leavenworth Valley ([2740m-3050m]) [June] (14; CAS, CNC, CUIC, MCZ, ROM, USNM, UWBM), Silver Plume ([2740m-3050m]) [June] (37; CAS, CUIC, FMNH, MCZ, UCR, USNM, UWBM); Garfield Co., New Castle (Colorado River) [Aug.] (2; USNM); Gilpin Co., East Portal (South Boulder Creek [2740m]) [July] (7; CArm, CUB), Rollinsville ([2440m-2530m] and 2.5 mi. w. on South Boulder Creek) [July-Aug.] (67; CArm, DHKa, UAFA); Grand Co., Berthoud Pass ([3050m]) [July] (3; CAS); Gunnison Co., Gothic ([2900m]) [July] (1; SJSC); Jefferson Co., Golden (Clear Creek [1680m]) [June] (2; EAMa, USNM); Lake Co., Independence Pass (5.1 mi. e.) [Aug.] (12; UAFA), Leadville [June] (9; CAS), Twin Lakes (and 4 mi. w., 7 mi. w., 12 mi. w. on Lake Creek [3200m]) [June, Aug.] (45; CAS, DHKa, EAMa); Larimer Co., Cameron Pass [June, Aug.] (3; EMUS, RTBe, UASM); Park Co., Santa Maria (North Fork South Platte River [2440m]) [June] (9; DHKa); Pitkin Co., Aspen (and 8 mi. e. on Roaring Fork River [2800m]) [July-Aug.] (18; AMNH, DHKa, UWBM); Rocky Mountain National Park, Ouzel Falls ([3050m]) [July-Aug.] (12; CArm, DHKa), Wild Basin (North St. Vrain Creek [2710m]) [July] (3; DHKa); Summit Co., Blue River (3 mi. s. of

Breckenridge) [July] (5; RTBe). IDAHO: Bear Lake Co., Montpelier Canyon [Sept.] (12; CAS); Bonner Co., Hope [Aug.] (6; MSU, OSUC), Pend Oreille Lake (near Sandpoint) [Oct.] (19; DHKa, UASM), Priest Lake [July, Sept.] (23; CAS, UIMI), Sandpoint [June, Aug.] (18; CNC, JSch, NMDo); Kootenai Co., Coeur d'Alene [June] (4; CAS, DEUN, UMMZ, USNM), Hayden Lake [Aug.-Sept.] (24; CAS, MCZ, UIMI, USNM); Madison Co., Green Canyon Hot Springs [July] (8; UWBM); County unknown, Beaver Canyon [July] (7; USNM). MONTANA: (2; UMMZ); Beaverhead Co., Big Hole River (at Highway 91 [1550m]) [Sept.] (5; UASM); Carbon Co., Bridger (Clark's Fork Yellowstone River) [Sept.] (1; DHKa), East Rosebud Lake [June-Aug.] (18; CUB, DHKa, USNM), Quad Creek (17 mi. sw. Red Lodge [3050m]) [July] (2; DHKa), Red Lodge (Rock Creek [1680m]) [July] (4; DHKa); Cascade Co., Belt (Little Belt Creek [1100m]) [July] (5; DHKa), Dry Fork Belt Creek (at Henn Gulch [1620m]) [July] (3; DHKa), Monarch (and 1 mi. s. on Belt Creek [1400m]) [July-Aug.] (30; BFCa, DHKa); Fergus Co., East Fork Rock Creek ([1710m]) [July] (44; DHKa); Flathead Co., Flathead Lake [Sept.] (1; MSU), Hungry Horse ([1220m]) [July] (18; LRus), Kalispell [June] (14; CAS, FMNH, KSUC, MCZ, ROM, UASM, USNM); Gallatin Co., Bozeman ([1430m]) [Aug.] (4; LRus), Gallatin [June] (3; NMDo), Squaw Creek [Sept.] (1; UIMI); Glacier Co., Babb (4.5 mi. n. at Kennedy Creek [1400m]) [July] (2; DHKa), St. Mary [Aug.] (2; MSU), St. Mary River [Aug.] (19; CAS); Glacier National Park, Baring Creek [Aug.] (4; UWBM), Fish Creek Camp [Aug.] (5; OSUO), Going-to-the-Sun Chalet [Aug.] (44; UWBM), Lake McDonald [Aug.] (10; UWBM), Kintla Lake [June] (4; CAS), St. Mary Lake [Aug.] (2; CAS), St. Mary River [July-Aug.] (24; CAS, CUIC, FMNH), Sprague Creek Campground (at Lake McDonald) [Aug.] (7; RTBe), West Glacier (Flathead River) [Aug.] (5; SJSC);

Lincoln Co., Troy (Kootenai River [550m]) [July] (20; CAS, CUIC, LRus); Madison Co., Beaver Creek ([1920m]) [Aug.] (1; KUSM); Mineral Co., Alberton ([910m]) [Aug.] (5; LRus), St. Regis [Sept.] (1; FMNH); Missoula Co., Lolo Pass (2 mi. e. on Lolo Creek [1520m]) [July] (1; DHKa), Missoula [Aug.] (1; DZEC); Park Co., Emigrant [Aug.] (10; BFCa); Powell Co., Elliston ([1370m]) [July] (2; LRus); Ravalli Co., Como Lake [July] (1; FMNH), Grantsdale [Aug.] (3; BFCa), Ross Hole [Aug.] (3; USNM); Sanders Co., St. Regis (12 mi. ne. [760m]) [June] (1; LRus); Yellowstone Co., Yellowstone River (near Laurel at Highway 310) [Sept.] (3; DHKa, UASM). OREGON: Hood River Co., Hood River [May, Sept.] (5; MCZ). UTAH: Uintah Co.,Big Brush Creek (7 mi.wnw.of Highway 44 [2620m]) [Aug.](48;DHKa). WASHINGTON: (12; ANSP, INHS, KSUC, MCZ, UMRM, USNM); Benton Co., Hanford [May] (2; UWBM), Kennewick [Sept.] (1; UWBM), Richland [May] (2; UWBM), White Bluffs [June] (1; WSU); Chelan Co., Lake Chelan [May] (1; UAFA), Manson [May] (1; UWBM), Stehekin [July] (3; UWBM), Wenatchee [May] (5; UWBM); Douglas Co., Moses Coulee Creek [May] (1; UWBM); Franklin Co., Pasco [May] (14; MCZ, UWBM); Kittitas Co., Cle Elum [May] (3; UWBM), Ellensburg [June, Sept.] (84; CAS, FMNH, UWBM), Thorp [May] (19; LRus, UWBM), Vantage [May] (1; UWBM); Spokane Co., Spokane (and at Spokane Falls) [July] (6; CAS, USNM, WSU); Yakima Co., Toppenish [June] (1; UWBM). WYOMING: Albany Co., Centennial ([2440m] and 0.5 mi. e. on North Fork Little Laramie River [2440m], 2.0 mi. nw. on Libby Creek [2620m]) [July-Aug.] (36; DHKa, MSU), Keystone (1 mi. sse. at Douglas Creek [2680m]) [July] (1; DHKa), Woods Landing (Laramie River [2290m]) [July] (16; DHKa); Grand Teton National Park [June] (2; CAS), Colter Bay Camp [July] (1; CUIC), Jenny Lake [June-July] (16; FMNH, SJSC); Laramie Co., Cheyenne [May] (1; ICCM); Lincoln Co., Alpine

Junction (15 mi. se. on Greys River at Murphy Creek [1920m]) [July] (5; DHKa), Hoback Junction (16 mi. sw. on Snake River at Wolf Creek [1770m-1780m]) [July-Aug.] (26; DHKa); Park Co., Cody [July] (4; ANSP; MCZ), Crazy Creek (at Crazy Creek Campground [2120m]) [Aug.] (12; DHKa); Sublette Co., Battle Mountain (0.5 mi. s.) [Aug.] (1; EAMa), Bondurant (8 mi. nw. on Hoback River [2100m]) [July-Aug.] (93; DHKa), Boulder (15 mi. ne. on Boulder Creek [2260m]) [July] (12; DHKa), Green River Lakes (west shore [2440m-2590m]) [July] (12; DHKa), Pinedale (39 mi. nnw. on Green River at Whiskey Grove Campground [2320m]) [July] (36; DHKa); Teton Co., Granite Creek (at junction with Little Granite Creek [2150m]) [Aug.] (4; DHKa), Jackson (9.8 mi. s. on Snake River [1830m]) [Aug.] (40; DHKa); Yellowstone National Park [July-Aug.] (19; CAS, USNM).

Doubtful Records. UNITED STATES OF AMERICA, CALIFORNIA: (2; ANSP, UMRM).

No Data. (5; ANSP, MCZ, UASM, USNM).

Nebria ingens Horn

Map: Figure 408.

Nebria ingens ingens Horn

Specimens examined: 123 (32♂, 91♀)

UNITED STATES OF AMERICA

CALIFORNIA: Fresno Co., Mt. Darwin ([4150m]) [Aug.] (1; CAS); Inyo Co., Big Pine Creek (above Finger Lake [3440m]) [Aug.] (1; CAS), George Creek ([3440m]) [July] (1; CAS), Jigsaw Pass (east side [3350m]) [Sept.] (1; CDA), Mt. Agassiz (east slope [3720m]) [Aug.] (1; CAS),

Mt. Whitney (Lone Pine Creek [3270m-3760m]) [July] (112; DHKa, UASM, USNM); Tulare Co., Franklin Lakes [July, Sept.] (4; CAS, FMNH), Mt. Whitney [Aug.] (1; SFVS).

Nebria ingens riversi Van Dyke, NEW STATUS

Specimens examined: 9 (2♂, 7♀)

UNITED STATES OF AMERICA

CALIFORNIA: Mono Co., Mill Creek (northeast slope of Mt. Conness [3300m]) [Aug.] (1; CAS), White Mtn. (cirque on northeast slope [3350m]) [July] (2; DHKa); Yosemite National Park, Mt. Lyell (north slope [3350m-3450m]) [July] (6; CAS, CDA).

Nebria kincaidi Schwartz

Map: Figure 405

Nebria kincaidi kincaidi Schwartz

Specimens examined: 245 (155♂, 90♀)

CANADA

BRITISH COLUMBIA: Inverness [July] (2; CAS, USNM), Metlakatla (1; CUIC), Mount Hayes (near Prince Rupert [610m]) [June] (10; CNC), Telegraph Point (Kwinitsa) [June] (3; CNC, UASM), Thornhill Mountain (near Terrace [1070m-1520m]) [July] (3; CNC, MCZ), Tyee (2.6 mi. nw.) [June] (14; CNC, UASM); Vancouver Island, Forbidden Plateau (Mount Becher [910m-1370m]) [Aug.] (10; MCZ, UBC, UWBM), Mount Arrowsmith Trail ([300m-980m]) [Aug.] (3; UASM).

UNITED STATES OF AMERICA

ALASKA: Farragut [illegible] [June] (1; USNM). WASHINGTON: Mason Co., Lake Cushman [July] (1; [illegible]Z); Olympic National Park [Aug.] (23; AMNH, CAS, MCZ, UASM, USNM), Boulder Peak ([1520m]) [Aug.] (1; CNC), Hurricane Ridge [July] (16; UWBM), Mount Steel [July] (4; MSU, UMMZ), Olympic Hot Springs (Boulder Creek [670m-760m]) [May-Aug.] (149; CAS, CNC, DHKa, JSch, MCZ, UIMI, UWBM), Seven Lakes Basin [Aug.] (1; USNM), Sol Duc Hot Springs [July] (2; OSUO, UWBM), Soleduck River ([490m-760m]) [Aug.] (1; LRus); County unknown, Stillaguamish River [June] (1; UWBM).

Doubtful Records. CANADA, ALBERTA: Mount Edith Cavell [July-Aug.] (1; ROM).

Nebria kincaidi balli Kavanaugh, NEW SUBSPECIES

Specimens examined: 360 (187♂, 173♀)

UNITED STATES OF AMERICA

OREGON: Hood River Co., Mount Hood ([910m-1830m] and Cloud Cap Road at TillieJane Road, Hood River Meadows Ski Area [1620m-1710m], Tillie Jane Creek [1830m], Umbrella Falls) [June-Sept.] (62; AMNH, CAS, CUIC, DHKa, MCZ, MSU, ODA, USNM, UWBM, WSU). WASHINGTON: Mount P[illegible]er National Park [July-Sept.] (4; CUIC, SJSC, WSU), Cayuse Pass ([1400m]) [June] (1; USNM), Fryingpan Creek ([1160m-1190m]) [July-Aug.] (2; CNC, DHKa), Louise Lake [July] (5; UASM), Mowich Lake [July] (4; OSUO, UWBM), Mystic Lake [July] (1; WSU), Nisqually River ([1220m]) [May] (4; CNC), Paradise area (Narada Falls [1520m], Paradise Park [1520m-1830m], Paradise River [1460m-1830m]) [June-Aug.] (255; CAS, CNC, CUIC, DHKa, FMNH, KUSM, LRus, MCZ, OSUO, UASM, USNM, UWBM), Ricksecker Point [Sept.]

(1; UWBM), Sluskin Falls [July] (1; UWBM), Snow Lake ([1520m]) [Aug.] (1; CNC), Spray Park ([1980m]) [Aug.] (1; LRus), Sunrise area [July] (2; CAS, LRus), Van Trump Creek (above Christine Falls [1220m-1280m]) [July] (7; DHKa), Van Trump Park ([1830m]) [Aug. 1; CNC), West Drive [July] (1; CAS); Pierce Co., Coplay Lake [May] (1; UWBM); Skamania Co., Spirit Lake [910m-1770m] [Aug.] (1; OSUO).

Doubtful Records. UNITED STATES OF AMERICA, OREGON: Deschutes Co., Bend [July] (8; LACM).

Nebria lacustris Casey

Map: Figure 384

Nebria lacustris lacustris Casey

Specimens examined: 2276 (1196♂, 1080♀)

CANADA

MANITOBA: Winnipeg [June] (1; CUIC). ONTARIO: (1; CNC); Elgin Co., New Sarum (e. of St. Thomas) [June] (3; CNC), Port Stanley [Sept.] (3; UASM); Essex Co., North Bay (1; ROM); Halton Co., Burlington [June, Sept.-Oct.] (4; DMad), Zimmerman [May-June] (53; DMad); Huron Co., Grand Bay [June] (1; CNC); Middlesex Co., Fanshawe Lake (near London) [Aug.] (8; UASM), Lobo Township [Aug.] (7; UASM); N folk Co., D ri (w. of Simcoe) [June] (1; CNC), Normandale [June] (7: C), Turkey Point [Aug.] (1; UAFA); Oxford Co., Drumbo [Sept.] (1; RTB Peterborough Co., Peterborough [Sept.] (1; UAFA); Simcoe Co., Bondhead (16 mi. w.) [Sept.] (3; UASM); York Co., Toronto [May-Sept.] (18; CUIC, ROM. USNM). QUÉBEC: Cté d'Arthabaska, St-Louis-de-Blandford [Aug.] (1; ALar);

Cté de Beauharnois, Beauharnois [Sept.] (5; ALar, DBUM); Cté de Brome, Knowlton (and 5 mi. se.) [July-Aug.] (2; CNC, UASM); Cté de Charlevoix-Est, Baie Ste-Catherine [June] (3; ALar), La Malbaie [July] (1; ALar), Port-au-Persil [June-July] (29; ALar, CNC, DBUM), Port-au-Saumon [June-July] (103; ALar, CNC, DBUM, DHKa), St-Fidèle [July-Aug.] (9; ALar), St-Siméon [June-Aug.] (24; ALar, CNC, DBUM); Cté de Charlevoix-Ouest, Île-aux-Coudres [June-Aug.] (16; ALar, CNC, USNM); Cté de Frontenac, Lac-Mégantic [Aug.] (1; CPQC); Cté de Levis, St-Étienne [Sept.] (1; LRus); Cté de Lotbinière, St-Sylvestre [Aug.] (1; ALar); Cté de Portneuf, Ste-Catherine [Aug.] (1; ALar); Cté de Saguenay, Chute-aux-Outardes [June-July] (9; ALar, DBUM), Grandes-Bergeronnes [June] (1; ALar), Tadoussac [June, Aug.] (2; ALar, LEMC); Île-de-Montreal, Île Ste-Hélène [June, Aug.] (7; CPQC, DJLa), Montréal (1; CNC); County unknown, Chanon (1; CAS).

UNITED STATES OF AMERICA

CONNECTICUT: (1; AMNH). DISTRICT OF COLUMBIA: Washington (and Rock Creek Park) [May, Sept.-Oct.] (7; MCZ, USNM). ILLINOIS: (4; RTBe); Champaign Co., Urbana (1; ICCM); Kankakee Co., Momence [July] (2; UWEM); Ogle Co., Grand Detour [June] (3; FMNH); Vermillion Co., Grape Creek (1 mi. n.) [May] (2; RTBe), Kickapoo State Park [May, Sept.-Oct.] (8; RTBe), Muncie (3 mi. s.) [Nov.] (1; RTBe). INDIANA: Fountain Co., [May] (3; LRus); Lawrence Co., Spring Mill State Park [Oct.] (1; RTBe); Marion Co., Indianapolis [May] (1; PURC); Montgomery Co., Shades State Park [May, Sept.] (5; PURC, RTBe); Parke Co., [Oct.] (2; NMDo), Annapolis (Devil's Den) [July] (1; DHKa), Turkey Run State Park [June, Sept.] (14; DHKa, FMNH, UCD); Putnam Co., Greencastle [Sept.] (8; LRus);

Tippecanoe Co., [May-Oct.] (11; JSch, NMDo, UMMZ), Lafayette (and 1 mi. ne., 8 mi. w., Wabash River) [May, Aug.-Oct.] (25; GRNo, PURC, UMMZ, USNM), Wildcat Creek (4 mi. e. of Lafayette [200m]) [May] (12; DHKa); Vigo Co., (2; PURC). IOWA: (2; UMMZ); Buchanan Co., Independence (3; CAS, USNM, UWEM). KENTUCKY: Jackson Co., [May] (2; MCZ); Powell Co., Slade [June] (2; MCZ). MAINE: Aroostook Co., Allagash area [Aug.] (8; MCZ); Oxford Co., Bethel [Sept.] (2; MCZ). MARYLAND: Allegany Co., Difficult Creek [June] (3; MCZ); Baltimore Co., North Point [May] (1; USNM); Calvert Co., Calvert Beach [May] (1; JSch), Plum Beach [May] (1; JSch); Frederick Co., Buckeystown [Aug.] (1; RTBe); Montgomery Co., [Nov.] (1; USNM), Cabin John [Sept.-Oct.] (4; USNM), Plummers Island [Mar.-May, Sept.-Nov.] (18; CAS, USNM); Washington Co., Harpers Ferry [May] (1; USNM). MASSACHUSETTS: (9; AMNH, MCZ, USNM); Franklin Co., Mount Toby [Sept.] (1; MCZ); Hampshire Co., Amherst [Oct.] (2; JSch), Cummington [July] (1; USNM); Middlesex Co., Framingham [June] (2; USNM). MINNESOTA: [Sept.] (8; INHS, JSch, WSU); Ramsey Co., St. Paul (1; INHS). NEW HAMPSHIRE: (7; ANSP, CAS, DHKa, FMNH, MCZ, RTBe); Belknap Co., Lake Winnipesaukee (and Three Mile Island) [June] (2; MCZ); Carroll Co., East Wakefield (1; MCZ), Mount Chocorua [June] (4; MCZ); Coos Co., Carter Notch ([1070m]) [June] (1; ANSP), Errol (Atkinson and Gilmanton Academy Grant at Dead Diamond River) [June] (10; PMCh), Fabyaus (Ammonoosuc River) [July] (10; ANSP, CAS, MCZ, UMMZ), Mount Jefferson ([1520m]) (3; FMNH), Mount Washington ([760m-1520m] and Base Station [520m], Great Gap, Halfway House [1160m], Hermit Lake [1220m], Lake of the Clouds [1550m], Pinkham Notch, summit [1920m], The Flume, Tuckerman Ravine [610m-1220m]) [June-Sept.] (121; ALar, AMNH, ANSP, CAS, CUIC,

DHKa, FMNH, HGou, MCZ, PADA, PMCh, RTBe, UASM, USNM), Peabody River [July] (1; USNM), Randolph [Aug.] (2; AMNH), Shelburne [July] (2; MCZ); Grafton Co., Monroe (Connecticut River) [Aug.-Sept.] (4; PMCh, RTBe), Mount Moo- -uke [July] (1; USNM), Plymouth [Aug.] (1; MCZ), Rumney [Sept.] Z); Hillsboro, Merrimack (Souhegan River) [Aug.] (3; PMCh); Sullivan Co., Claremont (Connecticut River) [June-July] (13; PMCh), Cornish Mills (Connecticut River) [Aug.] (4; PMCh). NEW JERSEY: Cape May Co., Anglesea (1; CAS); Warren Co., Phillipsburg [May, July-Sept.] (17; CAS, UASM). NEW YORK: (18; AMNH, CAS, DHKa, INHS, KUSM, MCZ, USNM); Broome Co., Chenango State Park [Aug.] (3; GRNo); Cattaraugus Co., Allegany State Park [July-Aug.] (7; CUIC, USNM); Chautauqua Co., [Aug.] (1; USNM), Ellington area [July] (1; UASM), Findley Lake [July] (16; UASM), Mayville [July] (1; UASM); Chenango Co., [July] (2; USNM); Clinton Co., Plattsburg [July] (1; USNM); Erie Co., Buffalo (4; ANSP, USNM), Colden [Aug.] (1; USNM), Hamburg [Sept.] (3; CAS), Lancaster (1; UCB); Essex Co., Heart Lake [Aug.] (8; CAS, CUIC), Keane Valley [Aug.] (1; CUIC), Lake Placid [July] (3; CAS), Mount MacIntyre [June, Aug.] (9; CUIC), Opalescent River ([530m]) [Aug.] (2; RTBe), Wallface Mountain [July] (1; CAS); Fulton Co., [June] (1; USNM); Greene Co., (1; ICCM); Herkimer Co., Darts [June] (1; FMNH); Livingstone Co., Dansville [Aug.] (1; USNM); Monroe Co., Forest Lawn [July] (1; AMNH), Rochester [Sept.] (2; LACM); Niagara Co., Niagara (2; AMNH, MCZ), Olcott [July] (2; CUIC); Orange Co., Mountainville [June] (1; FMNH); Putnam Co., Brewster (2 mi. nw.) [Aug.] (3; PURC); St. Lawrence Co., Lisbon [Sept.] (2; UMMZ), Waddington [June] (3; CAS, CUIC); Schuyler Co., [June] (1; UWBM), Watkins Glen [Aug.] (5; AMNH, MCZ, PURC);

Sullivan Co., Beaverkill (1; AMNH), Roscoe (Willowemoc Creek at Highway 17 [430m]) [June] (4; DHKa); Tompkins Co., Cayuga Lake [Oct.] (4; UASM), Dryden (5.5 mi. wsw. at Fall Creek [270m]) [May] (10; DHKa), Falls State Park (beach at Taughannoch) [May] (2; USNM), Ithaca (and Cascadilla Creek, 5 mi. sw. at Inlet Creek [150m]) [May-Oct.] (122; AMNH, CAS, CUIC, DEUN, DHKa, KSUC, MCZ, PURC, UASM), McLean [June, Aug.] (3; CUIC, UASM); Ulster Co., Oliverea (17 mi. sw. at West Branch Neversink Creek [610m]) [June] (7; DHKa); Warren Co., Lake George (Silver Bay) [Sept.] (2; CUIC); Washington Co., Hulett's Landing (6; ICCM), Lake George (1; ICCM); Wayne Co., [June, Sept.] (11; UASM); Wyoming Co., Pike [July] (1; MCZ); County unknown, Hemlock Mountain [June] (5; AMNH), Winton (1; MCZ). NORTH CAROLINA: Avery Co., Cranberry (1; FMNH); Yancey Co., Crabtree Falls (10 mi. e. of Mount Mitchell) [June] (1; RTBe). OHIO: Ashland Co., [May] (6; PURC), Vermillion Township [June] (11; PURC); Ashtabula Co., [Sept.] (6; PURC), Ashtabula [June] (4; PURC), Jefferson [June] (4; PURC), Rock Creek [May-June] (38; PURC); Athens Co., [Oct.] (2; USNM), Athens [May, Oct.] (2; LACM, OSUO), Canaan Township [May] (1; OSUO), Carbondale [July] (1; LACM), Frost [Sept.] (1; UIMI); Butler Co., Heuston Woods State Park [June] (3; RCGr); Columbiana Co., Lisbon [May] (3; PURC); Coshocton Co., Newcastle Township (Walhonding River) [July] (1;PURC), Tiverton Township [Apr.] (1; PURC); Crawford Co., Bucyrus area [June] (5; PURC), Jefferson Township (Sandusky River) [June] (3; PURC); Cuyahoga Co., Cleveland (and Rocky River Reservoir) [May-June, Aug.] (8; MCZ, RTBe, USNM); Delaware Co., [Sept.] (2; OSUC); Franklin Co., Columbus [Apr.-May] (20; PURC), Georgesville [May] (8; PURC); Greene Co., [Sept.] (1; OSUC); Hamilton Co., Cincinnati [May, Aug.] (2; MCZ, UMMZ); Hancock Co., Allen

Township [May] (9; PURC), Cass Township [June] (2; PURC), Madison Township (Eagle Creek) [June] (1; PURC), Mount Blanchard (Blanchard River) [May] (3; PURC), Orange Township (Little Riley Creek) [May] (2; PURC), Union Township [July] (1; PURC); Hocking Co., [June] (69; OSEC, OSUC, PURC), Cedar Falls State Park [June, Aug.] (2; OSUO, PURC), Old Man's Cave State Park [July-Aug.] (5; CAS, PURC); Holmes Co., [May] (15; PURC), Holmesville [May] (1; PURC); Licking Co., [Oct.] (3; OSUC); Lorain Co., Brownhelm Township [Aug.] (1; PURC); Lucas Co., (1; PURC); Mahoning Co., Youngstown (Mill Creek Park) [May, Sept.] (11; PURC); Medina Co., Valley City [May] (6; PURC); Preble Co., [Aug.] (1; PURC), West Alexandria [May, Sept.] (2; RTBe); Portage Co., Charleston Township [Aug.] (6; PURC), Nelson Ledges State Park [June] (12; PURC), Windham Township [Aug.] (3; PURC); Putnam Co., Cascade (Anglaize River) [June] (3; PURC), Jenning Township [July] (1; PURC), Sugar Creek Township (Sugar Creek) [June] (2; PURC), Union Township (Sugar Creek) [June] (2; PURC); Richland Co., Springfield Township (Lake Walker) [July] (1; PURC); Sandusky Co., [June] (1; PURC); Vinton Co., Salt Creek [Oct.] (2; LACM), Zaleski State Forest [June] (2; LACM); Wood Co., [Apr.] (11; PURC), Grand Rapids [Oct.] (3; RCGr); Wyandot Co., Richland Township [June] (2; PURC), Sycamore [Aug.-Sept.] (5; CAS). PENNSYLVANIA: (7; CAS, MCZ, UMMZ, USNM); Allegheny Co., [May-June, Oct.] (21; CUIC, ICCM), Allegheny (7; ICCM, KUSM, MCZ), Fair Oaks [July] (1; UASM), Pittsburg [May-Sept.] (46; CAS, DZEC, ICCM, KUSM, OSUC, OSUO, UASM), Wildwood [Sept.] (4; ICCM); Armstrong Co., Ford City [June] (11; ICCM); Beaver Co., Raccoon Creek State Park [Aug.] (1; ICCM); Blair Co., Hollidaysburg (6 mi. e. on Highway 22) [June] (2; DJLa); Bradford Co., Wilawana [July] (2; LACM); Bucks Co., Delaware River (near Uhlerstown) [Oct.] (3; USNM);

Center Co., Philipsburg [May] (11; CAS); Crawford Co., Meadville [Aug.] (1; VMKi); Dauphin Co., Clark's Ferry [May] (1; VMKi), Harrisburg [May-Oct.] (5; CUIC, PADA), Inglenook [Sept.] (3; CAS); Delaware Co., Broomall [May] (1; AMNH); Erie Co., North East [Sept.] (3; CUIC, PADA); Fayette Co., Ohiopyle [July] (8; PSUC); Forest Co., Cooksburg Forest State Park (Cooksburg) [June] (7; RTBe); Lebanon Co., Lebanon (2 mi. n.) [Sept.] (5; UMMZ); Mifflin Co., Poe Paddy Recreation Area [July] (2; PSUC); Monroe Co., Mount Pocono [Sept.] (1; CAS); Northampton Co., Easton [June] (3; CAS), Lehigh Gap [Sept.] (1; USNM); Perry Co., Crow's Ferry [Sept.] (6; USNM), Newport [May] (3; USNM); Snyder Co., Middleburg [July] (1; UMRM); Susquehanna Co., Montrose [Aug.] (2; CAS, UCD); Warren Co., [Sept.] (2; UMMZ); Washington Co., McConnells Mill [July] (2; ICCM); Westmoreland Co., Jeannette [May-July] (48; ICCM); County unknown, Galbraith Gap [July] (1; PSUC), "Gertie's Notch" [Oct.] (4; PADA). TENNESSEE: Carter Co., Elizabethton [Sept.] (2; CAS). VERMONT: Addison Co., Brandon Gap (2 mi. e.) [July] (1; RTBe), South Lincoln (Cooley Glen Trail) [Sept.] (1; RTBe); Bennington Co., (1; CAS), Bennington (South Stream) [July] (4; RTBe), Sunderland (Bourn Pond) [July] (1; RTBe), West Arlington (Battenkill River) [June] (10; RTBe); Caledonia Co., Burke Mountain [Aug.] (4; RTBe); Chittenden C , Bolton (Bolton Notch, Gleason Brook, Joiner Brook) [May, July] (12; DHKa, RTBe), Burlington [Sept.] (1; RTBe), Camel's Hump ([910m-1220m]) [July-Aug.] (5; RTBe), Colchester Point [Sept.-Oct.] (21; CAS, RTBe), Jerico (Browns River) [Oct.] (1; RTBe), Jonesville (Gillette Pond, Winooski River) [June, Sept.] (4; RTBe), Milton (Lamoille River) [June] (2; RTBe), Mount Mansfield (summit, Sunset Ridge Trail [700m]) [June, July] (3; DHKa, RTBe), Shelburne [Sept.] (3; RTBe), Underhill [July] (4;

RTBe), Westford [Oct.] (1; RTBe); Essex Co., Beecher Falls (1 mi. e. at Connecticut River [340m]) [July] (5; RTBe), Granby (Moose River [350m]) [July] (3; RTBe), Lemington (3 mi. n. at Connecticut River [300m]) [July] (6; HoKn, RTBe), Maidstone (Connecticut River) [July] (8; RTBe); Franklin Co., East Georgia (south bank Lamoille River) [June] (8; RTBe); Grand Isle Co., Grand Isle (Eagle Creek) [July] (1; RTBe), Isle La Motte (Fleury Bay) [Sept.–Oct.] (17; RDav, RTBe); Lamoille Co., Bingham Falls ([380m]) [May-Aug.] (35; HoKn, RTBe, USNM), Elmore (Bedell Brook, Elmore State Park) [July-Aug.] (42; RTBe), Jeffersonville (Brewster River) [May, July-Aug.] (12; RTBe), Johnson (Ithiel Falls, 3 mi. nw. at Judevine Brook, Lamoille River) [June] (8; RTBe), Morrisville (Beaver Meadow Trail) [Aug.] (3; RTBe), Moscow (Nebraska Notch) [July] (1; RTBe), Mount Mansfield (Pringle's Ravine, Smugglers Notch [550m-700m], Canyon Trail) [May-Aug.] (50; HoKn, RTBe), South Cambridge (Brewster River) [June] (4; RTBe), Spruce Peak (Sterling Brook, Sterling Pond, Sterling Pond Trail) [July] (13; RTBe), Stowe (and 6 mi. n. [340m], Little River) [July-Aug.] (12; PMCh, RTBe, USNM), Waterville (North Branch Lamoille River, 2 mi. e.) [June, Sept.] (15; DHKa, RTBe), West Elmore (Bedell Brook) [July-Aug.] (151; CAS, RTBe); Orleans Co., East Charleston [July] (2; RTBe), Westmore (Long Pond Stream) [July] (1; RTBe); Rutland Co., Danby (Flower Brook) [July] (2; RTBe), Mount Tabor (Big Branch Creek) [June] (35; HoKn, RTBe); Washington Co., North Duxbury (0.75 mi. to 3.0 mi. s. on Ridley Brook [150m-240m]) [May-July, Sept.] (30; DHKa, RTBe); Windham Co., Brookline (Grassy Brook, Putney Mountain) [June] (8; RTBe), Dover (Blue Brook, Mount Pisgah Trail) [Aug.] (3; RTBe), Grafton (Saxtons River) [Aug.] (1; RTBe), Guilford (Broad Brook) [Aug.] (3; RTBe), Jamaica (West River) [June] (7; RTBe),

Newfane (Rock River) [June] (3; RTBe), Putney (Sacketts Brook) [July] (4; RTBe); Windsor Co., Windsor (Brownsville Brook) [June] (1; RTBe); County unknown, Mud City [July] (2; RTBe). VIRGINIA: Arlington Co., Alexandria [Sept.] (1; USNM), Rosslyn [Aug.] (2; USNM); Bath Co., Williamsville [Sept.] (1; USNM); Bedford Co., Goose Creek (near Moneta) [Sept.] (1; HoKn); Bland Co., South Gap (Wolf Creek) (2; HoKn); Carroll Co., Big Reed Island Creek [Aug.] (3; HoKn); Fairfax Co., [Sept.–Oct.] (3; MCZ, USNM), Black Pond [Oct.] (6; USNM), Potomac River (at Great Falls) [Sept.] (1; UWBM), Turkey Run (2 mi. e. of McLean) [Sept.] (10; HoKn, LRus, RTBe); Giles Co., Eggleston (New River) [Oct.] (3; HoKn); Grayson Co., Volney (3 mi. e. on Highway 58) [June] (4; DJLa); Highland Co., Bullpasture River Gorge (3 mi. ne. of Williamsville) [June] (2; HoKn); Montgomery Co., Radford (2 mi. e.) [Oct.] (4; HoKn, LRus, RTBe); Washington Co., Damascus (1 mi. s.) [Sept.] (1; HoKn); Wythe Co., Carter Wayside (2 mi. e. of Fort Chiswell at Reed Creek) [Oct.] (15; HoKn, LRus). WEST VIRGINIA: (4; CAS, USNM); Jefferson Co., Harpers Ferry [July] (1; DHKa); Ohio Co., Wheeling [June] (1; ICCM); Pocahontas Co., Highway 250 (2.6 mi. nw. of Virginia border) [Sept.] (4; UASM), Cranberry Glades (10 mi. n. of Visitor Center on Highway 150 [1400m]) [June] (6; HoKn); Randolph Co., (1; ICCM), Cheat Bridge [Sept.] (3; UASM), Shaver Fork Cheat River [May] (2; LACM, UIMI); Taylor Co., Grafton (2; USNM); County unknown, "Ft. Pendltn" [Sept.] (1; USNM). WISCONSIN: (6; INHS, SDSU); Bayfield Co., Bayfield (8; AMNH, CAS, DEUN, MCZ, USNM, UWEM); Columbia Co., Kilbourn [July] (1; UMMZ); Grant Co., Wyalusing State Park [July] (2; RTBe).

Doubtful Records. UNITED STATES OF AMERICA, TEXAS: (1; USNM).

No Data. (13; LEMC, PSUC, ROM, RTBe, USNM, UWBM).

Nebria lacustris bellorum Kavanaugh, NEW SUBSPECIES

Specimens examined: 264 (131♂, 133♀)

UNITED STATES OF AMERICA

NORTH CAROLINA: Great Smoky Mountains National Park [June] (1; MCZ), Indian Gap [Sept.] (1; USNM), Kephard Prong Oconaluftee River [Aug.] (14; DHKa, TCBa), Newfound Gap ([1520m-1580m]) [Aug.] (1; MCZ), Oconaluftee River (11 mi. se. of Newfound Gap on Highway 441 [550m], 2.3 mi. nw. of Smokemont [610m]) [May] (47; DHKa, USNM), Smokemont Loop Trail ([760m-910m]) [July] (18; UAFA); Haywood Co., Beach Gap (7 mi. e. of Sunburst at Middle Prong West Fork Pigeon River [1520m]) [June, Aug.] (4; HoKn), Bubbling Spring Branch ([1520m]) [July] (10; DHKa, TCBa), Graveyard Fields (Blue Ridge Parkway at Yellowstone Prong Pigeon River [1540m]) [May] (1; DHKa), Mount Sterling ([910m]) [Oct.] (7; CAS, CUIC), Retreat [May] (6; USNM); Swain Co., Bryson City (Deep Creek [610m]) [Aug.] (2; MCZ). TENNESSEE: Great Smoky Mountains National Park, Alum Cave Creek ([1220m-1250m]) [May] (4; DHKa), Chimneys Camp ([910m]) [May, Sept.] (18; CAS, CUIC, USNM), Newfound Gap ([1520m-1580m]) [Aug.] (2; MCZ, UASM), Tennessee Branch Bradley Creek ([980m]) [May] (15; USNM), Walker Prong Little Pigeon River [Aug.] (1; DHKa), West Prong Little Pigeon River ([1040m-1220m] and Chimneys Picnic Area [910m], 3 mi. s. of Gatlinburg [520m], 3.7 mi. n. of Newfound Gap [1220m]) [May, July, Sept.] (109; DHKa, MCZ, UAFA, USNM); Sevier Co., Gatlinburg [June] (1; DHKa).

Doubtful Records. UNITED STATES OF AMERICA, COLORADO: Jefferson Co.,

Golden (Clear Creek) [June] (1; USNM). LOUISIANA: St. Tammany Parish, Highway 90 (10 mi. w. of Mississippi border) [...e] (1; CAS).

Nebria lyelli Van Dyke

Map: Figure 390

Specimens examined: 19 (15♂, 4♀)

UNITED STATES OF AMERICA

CALIFORNIA: Yosemite National Park, Mount Lyell (below Lyell Glacier [3350m-3510m]) [July-Sept.] (19; CAS, DHKa).

Nebria mannerheimii Fischer

Map: Figure 399

Specimens examined: 2948 (1546♂, 1402♀)

CANADA

BRIT... OLUMBIA: (5; AMNH, INHS, LEMC); Mount Revelstoke National Park [Ju... (2; CAS); Other localities, Agassiz [June] (1; INHS), Boswell [... Sept.] (5; CNC, UBC), CheeKye [Aug.] (4; UBC), Chilliwa... rea (MacGillivray Creek) [July] (1; CNC), Downie Creek [A... g.] ... CAS), Edgewood [Aug.] (4; CAS), Fraser River (and between Choat... Haig, between Hope and Lillooet) [June, Aug.] (12; ANSP, ...SNM ...WBM), Glenora (5; ANSP, ICCM, MSU, USNM), Hazelton [Aug.] (1; ...), Hope (and 1 mi. n. at Kokahaala Creek) [June-July, Sept.] (9; BFCa, UASM, UBC, UWBM), Hunter Creek (at Restmore Lodge) [July] (4; CAS, DHKa), Kaslo [June] (1; USNM), Kitseguecla River (76 mi. e. of Terrace

[210m]) [July] (2; CNC), Klehini River (Haines Highway mi. 50) [June] (4; CNC, UASM), Kootenay Bay [May] (1; UASM), Kootenay Lake (Lockhart Beach) [Aug.] (16; WSU), Ladner (10 mi. e.) [June] (1; UASM), Lake Alice Provincial Park (0.2 mi. n. of Stump Lake at CheeKye River [100m]) (47; CAS, DHKa), Lillooet (Seton Creek) [June] (11; CNC, UASM), Lake [Aug.] (1; BFCa), Mission City [June] (1; CNC), New Westminster (Fraser River) [June] (5; CNC, UASM), North Bend [June] (6; UWBM), North Vancouver [June] (6; UWBM), Price Creek (near Kitwanga) [June] (3; UASM), Quesnel Lake [Sept.] (4; CAS, KUSM), Revelstoke [Aug.] (8; BFCa, CUIC, MCZ), Riondel [Oct.-Nov.] (3; CNC, UBC), Seltat Creek (Haines Highway mi. 48.8) [June] (1; UASM), Shuswap Lake (Narrows) [Aug.] (1; UBC), Sicamous [July] (3;UASM), Terrace (and 7 mi. e.) [June] (5; CNC,MCZ,USNM),Thompson River(near Ashcroft)[June](1;JVMa), Vancouver [June] (3; ANSP, CAS, UWBM), Wigwam Inn [June] (6; CAS), Zymoetz River (ne. of Terrace) [June] (6; UASM); Queen Charlotte Islands, Graham Island (Masset and 10 mi. s., 2 mi. sw. and 5 mi. s. of Port Clements, Yakoun River) [July-Aug.] (63; CAS, CUIC, DHKa, ICCM, MCZ, UASM, UWBM, WSU); Vancouver Island [June] (13; CAS, CNC, JVMa, USNM), Abernathy Brook (e. of Youbou) [Aug.] (22; UASM), Cameron Lake [July] (2; BFCa), Chase River (near Nanaimo) [Aug.] (6; UASM), Cowichan Lake [June-July] (6; CAS, CNC), Departure Bay [June] (9; ROM), Duncan [Aug.-Oct.] (23; CAS, CNC, CUIC, MCZ, UASM, UBC), Englishman River Falls Provincial Park (8 mi. w. of Parksville) [Aug.] (6; UASM), Goldstream [May-June, Sept.] (4; CUIC, MSU, UWBM), Kennedy Lake [June] (1; UWBM), MacMillan Provincial Park (12 mi. e. of Port Alberni) [Aug.] (3; UASM), Nanaimo (Chase River) [Sept.] (3; USNM, UWBM), Nanaimo River (at Highway 1) [May] (21; CNC, UASM), Nanoose [Aug.] (3; UWBM), Parksville [July-Aug.]

(12; BFCa, LACM, UWBM), Port Hardy [June] (4; UBC, UWBM), Sidney [Sept.] (2; MCZ), Storms [July] (5; BFCa), Victoria [June-Aug.] (35; ANSP, CAS, DEUN, INHS, ISUI, LACM, MCZ, ROM, UASM, USNM, UWBM), Wellington [July] (1; UWBM), West Cameron Creek (9 mi. e. of Port Alberni) [Aug.] (1; UASM).

UNITED STATES OF AMERICA

ALASKA: Big Boulder Creek (Haines Highway mi. 34) [June] (18; MCZ, UASM), Cape Yakataga [June, July] (1; CAS, JVMa), Juneau [June] (23; CAS, CUIC, JSch, MCZ, OSUC), Lawing [June] (1; CNC), Little Boulder Creek (Haines Highway mi. 31) [June] (22; MCZ, UASM), Muir Glacier (1; USNM), Muir Inlet (Glacier Bay) [June-July] (23; MCZ, OSUC, USNM, UWBM), Sebree Island [July] (2; OSUC), Seward [June] (17; CNC), Sitka [June] (4; USNM), Skagway [July] (8; CAS), Snow River delta [June] (2; CNC), Worthington Glacier (Richardson Highway mi. 28.7) [Aug.] (4; UASM), Wrangell Island (Wrangell) (1; USNM), Yakutat [June] (1; USNM). IDAHO: (1; SDSU); Washington Co., Weiser [Oct.] (2; USNM). OREGON: (5; ANSP, CAS, INHS, MSU, USNM); Baker Co., Robinette [June] (1; UWBM); Benton Co., Corvallis [July] (1; USNM); Clackamas Co., (3; USNM), Brightwood (Salmon River [320m]) [May, July] (72; DHKa, MSU, OSUO), Clackamas River [May] (6; DHKa), Mollala River (at Highway 211 [80m]) [July] (15; DHKa), Rhododendron ([490m] and 1 mi. se. at Zigzag River [600m]) [July-Aug.] (62; CAS, DHKa); Gilliam Co., Arlington (and 5 mi. w. at Columbia River) [Apr.-May] (7; INHS, JSch, MSU); Hood River Co., Hood River (and 0.2 mi. s. on Hood River [60m]) [May-July, Sept.] (183; CAS, DHKa, MCZ, OSUO, USNM), Mount Hood (and 4.2 mi. s. of Mount Hood Post Office at East Fork Hood River [730m], White River) [July] (42; CAS, DHKa, MCZ, UASM, UWBM),

Parkdale (Hood River Rapids) [July] (24; AMNH, ANSP, CAS, ICCM, MCZ, PURC, USNM, WSU), Polallie Campground [May] (16; JSC, MSU, NMDo); Lane Co., Oakridge (at Salmon River [350m], 9.5 mi. se. at Salt Creek [610m]) [July] (171; DHKa), Nimrod (0.9 mi. w. at McKenzie River [270m]) [July] (70; DHKa), North Fork McKenzie River (at Boulder Creek [520m]) [July] (3; DHKa), Salmon Creek (10.6 mi. e. of Oakridge at Blue Pool Campground [610m]) [June] (2; USNM); Linn Co., Detroit (5 mi. e. and 13 mi. se. at North Santiam River) [Aug.] (3; OSUO); Marion Co., Detroit (and 2.5 mi. e. at North Santiam River [490m], 5 mi. n.) [June-Sept.] (41; CAS, DHKa, LRus), Marion Forks (3.2 mi. s. at North Santiam River [930m]) [Aug.] (4; CAS, DHKa), Mill City (7.4 mi. w. on Little North Santiam River [200m]) [July] (6; DHKa), North Santiam River [July] (2; FMNH); Morrow Co., Boardman [Oct.] (1; USNM); Multnomah Co., Multnomah Falls [May] (5; UWBM), Portland (1; ICCM); Tillamook Co., Lee's Camp (Wilson River) [Apr.] (2; MSU); Union Co., Elgin (3.1 mi. nw. at Little Phillips Creek [1030m]) [May] (2; DHKa), La Grande (1 mi. ne. at Grande Ronde River [1070m]) [May] (2; DHKa); Wallowa Co., Minam (0.2 mi. se. at junction of Minam River and Wallowa River [790m]) [May] (14; DHKa); Wasco Co., The Dalles [May, July] (2; FMNH, OSUO). WASHINGTON: [Aug.] (13; CAS, INHS, MCZ, PADA, USNM); Asotin Co., Grande Ronde River [Sept.] (1; SJSC); Chelan Co., Lake Wenatchee State Park [June] (8; ROM), Soda Springs Campground [May] (7; UWBM); Clallam Co., Dungeness [May] (1; UWBM), Elwha [June] (3; UWBM), Elwha River [July] (8; UWBM), Forks [July-Aug.] (6; CAS, UWBM), Klahowya State Park (Soleduck River) [June] (10; CAS), Mora [Sept.] (5; UWBM), Port Angeles (and 4 mi. w.) [May-June] (49; ALar, CAS, CDA, CUIC, DBUM, PADA), Sequim [Sept.] (2; UWBM), Soleduck River (at Bogachiel River) [Aug.] (1; USNM); Clark Co.,

Vancouver (2; CAS), Washougal [Sept.] (1; UWBM); Cowlitz Co., Ariel [May] (2; UWBM), Toutle (14 mi. e. at North Fork Toutle River [300m]) [Aug.] (37; CAS, DHKa), Toutle River [May] (8; UWBM); Grays Harbor Co., Quinault Lake [May] (2; CAS); Island Co., Whidbey Island (Coupeville) (1; CAS); Jefferson Co., Brinnon area [May] (2; LACM), Kalaloch Beach [Aug.] (6; RTBe), Port Townsend (6; MCZ, PADA); King Co., Carnation [May] (48; LRus, NMDo, UWBM), Cedar Mountain [May, July] (33; UWBM), Cedar River [May] (5; UWBM), Enumclaw [July] (6; UWBM), Fall City (Snoqualmie River) [Sept.] (2; UWBM), Green River [May] (1; UWBM), Greenwater (5 mi. w. at White River [490m], Greenwater Campground) [June, Aug.] (11; DHKa, UWBM), Issaquah (6 mi. e.) [June] (17; ALar, LRus), Maple Valley (Cedar River) [May] (2; UWBM), North Bend (and Snoqualmie River at Maloney's Grove) [May-Sept.] (60; CAS, CUIC, FMNH, MCZ, UASM, UIMI, UWBM), Renton (and at Cedar River) [May, Sept.] (29; UIMI, UWBM), Seattle [Apr.-May] (7; KSUC, UWBM), Skykomish area [July] (11; UASM), Snoqualmie [June] (1; UIMI), Snoqualmie Pass [July] (1; CAS), Snoqualmie River (at Snoqualmie Falls) [May, Sept.] (2; UWBM), White River (at Slippery Creek) [Aug.] (4; UWBM); Klickitat Co., Blockhouse (8.2 mi. nw. at Klickitat River [350m]) [May] (16; DHKa), Glenwood [July] (1; OSUO), Trout Lake [July] (2; ANSP), White Salmon [Aug.] (1; UWBM); Lewis Co., Carlson (8.4 mi. s. at East Fork Tilton River [350m]) [July] (18; DHKa); Mason Co., Lake Cushman [June-July] (1; UMMZ), Shelton [Aug.] (1; UWBM), Skokomish River [May-June] (4; ANSP, USNM), South Fork Skokomish River [July] (18; UWBM); Mount Rainier National Park ([1520m]) [July, Sept.] (34; CAS, DHKa, MCZ, MSU, UBC), Carbon Glacier [Sept.] (1; UWBM), Carbon River [July] (9; FMNH, UWBM), Fryingpan Creek ([1160m]) [Aug.] (19; CNC, SJSC), Kautz Creek (at

Nisqually River) [Sept.] (2; UWBM), Longmire [July-Sept.] (35; CAS, UWBM), Nisqually River (and at Cougar Rock Campground [960m], near Longmire, 0.1 mi. above Paradise River [980m], at Sunshine Point Campground [610m]) [July-Sept.] (100; CAS, DHKa, MCZ, UWBM), North Fork Puyallup River (below toe of Puyallup Glacier [1100m]) [Aug.] (3; DHKa), Ohanapecosh [Aug.] (1; USNM), Paradise area (Paradise Valley [1520m-1830m]) [Aug.] (1; CAS), Sunrise area [July] (24; CAS, LRus), White River (and at White River Campground [1190m-1520m]) [May, July-Sept.] (52; CAS, DHKa, FMNH, SJSC, UWBM); Okanogan Co., Dan's Creek [Aug.] (7; UWBM); Olympic National Park [July-Aug.] (23; AMNH, CUIC, LACM, MCZ, USNM), Elwha Campground [Aug.] (29; CUIC, RTBe), Hoh River ([150m], and 20 mi. e. of Highway 101, Hoh River Campground, Jackson Campground) [June-Aug.] (61; CAS, DHKa, FMNH, LRus, ROM, USNM, UWBM), Lake Crescent [June, Aug.-Sept.] (27; CAS, CUIC, UIMI, UWBM), Sol Duc Hot Springs [June, Sept.] (4; UWBM); Pacific Co., Bay Center [Aug.] (5; UWBM); Pierce Co., American Lake [Apr.] (6; UWBM), Ashford (4 mi. e. on Nisqually River at Goat Creek [590m]) [July] (74; DHKa), Elbe (Nisqually River [400m]) [July-Aug.] (196; DHKa), Fairfax (Carbon River) [Aug., Oct.] (2; FMNH, UWBM), Fort Lewis [May] (2; CAS), Nisqually River [May] (1; UWBM), White River (at Silver Springs Campground [760m-790m]) [June, Aug.] (92; DHKa, UASM, USNM); Skagit Co., Skagit River [Aug.] (3; UWBM), Van Horn [Apr.-May] (12; AMNH, UWBM); Skamania Co., Carson [Aug.] (4; UIMI), Columbia River (15 mi. w. of Underwood[90m]) [May] (39; DHKa), Cook [July] (1; UWBM), Mount St. Helens (north slope at Leschi Creek [980m]) [Aug.] (8; CAS, DHKa), North Fork Toutle River (at Spirit Lake Lodge [940m]) [Aug.] (1; DHKa), Stevenson [June] (1; UWBM), Wind River (8 mi. n. of Carson [340m]) [July] (3; DHKa); Snohomish Co., Arlington

(and at North Fork Stillaguamish River) [Aug.] (25; SDSU, UWBM), Cicero (North Fork Stillaguamish River) [Aug.] (1; UWBM), Fortson [Apr.] (1; UWBM), French Creek (at North Fork Stillaguamish River) [Aug.] (1; UWBM), Glacier Peak [July] (1; CAS), Hazel [May] (5; UWBM), Index [May] (8; UWBM), Monroe [July] (4; CAS), Silver Lake [Aug.] (4; UWBM), Stillaguamish River [Mar.-Apr., July] (6; UWBM); Thurston Co., Deschutes River [May] (1; UWBM); Walla Walla Co., Burbank [May] (1; ANSP), Walla Walla [Aug.] (11; MCZ, OSUO); Whatcom Co., Glacier (and 3 mi. e.) [July] (39; CAS, DHKa, LRus), Lynden [Apr.] (4; LRus), Mount Baker [Sept.] (4; CAS, UWBM), North Fork Nooksack River (4 mi. e. [380m] and 19 mi. w. [270m] of Glacier, Silver Fir Campground [610m]) [Aug.] (46; CAS, DHKa), Shuksan ([760m]) [Aug.] (1; LRus), Shuksan Creek [Aug.] (5; UWBM), Skagit River (at Newhalem Campground) [July] (2; UWBM); Whitman Co., Central Ferry [Sept.] (1; UWBM), Pullman [May-June] (4; NMDo, WSU), Riparia [Apr.] (1; USNM), Wawawai ([300m], and 2 mi. nw. at Snake River [290m]) [May, July-Aug.] (16; CAS, DHKa, USNM, WSU), Wilma [May] (3; ICCM); County unknown, Olympic National Forest [Aug.] (1; CAS).

Doubtful Records. CANADA, YUKON TERRITORY: Swift River (Alaska Highway mi. 733.3) [Aug.] (4; LRus). UNITED STATES OF AMERICA, CALIFORNIA: (14; ANSP, KUSM, MCZ). NEVADA: Washoe Co., Verdi (2; CAS).

No Data. (9; AMNH, OSUO, UWBM).

Nebria meanyi Van Dyke

Map: Figure 406

Nebria meanyi meanyi Van Dyke

Specimens examined: 617 (285♂, 332♀)

CANADA

BRITISH COLUMBIA: Chilkat Pass (Haines Highway) [June] (1; CNC), Clear Creek (Haines Highway mi. 61.3) [June-Aug.] (15; UASM), Garibaldi Provincial Park ([1550m] and south slope Black Tusk [1830m-2040m], Whistler Mountain [1830m]) [July-Aug.] (29; CAS, CNC, DHKa), Leduc Glacier (35 mi. nw. of Stewart) [Aug.] (1; UBC). YUKON TERRITORY: Whitehorse Pass [July] (1; CAS).

UNITED STATES OF AMERICA

ALASKA: Little Boulder Creek (Haines Highway mi. 31) [June] (1; MCZ). CALIFORNIA: Siskiyou Co., Mount Shasta (Mud Creek at Clear Creek [1980m]) [Aug.] (45; CAS, DHKa). OREGON: Clackamas Co., Mount Hood (headwaters of Salmon River near Timberline Lodge [1830m-1950m]) [Aug.] (21; CAS, DHKa); Deschutes Co., Middle Sister Peak (North Fork Squaw Creek [1950m-2190m]) [Aug.] (150; CAS, DHKa); Hood River Co., Mount Hood (White River ([1300m] and at White River Glacier) [July-Aug.] (63; AMNH, CAS, DHKa, KUSM, MCZ, UASM, USNM); Marion Co., Mount Jefferson (Russell Creek [1680m-2190m]) [Aug.] (17; CAS, DHKa). WASHINGTON: Mount Rainier National Park [July] (11; CAS, CUIC, MCZ, UASM), Carbon River ([610m-910m]) [Oct.] (1; FMNH), Narada Falls (Paradise River [1160m-1460m]) [July-Aug.] (3; DHKa, USNM, UWBM), Nisqually River ([1160m-1420m], at toe of Nisqually Glacier [1220m-1520m], 0.1 mi. above Paradise River [980m]) [July-Sept.] (132; CAS, DHKa, MCZ), North Fork Puyallup River ([1130m] and below toe of Puyallup Glacier (1100m-1650m]) [Aug.] (59; CNC, DHKa), Paradise area (Paradise

Glacier, Paradise Park, Paradise River [1400m-1830m], Paradise Valley) [June-Aug.] (26; CAS, CNC, CUIC, DHKa, USNM, UWBM), Sluskin Falls [July-Aug.] (33; JSch, UWBM), Van Trump Creek (above Christine Falls [1220m-1280m]) [July] (2; DHKa), White River (at White River Campground [1310m-1520m]) [July] (3; FMNH); Snohomish Co., Glacier Peak [July-Aug.] (3; CAS, UWBM); Whatcom Co., Mount Baker (Heather Meadows Ski Area near Austin Pass [1190m-1310m]) [Aug.] (1; DHKa).

Doubtful Records. CANADA, ALBERTA: Jasper National Park, Mount Edith Cavell (1; ROM). UNITED STATES OF AMERICA, CALIFORNIA: Mendocino Co., Longvale Creek [July] (1; CAS).

Nebria meanyi lamarckensis Kavanaugh, NEW SUBSPECIES

Specimens examined: 23 (7♂, 16♀)

UNITED STATES OF AMERICA

CALIFORNIA: Inyo Co., Big Pine Creek (below Finger Lake [3140m]) [Aug.] (2; CAS), Lamarck Creek (above Upper Lamarck Lake [3260m-3350m]) [July] (21; DHKa).

Nebria meanyi sylvatica Kavanaugh, NEW SUBSPECIES

Specimens examined: 179 (84♂, 95♀)

CANADA

BRITISH COLUMBIA: Vancouver Island, Alberni (38 mi. w.) [May] (1; CNC).

UNITED STATES OF AMERICA

WASHINGTON: Olympic National Park [Aug.] (11; ICCM, MCZ, UASM, USNM), Elwha River (at Elwha Campground) [Aug.] (1; CUIC), Dosewallips River

(at Muscott Campground) [July] (3; UWBM), Olympic Hot Springs (Boulder Creek [670m-760m]) [May-Aug.] (160; CAS, CNC, DHKa, JSch, UWBM), Sol Duc Hot Springs [July] (3; JSch, UWBM).

Nebria metallica Fischer

Map: Figure 407

Specimens examined: 2298 (1305♂, 993♀)

CANADA

ALBERTA: Entrance (40 mi. wnw. at North Fork Wildhay River [1460m]) [June] (2; UASM), Freeman Lake (10 mi. s. of Swan Hills) [Aug.] (2; HGou), Goose Mountain ([1400m]) [Aug.] (4; HGou). BRITISH COLUMBIA: (9; AMNH, ANSP, FMNH, MCZ); Glacier National Park, Glacier [July, Sept.] (4; CAS, USNM), Rogers Pass ([1310m]) [June] (1; CNC); Other localities, Agassiz [Sept.] (1; CNC), Barkerville (Grouse Creek [1280m]) [Sept.] (1; UBC), Chilkat Pass (Haines Highway mi. 65.1) [June] (1; UASM), Clear Creek (Haines Highway mi. 61.3) [June] (1; UASM), Copper Mountain [Aug.] (3; UBC), Fraser River (between Hope and Lillooet) [Aug.] (1; UWBM), Garibaldi Provincial Park (south slope Black Tusk [1830m-2040m], Diamond Head Trail [1070m]) [July-Aug.] (2; CNC, DHKa), Glenora (1; USNM), Hunter Creek (at Restmore Lodge) [July] (2; CAS), Manning Provincial Park (Pasayten River) [May] (11; CNC, USNM), Merritt (Midday Valley) [July] (2; CAS), New Westminster (Fraser River) [June] (2; CNC), Peachland [June] (1; UASM), Pine Pass [June] (1; CNC), Seltat Creek (Haines Highway mi. 49) [June] (4; CNC, UASM), Skagit River (= Hope Trail [760m]) [July] (5; UBC), Snass Creek (at Warburton

Trail [760m]) [July] (1; UBC), Spious Creek [May] (2; CAS), Stanley [June] (1; UBC), Stikine River (6; ANSP, CAS, DEUN, ICCM, USNM), Two Sisters Mountain (15 mi. e. of Barkerville [1370m]) [June] (1; CNC), Vancouver [June] (4; MCZ, NMDo, USNM), Whipsaw Creek (at Hope Trail [1220m]) [July] (6; UBC, USNM), Vancouver Island (1; MCZ).

UNITED STATES OF AMERICA

ALASKA: (72; AMNH, CAS, CUIC, DHKa, INHS, KSUC, KUSM, LACM, MCZ, UMMZ, UMRM, USNM); Afognak Island [June-Aug.] (22; FMNH, UWBM), Anchor Point (Anchor River) [July] (4; UASM), Anchorage (and Elmendorf area) [July] (4; MCZ, UWBM), Baranof Island (Sitka) (14; ANSP, ICCM, INHS, MCZ, UASM, WSU), Belkovsky [July] (1; USNM), Bird Creek (27 mi. se. of Anchorage) [July] (22; CNC, UASM), Bristol Bay (Lake Brooks) [June-Sept.] (2; UWBM), Cold Bay [July-Aug.] (260; CNC, DHKa, MCZ, UASM), Cooper Landing (Stetson Creek) [Aug.] (3; CNC), Goodnews Bay [July] (2; USNM), Haines (8 mi. nw.) [July] (1; CNC), Hope [670m] [July] (1; CNC), Izembek Wildlife Refuge (Frosty Creek [60m], Simeon Mountain [240m]) [July] (24; DHKa), Juneau [June] (10; CAS, ICCM), Katalla [July] (2; CAS), Katmai [July] (5; CAS, OSUC, USNM), Knik River (at Glenn Highway) [July-Aug.] (19; MCZ, UASM), Kodiak Island ([270m-730m] and Amara Lake [150m-370m], Anton Larson Bay, Bare Lake [370m-640m], Bear Lake, Kalsin Bay, Karluk Lake, Kodiak area, Olga Bay, Port Bailey, Old Womans Mountain, Pasagshak Bay, Pinguicula Lake, Shasta Creek [240m], Uyak) [May-Sept.] (267; CAS, CUIC, DHKa, FMNH, ICCM, MCZ, OSUC, UASM, USNM, UWBM), Lawing [May] (2; CNC), Moose Pass [July] (1; CNC), Mount Pavlof area [Sept.] (1; CAS), Muir Glacier (3; MCZ), Muir Inlet (Glacier Bay) [June] (7; OSUC, USNM), Old Crow Mine (near Girdwood [610m-760m]) [July] (8; UASM),

Palmer (25 mi. n. [1220m]) [Aug.] (4; UASM), Pilot Cove [July] (1; ICCM), Port Heiden [July] (2; UASM), Prince of Wales Island (Craig) [May] (4; UWBM), Savonoski (Naknek Lake) [June-Aug.] (13; CAS, OSUC, PURC, USNM), Sebree Island [July] (1; OSUC), Security Cove (Kuskokwim River) [July] (1; USNM), Seward [May-July] (25; ALar, CAS, CNC, DEUN, ICCM, MCZ), Skagway [June-July] (8; CAS, USNM), Snow River (delta area) [May] (9; CNC), Thompson Pass (Richardson Highway mi. 25 [820m]) [Aug.] (6; MCZ, UASM), Tiekel River (Richardson Highway mi. 57.5) [Aug.] (1; UASM), Valdez (14 to 16 mi. e. on Richardson Highway) [Aug.] (2; MCZ, UASM), White Pass [Aug.] (13; LACM), Worthington Glacier (at Richardson Highway) [Aug.] (1; MCZ); Aleutian Islands (724; DBUM, INHS, MCZ, USNM), Adak Island (Adak, Mount Moffett) [July] (8; MCZ), Akutan Island (Akutan) [Aug.] (9; AMNH, CAS), Amchitka Island [June-Sept.] (6; USNM, UWBM), Atka Island (Nazan Bay) [Aug.] (16; CAS, DBUM), Umnak Island (Crater Creek, Nikolski, Okmok Caldera, Tulik Volcano, Umnak and vicinity) [July] (120; MCZ, UASM, UWBM), Unalaska Island (Amaknak Island, Driftwood Bay, Dutch Harbor, Glacier River, Makushin River at Broad Bay, Mount Makushin [400m-460m], Unalaska and vicinity) [June-Sept.] (135; ANSP, CAS, CUIC, DHKa, ICCM, MCZ, PADA, UASM, USNM); Pribilof Islands, St. Paul Island [May] (3; USNM); Location unknown, Fern Mine [Aug.] (1; UWBM). MONTANA: (1; USNM); Ravalli Co., Sula [July] (1; CAS); County unknown, Bitterroot Mountains (6; CAS, KUSM, USNM). WASHINGTON: (1; CAS); Clallam Co., Forks [July] (1; CAS), Klahowya State Park (Soleduck River) [June] (5; CAS); Jefferson Co., Kalaloch Beach [Aug.] (4; RTBe); King Co., Greenwater [June] (1; UWBM), North Bend [June-July] (23; AMNH, MCZ,

UASM, USNM, UWBM), Slippery Creek (at White River) [Aug.] (1; UWBM), Snoqualmie [May] (1; UWBM), Snoqualmie Falls [May, Aug.-Sept.] (3; UWBM), Wellington [July] (1; KSUC); Mount Rainier National Park, Fryingpan Creek [Aug.] (1; SJSC); Olympic National Park [Aug.] (17; CNC, MCZ, USNM), Dosewallips River [July] (2; UWBM), Elwha River (at Elwha Campground) [Aug.] (1; CUIC), Hoh River Rainforest [May] (1; LRus), Olympic Hot Springs [July] (1; UWBM), Sol Duc Hot Springs [June-Sept.] (14; CAS, UWBM); Pierce Co., White River (at Silver Springs Campground [790m]) [June, Aug.] (178; DHKa, USNM); Snohomish Co., Darrington [May] (2; UWBM), Glacier Peak [July] (1; UWBM), Hazel (Stillaguamish River) (3; UWBM), Monroe [July] (20; CAS, UMRM, UWBM), Sultan [May] (1; UWBM); Whatcom Co., Lynden [June, Aug.-Sept.] (10; LRus, UWBM), North Fork Nooksack River (at Silver Fir Campground [610m]) [Aug.] (2; CAS, DHKa), Shuksan Creek [Aug.] (1; UWBM); Yakima Co., Bumping River [Aug.] (3; UASM, USNM); County unknown, Stillaguamish River [May-June] (3; UWBM).

Doubtful Records. FRENCH POLYNESIA, SOCIETY ISLANDS: Tahiti (1; MHNP). UNITED STATES OF AMERICA, ARIZONA: White Mountains [June] (1; CUIC). CALIFORNIA: Los Angeles Co., Mint Canyon [May] (2; LACM); San Bernardino Co., Lake Arrowhead [July] (4; LACM). OREGON: (1; KUSM).

No Data. (37; AMNH, ANSP, CAS, FMNH, INHS, ISUI, MCZ, MSU, PADA, USNM).

Nebria navajo Kavanaugh, NEW SPECIES

Map: Figure 400

Specimens examined: 2 (26)

UNITED STATES OF AMERICA

ARIZONA: Navajo Co., Kayenta (19 mi. sw. [1980m]) [June] (2; CAS).

Nebria nivalis Paykull

Map: Figure 385, 386

Nebria nivalis nivalis Paykull

Specimens examined: 1165 (647♂, 518♀)

CANADA

BRITISH COLUMBIA: Swift River (Alaska Highway mi. 733.3) [Aug.] (1; LRus). NORTHWEST TERRITORIES: District of Franklin, Baffin Island (Cumberland Sound on Blacklead Island, Frobisher Bay, Pangnirtung, Steensby Inlet area) [June, Aug.] (29; ALar, CNC, LEMC, MCZ, USNM), Southampton Island (Coral Harbor) [July] (4; CNC); District of Keewatin, Aberdeen Lake [July] (1; CNC), Baker Lake [July] (5; CNC), Yathkyed Lake [Aug.] (1; CNC); District of Mackenzie, Aklavik [July-Aug.] (34; CAS, USNM), Coppermine [July-Aug.] (13; CNC), Coppermine River (at Bloody Falls) [July] (1; CNC), Fort Smith [July] (1; ALar), Granet Lake [July] (6; CNC), Kazan River [Aug.] (1; CNC), MacKay Lake area (1; CNC), Perry River (8 mi. inland) [July] (3; DJLa, USNM). QUÉBEC: Terr. du Nouveau-Québec, Bellin (=Payne Bay) [July] (1; CNC), Rivière Arnaud (=Payne River) [Aug.] (1; DBUM), Saglouc (=Sugluk) [July] (6; CNC), Wolstenholme [July] (1; UASM). YUKON TERRITORY: (1; CAS); Dawson (14 mi. e. [400m]) [July-Aug.] (11; CNC), Dempster Highway (mi. 28 [760m], mi. 35 [880m], mi. 60 [1010m], mi. 64 [1010m], mi. 78 [1010m]) [July] (14; CNC), Duke River (Alaska Highway mi. 1098) [June]

(5; CNC, UASM), Firth River [Aug.] (1; CNC), Little Salmon Lake [Aug.] (1; CNC), Mayo [July] (1; BFCa), North Fork Pass ([1070m-1250m]) [June] (7; CNC), Rampart House (and 18 mi. s.) [Aug.] (3; CNC).

UNITED STATES OF AMERICA

ALASKA: (12; ANSP, UWBM); Mount McKinley National Park [July] (2; CUIC, USNM), Eilson ([1190m]) [Aug.] (2; MCZ, UASM), Igloo Creek [Aug.] (3; MCZ, UASM), Riley Creek (at Hines Creek [520m]) [July] (16; DHKa, LRus), Savage River (1.2 mi. n. of Denali Highway [730m-810m]) [June-Aug.] (63; CAS, DHKa, UASM); Other localities, Anuk Lake (14 mi. s. of mouth of Cutler River [490m]) [Aug.] (13; RCra), Atkasuk [July-Aug.] (25; LACM, MCZ, UASM), Bear Creek (Steese Highway mi. 97.3 [640m]) [July] (10; DHKa), Beaver Creek (west of) [Aug.] (1; CAS), Black Rapids Glacier (Richardson Highway mi. 227) [July] (14; UASM), Cape Lisburne (1; CAS), Cape Prince of Wales (at mouth of Village Creek) [Aug.] (1; USNM), Cape Thompson [June-July] (11; CNC, WSU), Chatanika River (at Chatanika River Campground [240m]) [July] (30; DHKa), Cold Bay [July] (43; MCZ, UASM), Collinson Point [May] (1; CAS), Deering (1; JVMa), Delta River (at Black Rapids) [July-Aug.] (19; JVMa, MCZ), Eagle Summit (Steese Highway mi. 109) [July] (4; MCZ, UASM), Faith Creek (at Chatanika River [440m]) [July] (17; DHKa), Feniak Lake ([490m]) [July] (48; RCra), Goodnews Bay [Aug.] (4; USNM), Grants Cabin (Toms Lake) [July] (2; CAS), Gulkana [June] (1; UWBM), Ikpikpuk River (at Valley of Willows) [July] (1; JVMa), Isabel Pass (Richardson Highway mi. 206 [880m]) [July] (2; CNC), Kaolak River [Aug.] (4; UCB), Katmai [June-July] (6; CAS, OSUC, USNM), King Salmon (at Naknek Lake) [July] (2; CNC), Koyukuk River (1; USNM), Kuzitrin River (at Coffee Creek) [July] (3; JVMa), Lake

Brooks [June-Sept.] (29; USNM, UWBM), Lake Peters [June] (3; JVMa), Little Nelchina River (Glenn Highway mi. 138) [July] (2; MCZ, UASM), Mammoth Creek (Steese Highway mi. 116) [July] (9; MCZ, UASM), McManus Creek (Steese Highway mi. 76 [590m] and mi. 81.3 [610m]) [July] (63; DHKa), Montana Creek (Steese Highway mi. 83.2 [640m]) [July] (19; DHKa), Naknek Lake (and at Tom's Village) [June-July] (15; CAS, OSUC), Nome (and 30 mi. e., 8 mi. n. at Nome River) [June-Aug.] (43; CAS, ICCM, INHS, JVMa, MCZ, MSU, UASM), North Fork Twelvemile Creek (Steese Highway mi. 93.3 [750m]) [July] (17; DHKa), Pitmegea River (15 mi. e. of Cape Lisburne) [June] (1; MSU), Port Heiden [July] (13; UASM), Ptarmigan Creek (Steese Highway mi. 101.1 [730m]) [July] (7; DHKa), Quinhagak [Aug.] (1; USNM), Reed Creek (at Middle Fork Twelvemile Creek [730m]) [July] (25; DHKa), Robertson River (Alaska Highway mi. 1348) [June] (3; MCZ, UASM), Russian Mission [Aug.] (3; USNM), Savonoski (at Naknek Lake) [July-Aug.] (86; CAS, DHKa, OSUC, PURC, USNM), Security Cove [July] (1; USNM), Seward [June] (2; ICCM), Sinoruk (15 mi. n. of Wales) [July] (3; USNM), Solomon River (37 mi. e. of Nome) [Aug.] (7; MCZ, UASM), Sourdough Creek (Steese Highway mi. 66 [430m]) [July] (13; DHKa), Stuyahok River [July] (1; USNM), Taylor Highway (mi. 27) [July] (2; CNC), Teller (1; CAS), Tiekel River (Richardson Highway mi. 57.5) [Aug.] (1; UASM), Tok River (Alaska Highway mi. 1309) [June] (8; MCZ, UASM), Umiat [June] (1; USNM), Willow Creek (Steese Highway mi. 95.5 [620m]) [July] (44; DHKa), York [July] (1; USNM), Yukon River (between Holy Cross and Paimuit, between Marshall and Old Andreanofski) [July-Sept.] (3; USNM); Pribilof Islands (3; CAS, USNM, UWBM), St. Paul Island (Big Lake at base of Polovino Hill, St. Paul and 2 mi. n.) [June-Aug.] (132; CAS, CNC, ICCM, MCZ, UASM, USNM, UWBM); St. Lawrence Island,

Koozata Lagoon (west end) [Aug.] (3; UASM); St. Matthew Island [June-Aug.] (17; CNC, JVMa, UASM).

Doubtful Records. CANADA, BRITISH COLUMBIA: Vancouver Island, Union Bay [Apr.] (1; USNM). UNITED STATES OF AMERICA, ALASKA: Sitka (6; ICCM).

Nebria nivalis gaspesiana Kavanaugh, NEW SUBSPECIES

Specimens examined: 289 (120♂, 169♀)

CANADA

NEWFOUNDLAND: Island of Newfoundland, Little Codroy River [July] (4; MCZ, USNM), St. John Bay (Doctors Brook) [July] (5; CNC, ZMLS), South Branch (Grand Codroy River) [July] (4; MCZ), Spruce Brook (1; MCZ). QUÉBEC: Cté de Bonaventure [July] (1; ALar); Cté de Gaspé-Ouest, Parc de la Gaspésie (Mont Albert at Ruisseau du Diable [980m-1070m]) [June-July] (261; ALar, CNC, DBUM, DHKa, RTBe), Territoire du Nouveau-Québec, Rivière Abloviak [July] (1; DBUM).

UNITED STATES OF AMERICA

MAINE: Piscataquis Co., Baxter State Park (Mount Katahdin [910m-1580m]) [June-Aug.] (10; CAS, MCZ, USNM).

Nebria obliqua LeConte

Map: Figure 395

Specimens examined: 3846 (1965♂, 1881♀)

CANADA

ALBERTA: Banff National Park, Banff (and 1 mi. s. on Bow River) [June-Sept.] (36; CAS, CUIC, DHKa, MCZ, RTBe, UASM, USNM), Bow River [Sept.] (2; USNM), Cascade River (near Banff) [Aug.] (3; UWBM), Lake Louise [Aug.-Sept.] (5; AMNH), Lake Minnewanka [July] (1; UASM), North Saskatchewan River (at Highway 93) [July] (1; DHKa); Jasper National Park, Athabasca River (15 mi. e. of Jasper) [July] (5; DHKa), Cottonwood Creek Campground [Sept.] (3; RTBe), Jasper Lake [Aug.] (1; UASM), Rocky Creek (at Highway 16) [Aug.] (1; UASM); Waterton Lakes National Park, Waterton [June] (3; DJLa); Other localities, Aldersyde area [July] (1; BFCa), Assineau River (near Lesser Slave Lake) [July] (1; DHKa), Athabasca River (3 mi. ne. of Chain Lakes) [Sept.] (31; UASM), Belly River [July] (2; CAS), Blindman River (at Red Deer River) [May] (1; UASM), Cardston (and at Lee Creek) [July] (9; UASM), Cypress Hills [May-June, Aug.] (37; CAS, MCZ, PURC, UASM), Devon (0.2 mi. n. at North Saskatchewan River [700m]) [June] (19; DHKa), Drumheller (2 mi. w.) [Sept.] (1; DHKa), Drywood Creek [May] (1; DJLa), Edmonton (at Emily Murphy Park and0.1 mi. e. of Groat Bridge on North Saskatchewan River [670m]) [May-June, Aug.-Oct.] (21; DHKa, RTBe, USNM), Elk Creek Campground (30 mi. w. of Caroline) [Aug.] (1; MSU), Forestry Trunk Road (at North Saskatchewan River) [June] (2; DHKa), Fort Macleod [May-June, Aug.] (15; FMNH, UASM, UCD, UMMZ, USNM), Fort McMurray [June-July] (7; CNC), Freeman Lake (10 mi. s. of Swan Hills) [Aug.] (3; HGou), High River [May, Sept.] (3; CAS), Hummingbird Creek area [July] (2; BFCa), James River area (near Willow Creek) [Aug.] (2; BFCa), Lethbridge (Oldman River, St. Mary River) [May-Sept.] (43; CNC, CUIC, DJLa, ICCM,

LRus, MCZ, UASM, USNM), Maycroft [Aug.] (1; DJLa), Medicine Hat (at South Saskatchewan River) [May-Oct.] (93; ALar, AMNH, BFCa, CAS, CNC, CUIC, DBUM, FMNH, KUSM, MCZ, UASM, USNM), Milk River (se. of Comrey, at Lost River Ranch [580m]) [May, July] (5; BFCa, UASM), Moose River [July] (2; DHKa), Morse River (near Fort Assiniboine) [July] (3; UASM), Nordegg [Aug.] (4; DRWh), North Saskatchewan River (near Nordegg, at Highway 11) [July] (9; RFre, UASM), Pincher Creek [May, Aug.] (9; ANSP, DBUM, UASM), Prairie Bluff Mountain [June] (1; UASM), Ram River area [July-Aug.] (2; BFCa), Red Deer [July, Sept.] (4; JVMa, UASM), Reesor Lake area [May] (1; USNM), Rock Lake ([1400m]) [June] (1; UASM), Sheep River (and at Gorge Creek) [Aug.] (7; UASM), Spring Creek Basin (Simonette River) [June] (24; UASM), Sundre [July] (7; BFCa), Taber Provincial Park (Oldman River) [July] (3; ROM), The Forks (North Saskatchewan River at Clearwater River [1280m]) [July] (3; ANSP), Wildhay River (20 mi. nnw. of Entrance on Grand Cache Road [1310m], 30 mi. nnw. of Entrance) [June] (2; DHKa, UASM); Location unknown, Morin [Aug.] (1; UASM). BRITISH COLUMBIA: Glacier National Park, Loop Creek [June] (1; UASM); Kootenay National Park, Highway 93 (30 mi. sw. of Highway 1) [June] (1; UASM); Yoho National Park [July] (1; UWBM), Chancellor Peak Campground (Kicking Horse River) [Aug.] (1; UASM), Field (at Kicking Horse River [1460m]) [July-Aug.] (22; CAS, CUIC, DJLa, KUSM, USNM), Kicking Horse Campground [July] (1; CAS); Other localities, Adsett Creek (Alaska Highway mi. 233) [Aug.] (2; UASM), Big Creek (Alaska Highway mi. 674) [Aug.] (1; DHKa), Blanchard River (Haines Highway mi. 93) [June] (8; CNC, UASM), Blue River [June] (1; JVMa), Chilcotin [May] (7; UBC), Chilkat Pass ([1070m], and at Kelsall Lake) [July] (4; CNC, UASM), Creston (2 mi. w. at Kootenay River) [July]

(4; DHKa), Elk Creek (e. of Fernie) [July] (2; UASM), Fernie [July-Aug.] (9; CAS, CNC, UBC), Fort Nelson [Aug.] (3; CNC, UASM), Glenora (8; ANSP, CAS, ISUI, USNM), Golden [July] (3; ANSP, UASM), Goodrich Creek (12 mi. w. of Little Prairie) [June] (2; UASM), Hyland River (Alaska Highway mi. 605) [Aug.] (1; DHKa), Kicking Horse River (13 mi. w. of Field) [June] (19; USNM), Kootenay River (17 mi. n. of Kimberley) [Aug.] (1; UASM), Le Moray [July] (1; BFCa), Liard River (Alaska Highway mi. 491) [June] (1; UASM), Midday Valley (near Merritt) [Aug.] (1; UBC), Morrissey [July] (2; UWBM), Mount Robson Provincial Park ([1830m]) [July] (1; ANSP), Muskwa River (Alaska Highway mi. 296) [June] (13; CNC, UASM), Peace River (at Alaska Highway) [June] (1; UBC), Perow [June] (1; CNC), Pine Pass (Pine River) [Aug.] (1; MSU), Pouce Coupe [July] (1; BFCa), Princeton [May, July] (7; CNC, UBC), Racing River (Alaska Highway mi. 418.7) [June] (4; CNC, UASM), Sikanni Chief River (Alaska Highway mi. 160) [June] (14; CNC, UASM), Spious Creek [July] (2; INHS, UBC), Stikine River (1; USNM), Summit Lake (Alaska Highway mi. 392 [1280m]) [July] (4; CNC), Terrace (7 mi. e.) [June] (1; CNC), Tetsa River (Alaska Highway mi. 376, 378, and 383) [June, Aug.] (5; DHKa, LRus, UASM), Toad River (at Alaska Highway) (7; JVMa), Trout Creek (13 mi. n. of Smithers) [June] (1; UASM), Upper Liard River (Alaska Highway mi. 642.6) [June] (1; UASM). NORTHWEST TERRITORIES: District of Mackenzie, Great Slave Lake (at Hay River) [Aug.] (3; USNM). SASKATCHEWAN: Fort Walsh [July] (16; CNC, UASM). YUKON TERRITORY: Burwash Landing (5 mi. n.) [July] (1; WSU), Carcross [July] (1; CUIC), Dawson (14 mi. e. [400m]) [Aug.] (2; CNC), Duke River (Alaska Highway mi. 1098.5) [June] (1; UASM), Kluane Lake (Burwash Flats) [Sept.] (1; MSU), Swift River (Alaska Highway mi. 725 and 733)

[June, Aug.] (20; CNC, DHKa, UASM), Watson Lake [Aug.] (1; CNC).

UNITED STATES OF AMERICA

ALASKA: Chilkat River (15 mi. n. of Haines) [June] (1; MCZ), Copper Center [June-July] (2; UWBM), Little Boulder Creek (Haines Highway mi. 31.5) [June] (1; UASM), Tiekel River (Richardson Highway mi. 58) [Aug.] (3; MCZ, UASM). CALIFORNIA: Alpine Co., Markleeville Creek [Aug.] (17; CAS). COLORADO: (30; ANSP, CAS, INHS, KUSM, MCZ, MSU, USNM); Archuleta Co., East Fork San Juan River (3 mi. se. of Highway 160) [Aug.] (4; DHKa, EAMa), Upper San Juan River [Aug.] (2; MCZ); Boulder Co., Barker Reservoir (Barker Dam [2620m]) [July] (2; CArm), Beaver Creek ([2430m]) [July] (2; CArm), Caribou Bog [June] (1; CArm), Coal Creek ([2100m-2290m]) [July] (10; CArm, CAS, CUB), Crisman (Sixmile Creek [1890m]) [July] (1; CArm), Eldora (South Fork Middle Boulder Creek [2530m]) [July] (3; CArm), Lefthand Creek ([1980m-2380m], and 6.1 mi. wsw. of Highway 36 [2010m]) [July-Aug.] (22; CArm, CUB, DHKa), Lyons (Middle St. Vrain Creek [1950m]) [July] (1; CArm), Nederland (Boulder Creek [2380m-2440m]) [July] (6; CArm), Pinecliffe (3 mi. w. on South Boulder Creek) [Aug.] (7; DHKa), South Boulder Creek (near Gross Dam [2130m]) [July] (1; CArm), Ward ([2500m], and 5 mi. e. on Lefthand Creek) [July-Aug.] (26; CArm, DHKa), Wondervu (near Cripple Creek) [July] (3; CArm); Chaffee Co., Nathrop (Chalk Creek, and 3 mi. n.) [Aug.] (6; CDA, GRNo, UWBM), Poncha Springs (5 mi. s.) [Aug.] (1; GRNo); Clear Creek Co., Empire (Clear Creek) [Sept.] (1; LRus), Georgetown (and Georgetown Reservoir [2740m]) [June-July] (7; CAS, DHKa, USNM), Graymont (Clear Creek) [July] (1; DHKa), Leavenworth Valley ([2740m-3050m]) [June-July] (2; AMNH, MCZ), Silver Plume ([2740m-3050m]) [June] (5; CAS,

MCZ, UMMZ); Conejos Co., Conejos River (16 mi. w. of Antonito [2650m]) [June] (11; DHKa); Costilla Co., El Pozo [June] (2; OSUO), Fort Garland [June, Aug.] (36; ANSP, CAS, KSUC, MCZ, MSU, PURC, UMMZ, USNM); Custer Co., Hardscrabble Creek (at Smith Creek [2270m]) [June] (8; DHKa), Wetmore (10 mi. s.) [Aug.] (1; USNM); Dolores Co., Rico area ([2590m-3050m], and Scotch Creek [2680m]) [July] (7; CAS, CNC, KUSM, MCZ); Douglas Co., Sedalia (3 mi. e. at Plum Creek) [May] (2; DHKa); Eagle Co., Gypsum (Eagle River) [Aug.] (5; USNM), Vail (5.0 mi. e. at Gore Creek [2740m]) [July] (1; USNM); El Paso Co., Colorado Springs (1; INHS), Fountain Creek (at Highway 29 [1830m]) [June] (9; DHKa, EAMa), Manitou Springs [June] (2; CAS); Fremont Co., Cañon City [June] (2; USNM), Wellville (Arkansas River [2120m]) [June] (72; DHKa); Gilpin Co., East Portal area (South Boulder Creek [2740m]) [July] (7; CArm), Rollinsville (South Boulder Creek [2440m-2530m], and 2.5 mi. w.) [July-Aug.] (12; CArm, DHKa, UAFA); Grand Co., Granby (Fraser River) [Aug.] (2; USNM); Gunnison Co., [Aug.] (5; MCZ), Gunnison [June, Aug.] (5; OSUC, USNM); Hinsdale Co., Lake City [June] (1; KUSM); Huerfano Co., La Veda (and 5 mi. s. at Cucharas River [2320m]) [June-July] (9; DHKa, USNM), North La Veda Pass (east side [2530m]) [June] (7; DHKa, EAMa); Jefferson Co., Bear Creek [Sept.] (4; UWBM), Denver (18 mi. sw.) [Aug.] (3; GRNo), Evergreen (Bear Creek) [Sept.] (1; DHKa), Golden (and 1 mi. w. on Clear Creek [1770m]) [May-June, Aug.-Sept.] (143; DHKa, EAMa, USNM), Morrison (2 mi. e. on Bear Creek) [Oct.] (8; DHKa, SJSG, USNM), Tinytown (1 mi. n.) [Aug.] (3; CDA), Waterton (South Platte River) [July] (4; DHKa); Lake Co., Climax (3.8 mi. sw. [3050m-3350m]) [Aug.] (12; UAFA), Independence Pass area ([3660m], and 5.1 mi. e.) [Aug.] (6; UAFA), Leadville ([3050m-3350m]) [June-July] (18; CAS, DEUN), Twin

Lakes (Lake Creek) [June, Aug.] (2; CAS, DHKa); La Plata Co., Durango area ([1680m-2130m]) [July-Aug.] (1; MCZ), Gold King Mill (Tirbircio Creek [2830m]) [Aug.] (6; UASM), Junction Creek [July] (1; USNM), Rockwood [July] (1; KUSM); Larimer Co., Bennett Creek [July] (2; RTBe), Buckhorn Creek [July] (6; RTBe) Crown Point Road (at Bennett Springs [2350m], 4.0 mi. sw. of highway junction [2290m]) [Aug.] (9; DHKa, UASM), Fort Collins area ([2440m]) [July-Aug.] (6; CAS, CDA, GRNo, ICCM), Kelly Flats (Cache La Poudre River) [Aug.] (3; RTBe), Laporte (2 mi. w. and 6 mi. nw. on Cache La Poudre River) [May, Aug.] (65; CDA, DHKa, EAMa), Sheep Creek [Aug.] (1; RTBe); Los Animas Co., Cucharas Pass (5 mi. s. at Bear Creek [2800m]) [June] (3; DHKa), Stonewall Gap (Middle Fork Purgatoire River [2500m]) [June] (4; DHKa), Weston (4.4 mi. e. at Purgatoire River [2130m]) [June] (4; DHKa); Mineral Co., Big Meadows Reservoir (8 mi. n. of Wolf Creek Pass [2650m]) [July] (4; CNC), Creede ([2740m]) [July] (8; MCZ), South Fork (4 mi. w. on Rio Grande River) [Aug.] (1; DHKa); Moffat Co., Dinosaur National Monument (Green River) [May] (2; MSU); Ouray Co., Ouray area ([2290m-3050m]) [June-July] (43; AMNH, ANSP, CAS, KSUC, MCZ, UMMZ, USNM); Park Co., Alma (Middle Fork South Platte River [3140m]) [July] (10; CAS, DHKa, EAMa), Bailey (North Fork South Platte River) [Aug.] (9; USNM), Como (5 mi. w. on Tarryall Creek [3200m]) [July] (11; DHKa, EAMa), Deer Creek [June] (1; USNM), Fairplay (South Platte River) [Aug.] (1; USNM), South Platte River Middle Fork([3510m]) [July] (2; DHKa), Kenosha Pass ([3050m]) [July] (26; CAS, FMNH, MCZ, UCD, UMRM), Santa Maria (and 0.7 mi. e. on North Fork South Platte River [2290m]) [June] (64; DHKa, USNM); Pitkin Co., Aspen [July] (1; CUIC); Rio Blanco Co., Buford (3 mi. ne. on North Fork White River [2160m]) [Aug.] (26; DHKa); Rio Grande Co., Monte

Vista [Aug.] (2; UMMZ), South Fork (1 mi. e. on Rio Grande River, 2 mi. sw.) [Aug.-Sept.] (8; CDA, DHKa); Rocky Mountain National Park, Fall River ([2440m]) [Aug.] (18; UASM); Routt Co., Clark [July] (1; CAS); San Juan Co., Silverton area ([3050m]) [Aug.] (1; MCZ); San Miguel Co., South Fork San Miguel River ([2590m]) [July] (21; AMNH, ICCM, KUSM, [illegible]MRM, USNM), Trout Lake (Rico Road [2590m-3050m]) [July] (3; MCZ, [illegible]); Summit Co., Frisco (Temmile Creek) [Aug.] (2; RDav), Snake River (near Dillon Reservoir) [Aug.] (1; USNM); Teller Co., Florissant [June] (16; MCZ, PADA), Phantom Canon ([2960m]) [July] (1; CAS); County unknown, Bendimeer [July] (11; CAS), Douglas Pass ([2500m]) [Aug.] (1; MCZ), Evergreen Lakes [Aug.] (4; MCZ), Monument Gulch ([2130m-2740m]) [July] (1; CAS), North Fork South Platte River ([2130m-2440m]) [Aug.] (1; MCZ), San Luis Valley ([2350m]) [Aug.] (2; CAS, MCZ), Thayer (1; KSUC). IDAHO: (2; KSUC); Ada Co., Boise (2; UMMZ); Blaine Co., North Fork Warm Springs Creek (10 mi. w. of Ketchum [1890m]) [Aug.] (2; DHKa), Sun Valley [Sept.] (3; JSch); Boise Co., Crouch area (South Fork Payette River [910m]) [Aug.] (5; RTBe), Lowman [July] (1; BFCa); Camas Co., Carrie Creek (36 mi. wsw. of Ketchum [2100m]) [Aug.] (2; DHKa), Skeleton Creek (14 mi. e. of Featherville [1550m]) [Aug.] (3; DHKa), South Fork Boise River (at Bear Creek [1830m]) [Aug.] (1; DHKa); Cassia Co., Rock Creek Canyon (15 mi. s. of Rock Creek) [June] (9; UIMI); Custer Co., Challis (9 mi. n.) [Sept.] (2; UIMI), Rothas (8 mi. ne. at Pass Creek [1980m]) [Aug.] (1; DHKa), Salmon River (at Bayhorse Creek [1620m], 12 mi. n. of Challis) [July-Aug.] (12; DHKa, UWBM), Summit Creek (9 mi. ne. of Trail Creek Summit [2130m]) [Aug.] (5; DHKa); Elmore Co., Pine (3 mi. n. on South Fork Boise River at Dog Creek Campground [1460m]) [Aug.] (23; DHKa); Nez Perce Co.,

Lewiston [May] (8; UIMI, UWBM); Twin Falls Co., Magic Hot Springs [July] (4; FMNH, UWBM); Valley Co., Payette Lake [Aug.] (1; NMDo); Washington Co., Weiser [Oct.] (11; USNM). MONTANA: Big Horn Co., Hardin (2 mi. se. at Bighorn River [940m]) [July] (126; DHKa), Wyola (9 mi. se. at Little Bighorn River [1280m]) [July] (26; DHKa); Carbon Co., Bridger (Clarks Fork at Highway 310) [Sept.] (1; UASM); Cascade Co., Belt (Little Belt Creek [1100m]) [July] (19; DHKa), Belt Creek (at Highway 87) [June] (2; DJLa, RFre), Sun River (on Sun River at Highway 200 [1010m]) [July] (1; DHKa); Chouteau Co., Highwood Creek (26 mi. ne. of Belt [1310m]) [July] (41; DHKa), Loma (Marias River) [June] (1; UASM), North Fork Highwood Creek (at Briggs Creek [1370m]) [July] (34; DHKa), South Fork Highwood Creek (at Big Coulee [1490m]) [July] (14; DHKa); Flathead Co., Flathead Lake [Aug.] (1; USNM), Kalispell [June] (1; USNM), North Fork Flathead River (at Middle Fork Flathead River) [Aug.] (1; OSUO), West Glacier (Middle Fork Flathead River) [July] (2; DHKa); Gallatin Co., Bozeman ([1430m]) [Aug., Oct.] (4; DZEC, LRus), Cabin Creek (at Madison River) [July] (1; ICCM), Madison River (25 mi. sw. of Bozeman) [June] (1; MSU), Manhattan ([1430m]) [Aug.] (3; LRus); Glacier Co., Cut Bank Creek (n. of Browning) [July] (3; UASM); Glacier National Park, St. Mary entrance [July] (2; SJSC), West Glacier entrance [Aug.] (1; SJSC); Judith Basin Co., Hobson (0.2 mi. nw. at Judith River [1280m]) [July] (8; DHKa); Lewis and Clark Co., Helena [Aug.] (1; USNM); Lincoln Co., Troy (at Kootenai River [550m]) [July-Aug.] (3; CUIC, LRus); Yaak River (at Kootenai River) [Aug.] (1; MSU); Mineral Co., Alberton ([910m]) [Aug.] (7; LRus); Powell Co., Lincoln (10 mi. w. [1130m]) [July] (2; LRus); Ravalli Co., Hamilton [Sept.] (1; UIMI); Sanders Co., St. Regis (12 to

13 mi. ne. [760m]) [June-July] (2; LRus); Teton Co., Dutton (5 mi. n. at Teton River [1070m]) [July] (5; DHKa); Toole Co., Marias River [Sept.] (3; CNC), Shelby (6 mi. s. at Marias River [980m]) [July, Sept.] (11; DHKa, UASM); Yellowstone Co., Billings (Yellowstone River at Highway 87 [980m]) [July] (8; DHKa), Laurel (Yellowstone River at Highway 310) [Sept.] (2; DHKa, UASM). NEBRASKA: Sioux Co., Glen [Aug.] (1; DEUN). NEVADA: (3; ANSP); Elko Co., Contact [Aug.] (1; BFCa), Lamoille Creek (at Lower Lamoille Campground [1920m]) [Aug.] (3; DHKa), Wildhorse Dam (0.1 mi. nw. on Owyhee River [1870m]) [Aug.] (17; DHKa); Nye Co., Reese River (0.3 mi. s. of Reese River Ranger Station [2090m]) [July] (12; DHKa). NEW MEXICO: (6; ANSP, LACM, MCZ, UMRM); Mora Co., Gãscon (2 mi. w. at Rio de Gascon [2440m]) [Aug.] (6; UASM); Rio Arriba Co., Canjilon (9.5 mi. ne. at Canjilon Creek [2770m]) [June] (2; DHKa), Cañones Creek (at Highway 96 [2010m]) [June] (4; DHKa), Rio Puerco (at Rio Puerco Campground [2350m-2440m]) [June] (1; DHKa), Rio San Antonio (14 mi. e. of Lagunitas [2730m]) [June] (5; DHKa), Rio Tusas (at Highway 553 [2730m]) [June] (3; DHKa); Sandoval Co., Rio de Las Vacas (at Highway 126 [2480m]) [June] (2; DHKa); San Miguel Co., Beaver Creek (sw. of Rincon Montoso [2620m]) [Aug.] (1; UASM), Cowles ([2440m], and 2.0 mi. n. on Panchuela Creek at Panchuela Campground [2530m]) [June] (57; DHKa, UASM), Gallinas (5.5 mi. w. [2260m-2440m]) [June, Aug.] (39; UASM), Holy Ghost Canyon (14 mi. n. of Pecos [2440m]) [June] (8; UASM), Jack's Creek (at Pecos River [2480m]) [June] (4; DHKa), Pecos (0.5 mi. n. [2090m] and 9.9 mi. n. at Windy Bridge [2260m] on Pecos River) [June] (50; DHKa), Rio Moro (at Pecos River [2410m]) [June] (33; DHKa), Sapello (15.7 mi. w. at Mosimann Ranch [2440m]) [June] (5; UASM), Tererro

(3.0 mi. w. at Holy Ghost Creek [2480m]) [June] (4; DHKa), Upper Pecos River [June] (4; CAS), Winsor Creek ([2560m-2590m]) [June] (4; DHKa); Santa Fe Co., Black Cañon Campground ([2590m]) [Aug.] (1; RCGr), Santa Fe (Santa Fe Cañon [2130m]) [June-Aug.] (29; CAS, KSUC, KUSM); Taos Co., Angostura Creek (0.3 mi. s. of Highway 3 [2710m]) [June] (8; DHKa), Questa (2.0 mi. e. on Red River [2330m]) [June] (52; DHKa), Red River (2.4 mi. se. [2730m], 8.0 mi. s. [2870m], 2.2 mi. w. at June Bug Campground [2610m], and 4.1 mi. w. [2580m] on Red River) [June] (182; DHKa), Rio Pueblo (1.7 mi. [2390m] and 5.4 mi. [2510m] e. of junction of Highways 3 and 3/75) [June] (26; DHKa), Shady Brook (2.0 mi. e. at Rio Fernando de Taos [2440m]) [June] (4; DHKa), Tres Ritos [July] (8; CAS, CNC). OREGON: Baker Co., North Powder River (10 mi. nw. of Haines [1040m]) [May] (4; DHKa); Crook Co., Ochoco Creek (14 mi. e. of Prineville [1020m]) [May] (1; DHKa); Grant Co., Dale (2.4 mi. s. at Meadow Brook [1050m]) [May] (4; DHKa); Mount Vernon (1.5 mi. e. on John Day River [940m]) [May] (3; DHKa), Prairie City (John Day River) [Sept.] (5; JSch); Lake Co., Adel (5 mi. sw.) [June] (1; JSch); Malheur Co., Farewell Bend State Park [Sept.] (1; UASM); Umatilla Co., Dale (1 mi. n. at North Fork John Day River [910m]) [May] (5; DHKa), Echo (Umatilla River [290m]) [May] (1; DHKa), Freewater [Sept.] (3; OSUO, USNM), Rieth (5.9 mi. w. at Umatilla River [370m]) [May] (1; DHKa); Wallowa Co., Minam [May] (2; UWBM); Wasco Co., Tygh Creek (at Highway 197) [June] (1; JSch). SOUTH DAKOTA: Custer Co., Custer (2 mi. s.) [Aug.] (2; UASM), Sylvan Lake [Aug.] (1; DHKa); Fall River Co., Hot Springs [Sept.] (1; VMKi); Lawrence Co., Cheyenne Crossing (2.2 mi. se. at East Fork Spearfish Creek [1830m]) [July] (3; DHKa), Nemo [Aug.] (1; UMMZ), Spearfish (and 5 mi. [1340m] and 10 mi. [1520m] ssw. at

Spearfish Creek) [July-Sept.] (63; DHKa, VMKi); Pennington Co., Hill City (Castle Creek [1460m]) [July] (8; DHKa), Rochford (2 mi. ese. at Rapid Creek [1570m]) [July] (29; DHKa); County unknown, Palmer Creek [Aug.] (8; MSU). UTAH: (1; ANSP); Beaver Co., ([2440m-3050m]) [Aug.] (2; CAS, USNM), Beaver (and 4.1 mi. e. on Beaver River at Little Cottonwood Campground [2100m]) [June, Aug.] (4; BFCa, DHKa), North Creek [July] (5; CAS, MCZ, USNM); Cache Co., Logan [June-July] (4; CAS, EMUS), Providence [Aug.] (1; EMUS); Garfield Co., Antimony (8 mi. s. on Sevier River) [July] (9; UAFA), Hatch [Aug.] (2; BFCa), Panguitch (2.5 mi. se. on Sevier River [2010m]) [July] (32; DHKa), Sevier River (at Highway 12) [July] (5; UASM); Iron Co., Parowan (and 2.7 mi. s. on Parowan Creek [1920m]) [June-July] (44; DHKa, USNM), Vermillion Castle Campground [July] (2; UIMI); Kane Co., Glendale (4.9 mi. [1860m] and 6.0 mi. [1890m] ne. at East Fork Virgin River, 21.6 mi. n. on Highway 89 [1920m]) [June, Aug.] (30; DHKa, UASM); Millard Co., Fillmore [Aug.] (2; CNC); Morgan Co., Mountain Green (Weber River [1510m]) [Aug.] (12; DHKa); Piute Co., Kingston (9 mi. e. at East Fork Sevier River [2350m]) [June] (3; DHKa), Marysvale (2.2 mi. w. at Beaver Creek [1830m]) [July] (2; DHKa); Summit Co., East Fork Bear River (31.1 mi. s. of Evanston [Wyoming] [2500m]) [Aug.] (7; DHKa), Kamas (5.2 mi. e. at Beaver Creek [2130m]) [Aug.] (1; DHKa), North Fork Provo River (at Highway 150) [Aug.] (1; USNM), North Fork Upper Provo River (12.5 mi. [2300m] and 15.8 mi. [2390m] e. of Kamas) [Aug.] (4; DHKa); Utah Co., American Fork Canyon [June] (26; ANSP, CAS, INHS, USNM), Provo [June] (1; USNM), Provo River (at Upper Falls [1570m]) [Aug.] (1; DHKa); Wasatch Co., Daniels Creek (near Heber) [Aug.] (3; UASM), Deer Creek Reservoir [Aug.] (1; BFCa), Hailstone Junction (3.4 mi. e. on Upper

Provo River [1890m]) [Aug.] (4; DHKa), Provo River (12.2 mi. ne. of Provo [1630m]) [Aug.] (1; DHKa); Wayne Co., Capitol Reef National Monument (2.1 mi. e. of Capitol Reef Lodge on Fremont River [1710m]) [Aug.] (2; DHKa); Weber Co., Ogden [July] (4; USNM). WASHINGTON: (5; MCZ, USNM, WSU); Asotin Co., Asotin (Asotin Creek [370m]) [May] (1; DHKa); Benton Co., Hanford [Apr.-May] (3; UWBM), Kennewick [Sept.] (1; UWBM), Richland [Apr.-May] (11; FMNH, UWBM); Chelan Co., Cashmere [July-Aug.] (5; CAS, UWBM), Leavenworth [July] (8; AMNH, MCZ, UCR, USNM), Wenatchee [Aug.] (3; UWBM); Columbia Co., Dayton [Sept.] (3; CUIC); Franklin Co., Pasco [May] (22; MCZ, UWBM), Perry [Aug.] (1; USNM); Kittitas Co., Cle Elum [June-July] (46; UWBM), Easton (2; CAS, USNM), Ellensburg [May-July, Sept.] (10; CAS, CNC, FMNH, UWBM), Swauk Creek [June] (1; UWBM), Thorp [May] (37; LRus, UWBM), Vantage [May] (4; UWBM); Okanogan Co., Nine Mile [Sept.] (1; LACM); Skamania Co., Stevenson (1; UWBM); Walla Walla Co., Burbank [May] (1; WSU), Snake River (at Columbia River) [Aug.] (2; CAS), Touchet River (near Waitsburg) [July] (8; DJLa), Walla Walla (2 mi. s. at Walla Walla River [320m]) [May] (3; DHKa); Whitman Co., Central Ferry (Snake River) [Aug.-Sept.] (2; UWBM), Pullman [Apr.-May] (2; WSU), Wawawai [May] (1; JSch); Yakima Co., Cliffdell (4.3 mi. se. on Naches River [730m]) [July] (2; DHKa), Naches [July, Sept.] (74; KUSM, UWBM), Naches River (and at Tieton River [560m]) [July-Aug.] (47; DHKa, USNM), Yakima [May, Sept.] (7; JSch, USNM, WSU); County unknown, East Bar [Apr.] (1; USNM). WYOMING: (1; USNM); Albany Co., Keystone (1 mi. sse. at Douglas Creek [2680m], 5 mi. sse. at Lake Creek [2620m]) [July] (31; DHKa), Woods Landing (Laramie River [2290m]) [July] (26; DHKa); Carbon Co., Medicine Bow (4 mi. n. at Little Medicine Bow River) [Aug.] (1; RCGr), Riverside

(Encampment River [2180m]) [July] (26; DHKa); Converse Co., Horseshoe Creek (34 mi. s. of Douglas [1890m]) [July] (22; DHKa); Fremont Co., Fort Washakie (Little Wind River) [Aug.] (11; EAMa), Wind River (38.8 mi. e. of Moran Junction [2290m]) [June] (1; RFre); Grand Teton National Park [July] (4; CAS), Colter Bay Campground [July] (1; CUIC); Johnson Co., Clear Creek (12 mi. w. of Buffalo [2190m]) [July] (18; DHKa); Lincoln Co., Greys River (15 mi. se. of Alpine Junction at Murphy Creek [1920m]) [July] (21; DHKa), Salt Creek (12.5 mi. ne. of Geneva [2060m]) [Aug.] (3; DHKa), White Creek (20 mi. se. of Alpine Junction [2190m]) [July] (3; DHKa); Park Co., Cody (and at Morris Ranch [2040m]) [July, Sept.] (2; ANSP, CUIC); Platte Co., Bluegrass Creek (36 mi. ne. of Bosler [1620m]) [July] (6; DHKa); Sheridan Co., Dayton (Tongue River [1190m]) [July] (2; DHKa), Piney Creek (19 mi. ssw. of Sheridan [1370m]) [July] (30; DHKa); Sublette Co., Battle Mountain (0.5 mi. s. on Hoback River) [Aug.] (17; EAMa), Big Sandy (4.5 mi. nw. at East Fork River [2190m]) [July] (7; DHKa), Bondurant (8 mi. nw. on Hoback River [2100m]) [July-Aug.] (74; DHKa), Boulder Creek (15 mi. ne. of Boulder [2260m]) [July] (7; DHKa), Green River (39 mi. nnw. of Pinedale at Whiskey Grove Campground [2320m]) [July] (1; DHKa), Hoback River (14 mi. sw. of Highway 187/189 [2440m]) [July] (38; DHKa), Pinedale (Pine Creek [2180m]) [July-Aug.] (2; DHKa, MSU), Pole Creek (at Highway 187/189, 6 mi. se. of Pinedale [2160m]) [July-Aug.] (2; DHKa, EAMa); Sweetwater Co., Farson (Little Sandy River [Sept.] (1; UASM), Green River ([1830m-2130m]) [July-Aug.] (12; CAS, KUSM, MCZ, MSU, USNM); Teton Co., Granite Creek (at Little Granite Creek [2150m]) [Aug.] (4; DHKa), Togwotee Pass (3.7 mi. wnw. at Blackrock Creek [2770m]) [Aug.] (8; DHKa); Washakie Co., Tensleep Creek (11 mi. [1890m] and 16.6 mi.

[1550m] ne. of Tensleep) [July] (15; DHKa); Yellowstone National Park [July-Aug.] (17; AMNH, INHS, USNM), Astringent Creek [July] (1; UCB), Gardner River (and at Mammoth Hot Springs) [Aug.-Sept.] (24; JSch, NMDo, UWBM), Norris Geyser Basin ([2130m]) [May-June, Aug.] (12; LRus, UASM, UMMZ), Slough Creek [Aug.] (1; SJSC), The Thumb [June] (9; CAS), Upper Geyser Basin [July] (5; USNM); County unknown, Tie Hack Campground [Aug.] (4; SJSC, USNM).

Doubtful Records. CANADA, BRITISH COLUMBIA: Vancouver Island, Campbell River [Aug.] (7; CAS, CNC). ONTARIO: Middlesex Co., Lobo Township [Aug.] (3; UASM). UNITED STATES OF AMERICA, INDIANA: (1; USNM). NEBRASKA: Lancaster Co., Lincoln [Apr.] (1; CAS). TEXAS: (1; USNM). WASHINGTON: King Co., Seattle (1; KSUC).

No Data. (1; CDA).

Nebria ovipennis LeConte

Map: Figure 404

Specimens examined: 269 (127♂, 142♀)

UNITED STATES OF AMERICA

CALIFORNIA: (3; ANSP, CAS); Alpine Co., Ebbetts Pass ([2670m]) [June] (1; MCZ); El Dorado Co., (3; CAS), Glen Alpine [July] (2; CAS, USNM), Pyramid Peak ([2440m]) [Aug.] (2; CAS), Strawberry Valley [Aug.] (5; CAS), Tallac [July] (11; AMNH, CAS, KSUC, LACM, UMRM); Fresno Co., Kaiser Peak ([3050m]) [July] (1; CAS), Piute Creek ([3020m]) [Aug.] (1; CAS), Snow Bend Creek (near Kaiser Pass) [Aug.] (11; CAS, DHKa); Inyo Co., Big Pine Creek (near Willow Lake [2930m]) [Aug.] (1; CAS); Kings

Canyon National Park, Bubbs Creek Canyon ([3050m]) [July] (1; CAS), Bullfrog Lake ([3230m]) [July] (8; CAS, UWBM), Kearsarge Lakes ([3510m]) [July] (2; CAS), North Fork Woods Creek [Sept.] (9; CAS, CNC, MCZ), Sixty Lake Basin ([3200m]) [July] (1; CAS); Mono Co., H. M. Hall Natural Area ([3050m-3350m]) [July-Sept.] (4; RPPa), Leavitt Meadows [Aug.] (1; UCB), Mill Creek (above Lundy [2740m-3350m]) [July-Aug.] (10; CAS, USNM), Mount Conness (falls above Greenstone Lake) [July] (17; DHKa), Saddlebag Lake [Sept.] (2; CAS), Slate Creek Basin (North Branch Slate Creek [3100m-3320m]) [July] (9; DHKa), Sonora Pass (and 1.0 mi. e.) [June, Aug.] (2; DHKa, UCB), White Mountain (east slope between Green Treble Lake and Big Horn Lake [3110m-3260m]) [July] (3; DHKa); Placer Co., [May-June, Sept.] (31; CAS, FMNH, ICCM, KUSM, USNM), Deer Park (Alpine Meadows Ski Area) (1; CAS), Donner Summit [June-July] (3; CAS); Sequoia National Park, Mount Sillman ([3050m]) [Aug.-Sept.] (3; CAS, OSUC, USNM); Sierra Co., Yuba Pass (2.2 mi. s. at Berry Creek [2040m]) [July] (2; CAS, DHKa); Tulare Co., [Sept.] (2; KUSM), Farewell Gap ([3050m]) [Aug.] (4; CAS), Franklin Lakes ([3050m-3140m]) [July, Sept.] (20; CAS, CNC, DHKa, KUSM, MCZ, UASM), Mineral King [Aug.] (5; CAS), Monarch Lake [Sept.] (2; CAS, INHS); Tuolumne Co., Chipmunk Flat [Aug.] (6; UCD, USNM), Sonora Pass ([2740m-3350m] and 2 mi. w.) [June-Sept.] (30; CAS, CDA, DHKa, UCB, UCD, UIMI, USNM); Yosemite National Park, Donahue Pass ([3050m-3350m]) [Aug (2; RTBe), Elizabeth Lake [3200m-3350m]) [Aug.] (4; CAS, RTBe), Lyell Fork Tuolumne River (John Muir Trail [2990m]) [Sept.] (12; DHKa), Mount Dana [Sept.] (2; CAS), Mount Lyell ([3350m]) [July] (6; CAS), Tilden Lake [July] (1; CAS), Tuolumne Meadows ([2820m]) [July-Aug.] (6; CAS, MCZ, UMMZ); County

unknown, Sierra Nevada (1; MCZ). NEVADA: Washoe Co., Mount Rose (east slope, 0.5 mi. e. of Mount Rose Pass on Brown Creek [2690m], 11 mi. w. of Highway 395 at Galena Creek [2290m]) [July-Aug.] (15; CAS, DHKa, WSU).

Doubtful Records. UNITED STATES OF AMERICA, OREGON: Lane Co., Eugene [May] (1; MCZ).

Nebria pallipes Say

Map: Figure 396

Specimens examined: 2069 (1063♂, 1006♀)

CANADA

NEW BRUNSWICK: [Aug.] (2; MCZ); Albert Co., West River [Aug.] (8; CUIC); Kings Co., Grand Bay [July] (2; DJLa); York Co., Tay River (near Taymouth) [July] (16; DJLa). NOVA SCOTIA: Colchester Co., Truro [June, Aug.] (6; CAS, CUIC). ONTARIO: Carleton Co., Ottawa [June-July] (6; ALar, HGou, USNM). QUÉBEC: Cté d'Abitibi, Stem [Aug.] (9; HGou, USNM); Cté d'Arthabaska, St-Louis-de-Blandford [Sept.] (1; ALar); Cté de Berthier, Berthierville [July-Sept.] (19; ALar, DBUM), Lanoraie [June] (3; CNC); Cté de Beauharnois, Beauharnois [Sept.] (1; DBUM), Cté de Bonaventure, Escuminac [July] (18; ALar), Matapédia [July] (2; ALar), Nouvelle [July] (6; ALar); Cté de Brome, Brome [Aug.] (3; CNC), Knowlton (and 5 mi. se.) [June-Aug.] (11; CNC, UASM), Orford Lake [Aug.] (1; CPQC); Cté de Champlain, Ste-Thècle (Lac Long) [July] (1; CPQC); Cté de Charlevoix-Ouest, Île-aux-Coudres [Aug.] (1; CNC); Cté de Chicoutimi, St-Ambroise [June] (4; ALar); Cté de Frontenac, Lac-Mégantic [Aug.]

(1; CPQC); Cté de Joliette, Joliette [July-Aug.] (8; ALar, CNC, DBUM, KUSM), Ste-Melanie [July] (16; ALar, CNC); Cté de Levis, St-Nicolas [July] (1; CDA); Cté de Lotbinière, St-Sylvestre [Aug.] (2; ALar, CDA), Val-Alain [Sept.] (1; ALar); Cté de Montcalm, Rawdon [Aug.] (1; DBUM), St-Émile-de-Montcalm [Aug.] (6; ALar, CNC); Cté de Nicolet, Becancour [Sept.] (5; ALar, CDA, LRus); Cté de Portneuf, Rivière-à-Pierre [Aug.] (1; LRus), Ste-Catherine [Aug.] (1; ALar), St-Léonard-de-Portneuf [Sept.] (1; ALar); Cté de Richelieu, St-Ours [Aug.] (3; ALar, LRus); Cté de Rouville, Mont Yamaska [Aug.] (1; LRus); Cté de Standstead, Ayer's Cliff [July] (18; ALar, CNC), Coaticook [Sept.] (1; CPQC), Lake-Memphrémagog [June] (4; MCZ); Cté de Vaudreuil, Choisey [Sept.] (9; ALar, CNC), Rigaud [Aug.-Sept.] (5; ALar, HGou); Île-de-Montréal, Montréal [May, Oct.] (2; CPQC, DBUM); County unknown, Ste-Marguerite [Aug.] (1; ALar), St-Hilaire (1; UASM).

UNITED STATES OF AMERICA

CONNECTICUT: (1; AMNH); Fairfield Co., Shelton [June] (3; MCZ); Hartford Co., Burlington [Aug.] (1; UMMZ), Hartford (10; PMNH), Plantsville (1; PMNH); Litchfield Co., Cornwall [May-Aug.] (5; CUIC, LACM), Kent [June] (1; CUIC), Litchfield [June-July] (22; AMNH, CUIC, LACM); Middlesex Co., Durham [Aug.] (1; LACM), Rockfall [Oct.] (1; MCZ); [illegible] Co., Meriden (south) [Sept.] (1; DENH), Mount Carmel [June] (1; PMNH), New Haven [Oct.] (1; PADA); Tolland Co., Union [June] (3; UMMZ), [illegible]ham Co., Pomfret (2; AMNH, MCZ). DISTRICT OF COLUMBIA: [July] (1; USNM); Washington (and Glover Archbold Park, Pimmit River, Rock Creek Park) [May-June, Aug.-Sept., Nov.] (20; MCZ, USNM). ILLINOIS: (3; INHS, MCZ); Champaign Co., Champaign [Oct.] (1; UBC); Coles Co.,

Fox Ridge State Park [Oct.] (4; RTBe); La Salle Co., Starved Rock State Park [Aug.] (11; CSU, RTBe); Peoria Co., Peoria [June] (1; FMNH); Vermillion Co., Danville (Harrison Park) [July] (1; RTBe), Kickapoo State Park [Sept.-Oct.] (7; RTBe). INDIANA: (3; AMNH, INHS); Allen Co., [Sept.] (1; UMMZ); Clark Co., Clark County State Forest and Nursery [June] (2; PURC); Fountain Co., [May] (1; NMDo); Franklin Co., [June] (1; PURC); Lawrence Co., Spring Hill State Park [Aug.] (2; SJSC); Marion Co., [Sept.] (1; PURC); Monroe Co., Belmont area [Oct.] (2; IUIC), Bloomington [May, Oct.] (2; IUIC); Morgan Co., [June] (2; PURC); Montgomery Co., Shades State Park [Sept.-Oct.] (3; NMDo, RTBe); Parke Co., Turkey Run State Park [June] (2; INHS, UCD); Tippecanoe Co., [Oct.] (3; UMMZ), Lafayette [May, Oct.] (2; PURC, UMMZ). KENTUCKY: (1; MCZ); Jessamine Co., Marble Creek (at Kentucky River [200m]) [May] (15; DHKa); Mammoth Cave National Park [Aug., Oct.-Nov.] (10; MCZ, RTBe, UWBM); Powell Co., Natural Bridge State Park [Aug.] (8; CNC); Wolfe Co., [June] (4; MCZ). MAINE: Aroostook Co., Allagash area [Aug.] (4; MCZ); Franklin Co., Weld [Sept.] (3; CUIC); Hancock Co., Lamoine (1; MCZ); Kennebec Co., Monmouth [June] (1; MCZ); Oxford Co., Bethel (1; MCZ), Paris [Sept.] (1; SJSC); Penobscot Co., East Branch Penobscot River (at Lunksoos) [July] (1; MCZ); Piscataquis Co., Greenville [Aug.] (1; MCZ). MARYLAND: (2; MCZ); Anne Arundel Co., Odenton [June] (4; CUIC); Baltimore Co., [July] (2; CNC), Baltimore [May-June, Aug.-Sept.] (10; CAS, DHKa, USNM), Homewood [May] (1; USNM), Hereford [Aug.] (3; USNM), Parkton [July] (1; USNM); Frederick Co., Buckeystown [Aug.] (1; RTBe), Frederick (and Old Mink Farm Camp, Monocacy River at Linganore Creek) [May-June, Aug.] (7; GRNo, RTBe, USNM); Harford Co., Franklinville

(Gun Powder River) [Aug.] (15; USNM); Montgomery Co.,[Sept.] (1; USNM), Cabin John [Sept.-Oct.] (17; USNM), Plummers Island (adjacent to) [Oct.] (15; USNM); Prince George Co., Branchville [May] (1; USNM), Laurel (1; CUIC); Washington Co., Boonesboro (1 mi. s.) [Oct.] (1; USNM); County unknown, Prettyboy Reservoir [May] (2; USNM). MASSACHUSETTS: (10; AMNH, DHKa, MCZ); Berkshire Co., Mount Washington [July] (1; UIMI), Tyringham (2; MCZ); Franklin Co., Mount Toby [Sept.] (1; MCZ), Northfield [Aug.] (2; CNC, MCZ); Hampden Co., Montgomery [Aug.] (1; USNM); Hampshire Co., Amherst [Sept.] (1; JSch), Cummington [July] (1; USNM), Hadley [Sept.] (1; CAS); Middlesex Co., Bedford Center (0.1 mi. e. at Bedford Reservoir [30m]) [June, Aug.] (6; DHKa, USNM), Dunstable (Salmon Brook) [Sept.] (2; PSMi), Framingham [June] (2; UMMZ), Natick [Sept.] (1; UASM), Stoneham [Oct.] (1; CAS); Norfolk Co., Needham [Oct.] (4; MCZ); Worcester Co., Barre [June] (7; UASM), East Northboro [July] (1; MCZ). MICHIGAN: Chippewa Co., Whitefish Point [July] (1; UMMZ); Oakland Co.,[Aug.] (2; UMMZ), Southfield [Sept.] (2; UMMZ); Wayne Co., Detroit [Apr.] (2; UMMZ). NEW HAMPSHIRE: Belknap Co., Center Harbor [July] (5; AMNH); Carroll Co., Glen (9.6 mi. n. on Ellis River) [May] (2; PMCh), Mount Chocorua [June] (2; MCZ); Cheshire Co., Cold River (Connecticut River) [Aug.] (2; PMCh), West Swazey [June] (1; MCZ); Coos Co., Crawford House [July] (1; CAS), Errol (Atkinson and Gilmanton Academy Grant at Dead Diamond River) [June-July] (5; PMCh), Fabyaus (Ammonoosuc River) [July] (4; MCZ, UMMZ), Jefferson Notch Road ([910m]) [July] (1; MCZ), Mount Madison (1; CUIC), Mount Washington ([460m-760m] and Base Station, Mount Pleasant House, Pinkham Notch) [June-Sept.] (53; ALar, CAS, CNC, HGou, MCZ, UASM), Peabody River [July] (3; AMNH, USNM), Randolph ([400m]) (2; CUIC), Shelburne [July]

(2; MCZ); Grafton Co., Monroe [Apr., June, Aug.-Sept.] (17; PMCh, RTBe), Rumney [June-July, Sept.] (12; MCZ, USNM); Hillsboro Co., Hollis [June-July] (2; PMCh), Merrimack (Souhegan River) [Sept.] (1; PSMi); Merrimack Co., Warner (Warner River) [July] (4; PMCh, PSMi); Rockingham Co., Exeter [June] (1; MCZ); Strafford Co., Dover (Mast Road Gravel Pit) [May] (12; PMCh), Durham [June] (5; DENH), Lee (Lamprey River) [Sept.] (10; PMCh); Sullivan Co., Claremont (Connecticut River) [June-July] (10; PMCh), Cornish Mills (Connecticut River) [Aug.] (3; PMCh). NEW JERSEY: (4; AMNH, USNM); Bergen Co., Hillsdale [Sept.] (4; USNM), Montvale [July] (2; MCZ), Riverdale [May] (1; MCZ); Essex Co., Montclair [Oct.] (1; AMNH), Upper Montclair [June] (2; MCZ); Hunterdon Co., Croton (branch of Wickecheoke Creek) [July] (2; OSUO), Hamden [May] (2; AMNH), Lambertville [May] (5; DRWh); Middlesex Co., Avenel [June] (2; UMRM); Morris Co., Budd Lake [Aug.] (6; AMNH), Morris Plains [May] (9; DRWh); Somerset Co., North Branch [May] (5; DRWh); Union Co., Rahway (South Branch Rahway River) [June] (1; CUIC); Warren Co., Hackettstown [May] (3; AMNH), Phillipsburg [July] (1; UASM); County unknown, Hemlock Falls [May] (1; AMNH). NEW YORK: (17; AMNH, ANSP, CAS, UMRM, USNM); Allegany Co., Rushford Lake [July] (1; UASM); Bronx Co., New York City (Bronx Park) [Aug.] (3; USNM); Broome Co., Chenango State Park [Aug.] (6; GRNo), New Windsor (4; USNM); Cattaraugus Co., Allegany State Park [July-Aug.] (7; CUIC, UASM, USNM); Dutchess Co., Pawling [Aug.] (1; DHKa), Poughkeepsie [June, Aug.] (15; RDav), Red Oak Mills [Aug.] (19; PMCh, RDav); Erie Co., Colden [July] (1; UCB); Essex Co., Chapel Pond [June] (2; CUIC), Opalescent River ([840m]) [Aug.] (1; RTBe), Pitchoff Mountain [May] (1; RTBe), Wallface Mountain [July] (5; AMNH, CAS, MCZ, USNM); Franklin Co., Lake Chateaugay ([610m]) [Aug.-

Sept.] (2; AMNH, MCZ); Fulton Co., [June] (1; USNM); Greene Co., [July] (2; ICCM); Monroe Co., Rochester [Aug.] (2; LACM); Ontario Co., [July] (6; UASM); Orange Co., Harriman State Park [Aug.] (3; HGou), Poplopen Pond [Aug.] (3; CAS), West Point [Aug.-Sept.] (2; USNM); Putnam Co., Brewster (2 mi. nw.) [Aug.] (9; PURC); Richmond Co., Staten Island (and Great Kills) [May-June, Oct.] (9; CAS, FMNH); St. Lawrence Co., Canton [Sept.] (3; LACM, NMDo, OSUO), Childwold [July] (1; CUIC); Suffolk Co., Long Island (Orient) [July-Aug.] (3; CUIC); Sullivan Co., Beaverkill (1; AMNH), Mountain Dale [July] (1; FMNH), Roscoe (Willowemoc Creek [430m]) [June] (2; DHKa); Tompkins Co., Dryden (5.5mi.wsw.at Fall Creek [270m]) [May] (7; DHKa), Groton [Aug.] (2; JSch), Ithaca (and Cascadilla Creek, Coy Glen, 5 mi. sw. at Inlet Creek [150m]) [May-Aug., Oct.] (51; CAS, CUIC, DHKa, INHS, UASM, UCB, USNM); Ulster Co., (5; ICCM); Warren Co., Lake George [Aug.] (1; USNM), Ticonderoga (10 mi. s.) [June] (2; DJLa, USNM); Washington Co., West Hebron [June] (6; AMNH, CAS); Wayne Co., [June, Sept.] (3; UASM), Butler [Sept.] (1; FMNH); Westchester Co., Croton Reservoir [Sept.] (1; DHKa), Mosholu (3; CAS); Wyoming Co., Pike (2; CSU); County unknown, Catskill Mountains (7; MCZ), East Varick [Aug.] (1; PSUC), Hemlock Mountain [June] (4; AMNH). NORTH CAROLINA: (4; MCZ, USNM); Avery Co. [Aug.] (1; MCZ), Cranberry [July] (1; HoKn), Linville [Sept.] (13; MCZ); Boncombe Co., Black Mountain (North Fork Swannanoa River) [May-July] (6; AMNH, EDNC, MCZ), Swannanoa [May-June] (1; EDNC); Cherokee Co., Andrews [May] (3; EDNC); Great Smoky Mountains National Park, Indian Gap ([1520m]) (1; USNM), Oconaluftee River (11 mi. se. of Newfound Gap [550m], 2.3 mi. nw. of Smokemont [610m]) [May] (16; DHKa, USNM), Smokemont Loop Trail ([760m]) [July] (4; UAFA); Haywood Co., Retreat

[May-June] (3; USNM); Henderson Co., Bearwallow Creek [June] (1; USNM); Jackson Co., Balsam Gap ([1010m]) [Aug.] (2; MCZ), Dillsboro [Aug.] (1; AMNH), Round Knob [June] (1; USNM); Macon Co., Aquone [May] (2; EDNC), Highlands ([910m-1220m]) [June] (7; MCZ, RCGr), Scaly ([1020m]) [June] (1; RCGr); McDowell Co., Linville Falls ([910m]) [June] (2; EDNC, USNM), Old Fort [Oct.] (1; EDNC); Mitchell Co., Little Switzerland ([1040m]) [Sept.] (1; MCZ); Swain Co., Bryson City ([610m]) [Aug.] (1; MCZ), Nantahala Gorge ([610m]) [Aug.] (1; MCZ); Transylvania Co., Brevard (3 mi. e., 7 mi. ne., and 11 mi. n. on Highway 276) [Aug.-Sept.] (3; HoKn, UASM); Yancey Co., Celo ([840m]) [Aug.] (1; USNM), Crabtree Falls (10 mi. e. of Mount Mitchell) [June] (1; RTBe); County unknown, Black Mountains [May-July] (28; AMNH, CAS), Owens Gap (Tennessee Ridge [1220m]) [Aug.] (1; MCZ). OHIO: [July] (3; JSch, UMMZ); Adams Co., [Sept.] (1; UMMZ); Ashtabula Co., [Sept.] (1; PURC), Jefferson [Aug.] (1; OSUC); Athens Co., Athens [June] (4; LACM, UIMI, UWL), Canaan Township [May-June] (4; LACM, OSUO), Waterloo Township [May] (1; UWL); Cuyahoga Co., Cleveland [June] (1; MCZ); Hamilton Co., Cincinnati [May-June, Aug.-Sept.] (10; IUIC, MCZ, UMMZ); Hocking Co., [June, Aug.] (27; OSEC, OSUC, PURC), Old Man's Cave State Park [Aug., Oct.] (3; PURC); Holmes Co., Lakeville [July] (1; MCZ); Medina Co., [May] (2; RTBe); Meigs Co., Tuppers Plains [Sept.] (1; LACM); Preble Co., [Aug.] (1; PURC), Houston Woods State Park [June] (10; RCGr), West Alexandria [Sept.] (3; RTBe); Ross Co., Bainbridge [June] (1; MSU); Summit Co., Virginia Kendall State Park [July] (2; RTBe); Vinton Co., Zaleski State Forest [June] (2; LACM, UWL). PENNSYLVANIA: (16; AMNH, ANSP, CAS, CSU, KSUC, MCZ, PSUC, UMMZ, USNM); Allegheny Co., [Apr.-May] (8; ICCM), Pittsburg [May-July] (22; CAS, ICCM, OSUO, UASM), Upper

St. Clair Township [June] (1; UCR); Beaver Co., Raccoon Creek State Park [Aug.] (2; ICCM); Berks Co., French Creek State Park [May] (1; RTBe); Blair Co., Hollidaysburg (6 mi. e. on Highway 22) [June] (3; DJLa); Bucks Co., [Aug., Oct.] (2; ICCM), Delaware River (near Uhlerstown) [Oct.] (7; USNM), Forest Park [June] (1; AMNH); Center Co., Philipsburg [May] (4; CAS), State College (1; PSUC); Chester Co., West Chester [July] (1; UWEM); Cumberland Co., Camphill [Sept.] (1; PADA), Carlisle [Sept.] (1; WSU), New Cumberland [May, July] (3; PADA, VMKi); Dauphin Co., Beaver Creek [Oct.] (2; PADA), Harrisburg [May, Aug., Oct.] (11; PADA, VMKi), Rockville [Oct.] (6; PADA, VMKi); Delaware Co., Darby [May] (5; CAS), Glenolden [May] (2; FMNH), Swarthmore [Mar.] (3; USNM); Fayette Co., Ohiopyle [July] (9; PSUC), Uniontown [Oct.] (3; UMMZ); Forest Co., Cook Forest State Park [July] (1; PSUC); Lancaster Co., Lancaster [Aug.] (8; CNC, KSUC, USNM); Lebanon Co., Lebanon (2 mi. n.) [Sept.] (5; UMMZ); Luzerne Co., Conyngham [Sept.] (1; CAS), Wyoming [Sept.] (4; USNM); Monroe Co., [Aug.] (5; MCZ), Delaware Water Gap (1; AMNH); Montgomery Co., Glenside [June] (1; USNM), Merion [Sept.] (7; USNM); Northampton Co., Bethlehem [May] (9; FMNH, MCZ, PSUC), Easton [June, Aug.] (9; CAS, FMNH, UASM, UBC), Lehigh Gap [July] (5; USNM); Northumberland Co., Sunbury [July] (1; MCZ); Perry Co., Blain [Aug.] (2; USNM), New Bloomfield [July] (2; PADA); Philadelphia Co., Chestnut Hill [June-Sept.] (7; ANSP, MCZ), Frankford [Sept.] (1; USNM), Germantown [June, Oct.-Nov.] (10; ANSP, MCZ, USNM), Philadelphia [May] (6; ANSP, LACM, MCZ, USNM); West Park [May] (1; USNM), Wissahickon [Sept.] (2; MCZ); Pike Co., [Aug.] (10; ANSP, MCZ), Greentown [July] (2; USNM); Susquehanna Co., Montrose [Aug.] (4; CAS, UCD); Tioga Co., Holiday (1; UMRM); Warren Co.,

Allegheny State Park [Aug.] (1; PURC), Warren (1; CAS); Washington Co., McConnells Mill [July] (3; ICCM); Westmoreland Co., Jeannette [May-June] (20; ICCM); York Co., Davidsburg (5 mi. w.) [June] (4; GRNo); County unknown, "Gertie's Notch" [Oct.] (1; PADA), "Squaw Run Fox Chapel" [May] (2; INHS). RHODE ISLAND: Providence Co., North Sciuate [May] (1; PMNH). SOUTH CAROLINA: Oconee Co., Salem (and at Little River) [Apr.] (4; USNM). TENNESSEE: Anderson Co., Norris [June] (2; FMNH); Great Smoky Mountains National Park, Little River (at Elkmont Campground) [June] (1; RCGr), West Prong Little Pigeon River (3 mi. s. of Gatlinburg [520m]) [May] (6; DHKa); Sevier Co., Gatlinburg ([760m]) [May-June, Sept.] (5; CNC, DHKa, SJSC, USNM). VERMONT: Addison Co., [July] (6; CUIC), South Starksboro [Aug.] (3; RDav), West Lincoln (2 mi. s.) [Sept.] (1; RTBe); Bennington Co., Bennington (South Stream) [July] (9; RTBe), Pownal (Hoosick River) [July] (2; RTBe), Heartwellville [Aug.] (1; AMNH), West Arlington (Battenkill River) [June] (8; RTBe); Caledonia Co., Croton (Wells River) [June] (2; PSMi), Lower Waterford (3 mi. w.) [June] (2; RTBe), St. Johnsbury (2 mi. e. at Moose River [170m]) [June] (4; DHKa), West Barnet (Harvey Lake) [July-Aug.] (13; PMCh); Chittenden Co., Bolton (Joiner Brook) [July] (15; DHKa), Burlington (and East Woods) [Sept.-Oct.] (10; RTBe), Hinesburg [Oct.] (1; RTBe), Jerico (Browns River) [Oct.] (1; RTBe), Jonesville (and 0.5 mi. e. and 2 mi. e. on Winooski River) [June, Sept.] (10; RTBe), Gillette Pond [June-July, Sept.] (15; RDav, RTBe), Milton (Lamoille River) [June] (1; RTBe), Richmond (2 mi. w.) [Sept.] (2; RTBe), Shelburne [Aug.] (1; CAS), South Burlington (Potash Brook) [Sept.-Oct.] (2; RTBe), Underhill [Sept.] (2; RTBe), Winooski [Sept.] (1; RTBe), Winooski River (1 mi. e. of River Road [90m]) [June] (2; DHKa);

Essex Co., Beecher Falls (Connecticut River [340m]) [July] (18; RTBe), Brighton (Lewis Road) [July] (5; RTBe), Ferdinand (Nulhagen River, Paul Stream) [July] (5; PSMi, RTBe), Granby (Moose River [350m]) [July] (9; RTBe), Lem[illegible]on (Connecticut River [300m]) [July] (16; RTBe), Maidstone (Connecti[illegible] River) [July] (1; RTBe), Victory (Moose River [340m]) [July] (5; RTBe); Franklin Co., East Georgia (Lamoille River) [June, Sept.] (31; RTBe), Fairfax [June] (15; RDav); Lamoille Co., Bingham Falls ([370m-400m]) [May, Oct.] (5; RTBe), Elmore (Bedell Brook, Elmore State Park) [June-Aug.] (19; RTBe), Jeffersonville (Brewster River) [Aug.] (4; RTBe), Johnson (and Cranberry Bog, Ithiel Falls) [June-Oct.] (15; RTBe), Long Pond [Aug.] (3; RTBe), Mount Mansfield (Pringle's Ravine) [July] (1; RTBe), Moscow (Mansfield Trout Club) [July] (8; RTBe), South Cambridge (Brewster River) [May] (1; RTBe), Spruce Peak (Sterling Brook) [July] (4; RTBe), Stowe (and Little River, Luce Hill) [July-Sept.] (12; PMCh, RTBe), Waterville (and 2 mi. se., North Branch Lamoille River) [June, Sept.-Oct.] (9; DHKa, RTBe), West Elmore (Bedell Brook) [June-Aug.] (56; RTBe); Orange Co., Williamstown [Aug.] (5; CUIC); Orleans Co., East Charleston [July] (11; RTBe), Greensboro (Lake Caspian) [July-Aug.] (4; RTBe), Holland Pond [illegible]0m]) [July] (5; RTBe), Lake Salem (3 mi. s. of Derby) [Sept.] (1; RTBe), Lake Willoughby (1.5 mi. s.) [Aug.] (1; RDav), Morgan (Underpass Pond Road) [July] (3; RTBe), North Troy (and 2 mi. s. at Jay Branch) [Aug.-Sept.] (9; RDav, RTBe), Orleans (Willoughby River [210m]) [July] (2; RTBe), Pherrins River (e. of Morgan) [July] (2; RTBe), Troy (Big Falls) [Aug.] (1; RTBe), Westmore (and Bald Mountain Trail) [July] (4; RTBe); Rutland Co., Danby (Flower Brook) [July] (3; RTBe), Ira (Ira Brook) [Aug.] (6; RTBe), Mount Tabor (Big Branch Creek) [June] (5; RTBe); Washington Co.,

Duxbury [July] (1; RTBe), Irasville (1 mi. w. at Mill Brook) [Sept.] (1; RTBe), Molly Falls Pond (2.5 mi. e. of Marshfield [120m]) [June] (1; DHKa), North Duxbury (0.75 mi. to 2.25 mi. s. on Ridley Brook [150m-240m]) [June, Sept.] (15; DHKa, RTBe); Windham Co., Bellows Falls [Aug.] (1; RTBe), Brookline (Grassy Brook, Putney Mountain) [June-July] (25; RTBe), Dover (Blue Brook) [Aug.] (3; RTBe), Grafton (Saxtons River) (5; RTBe), Guilford (Broad Brook) [Aug.] (9; RTBe), Newfane (Rock River, West River) [June] (3; RTBe), Putney (and Hemlock Ravine, Sacketts Brook) [June, Aug.] (19; CAS, RTBe); Windsor Co., Quechee Gorge (1 mi. s. of Quechee) [Aug.] (1; USNM), Woodstock [Aug.] (5; MCZ, RTBe).

VIRGINIA: (2; MCZ, RTBe); Arlington Co., [June] (2; USNM), Barcroft [Sept.] (2; USNM), Rosslyn [Sept.] (4; USNM, UWBM); Alleghany Co., Cliffdale (Roaring Run) [Sept.] (2; HoKn); Amherst Co., Otter Creek area (Blue Ridge Parkway mi. 56 [520m]) [May] (8; USNM); Bath Co., Williamsville [Sept.] (7; USNM); Clarke Co., Shenandoah River (4.1 mi. w. of Paris) [June] (11; GRNo); Dickenson Co., Breaks Interstate Park (8 mi. n. of Haysi) [June] (2; HoKn); Fairfax Co., [Sept.] (1; USNM), Black Pond [May] (1; MCZ), Turkey Run (2 mi. e. of McLean) [Sept.] (1; HoKn); Floyd Co., Copper Valley (2 mi. sw.) [Aug.] (3; HoKn, LRus); Franklin Co., Endicott (4 mi. sw.) [May] (1; RTBe); Grayson Co., Troutdale (4.5 mi. w. at Lewis Fork [1100m]) [June] (5; HoKn); Highland Co., Hightown (8 mi. nw. of Locust Springs [1160m]) [June] (3; HoKn); Montgomery Co., Radford (2 mi. e., Wildwood Park) [Oct.] (9; HoKn, LRus); Nelson Co. [July] (1; USNM); Patrick Co., Pinnacles of Dan (4 mi. sw. of Vesta [370m]) [July] (2; HoKn); Pulaski Co., Snowville (2 mi. s. at Laurel Creek) [Sept.] (5; DHKa); Rockbridge Co., Cave Mountain (8 mi. se. of Natural Bridge) [June] (1; RTBe), Natural Bridge [Sept.]

(2; MCZ); Shenandoah Co., Strasburg (6 mi. se. at Passage Creek) [Oct.] (4; HoKn, LRus), Waterlick (4.5 mi. s. at Elizabeth Furnace Campground) [July] (1; USNM); Smyth Co., Sugar Grove (3.5 mi. sw. at Dickey Creek [910m]) [Sept.] (3; HoKn), Little Laurel Creek (at Highway 600 [980m]), 2.0 mi. nw. of Konnarock [180m]) [May, Sept.] (20; DHKa, HoKn); Washington Co., Bristol (6 mi. nw. at Abrams Falls) [Sept.] (6; HoKn, LRus); County unknown, Ash Grove (2; CUIC), Big Meadows ([1070m]) [Sept.] (1; USNM). WEST VIRGINIA: Hardy Co., Wardensville (6 mi. s. [370m]) [Oct.] (15; USNM); Jefferson Co., Harpers Ferry [Sept.] (4; USNM); Pocahontas Co., Cranberry Glades (10 mi. n. of Visitor Center on Highway 150 [1400m]) [June] (8; HoKn); Randolph Co., Cheat Bridge [Sept.] (1; UASM), Mingo ([760m]) [July] (12; DHKa, ROM); Taylor Co., Grafton (3; USNM).

Doubtful Records. CANADA, BRITISH COLUMBIA: Vernon (1; CAS). UNITED STATES OF AMERICA, COLORADO: (1; MCZ).

No Data. (7; AMNH, INHS, ROM, RTBe, USNM).

Nebria paradisi Darlington

Map: Figure 382

Specimens examined: 1572 (751♂, 821♀)

UNITED STATES OF AMERICA

OREGON: Hood River Co., Mt. Hood ([1740m] and Hood River Meadows Ski Area [1920m-1950m], Sand Creek, Tillie Jane Creek [1830m]) [June-Aug.] (73; CAS, DHKa, UWBM). WASHINGTON: Lewis Co., Elk Pass (Goat Rocks Wilderness [1680m]) [Sept.] (1; PUCA); Mount Rainier National Park

([1830m-2130m]) [July-Aug.] (54; CAS, CUIC, DHKa, KUSM, MCZ, OSUO, USNM, UWBM, WSU), Burroughs Mountain (east slope [1890m-2130m]) [Aug.] (273; DHKa), Fryingpan Creek ([1160m]) [Aug.] (1; CNC), Mazama Ridge [July] (1; CAS), Nisqually Glacier (1; MCZ), Paradise area (Edith Creek Basin [1710m-1920m], Golden Gate [1920m-2010m], Paradise Park [1830m], Paradise Valley [1520m-1830m]) [July-Aug.] (970; ANSP, CAS, CNC, CUIC, DHKa, ICCM, KSUC, KUSM, MCZ, NMDo, OSUC, OSUO, UASM, UCB, UCD, UMRM, USNM, UWBM, WSU), Sluskin Falls [July] (1; UWBM), Snow Lake ([1520m]) [Aug.] (13; CNC), Van Trump Park ([1830m]) [Aug.] (4; CNC), Yakima Park ([2290m]) [Aug.] (4; RTBe); Skamania Co., Mount St. Helens (Forsyth Glacier at toe [1620m-1650m], below Leschi Glacier [1580m-1680m], northeast open slope [1340m-1620m], Windy Pass [1540m]) [July-Aug.] (138; CAS, DHKa, LRus); Snohomish Co., Glacier Peak [July] (2; CAS, UWBM); Yakima Co., Mount Adams (Bird Creek [1830m-2440m]) [July] (10; CAS, NMDo, UIMI, UWBM, WSU).

Doubtful Records. CANADA, ALBERTA: Lake Louise [Aug.] (6; GRNo, KUSM).

Nebria piperi Van Dyke

Map: Figure 409

Specimens examined: 1156 (587♂, 569♀)

CANADA

BRITISH COLUMBIA: (2; CAS, USNM); Copper Mountain [July] (18; CNC, MCZ, UASM, UBC, USNM, UWBM), Engineer [June] (1; CNC), Glenora (3; ANSP, MCZ, USNM), Kleanza Creek (near Terrace) [July] (3; CNC), Klehini River (Haines Highway mi. 50) [June] (2; CNC, UASM), Lake Alice Provincial

Park (0.2 mi. n. of Stump Lake at CheeKye River [100m]) [Aug.] (62; CAS, DHKa), Lillooet [June] (7; CNC, UASM), Merritt (Midday Valley) [July] (1; INHS), Muncho Lake Provincial Park (Alaska Highway mi. 445 at Peterson Creek, Alaska Highway mi. 459) [July] (3; BFCa, CNC), Seltat Creek (Haines Highway mi. 48.8) [June] (1; UASM), Spious Creek (near Merritt) [May, July] (15; CAS, CNC, DBUM, MCZ, UBC, UMMZ), Terrace (7 mi. e.) [June] (2; CNC), Whipsaw Creek (near Princeton) [May] (1; CNC), Zymoetz River (ne. of Terrace) [June] (3; CNC, UASM).

UNITED STATES OF AMERICA

ALASKA: Big Boulder Creek (Haines Highway mi. 34) [June] (16; CNC, UASM), Little Boulder Creek (Haines Highway mi. 31.5) [June] (14; MCZ, UASM), Skagway [July] (3; CAS). OREGON: Lane Co., Nimrod (0.9 mi. w. at McKenzie River [270m]) [July] (2; DHKa). WASHINGTON: (2; NMDo); King Co., Greenwater (5 mi. w. at White River [490m]) [Aug.] (17; DHKa), North Bend (Snoqualmie River) [Aug.] (2; UWBM); Mason Co., Lake Cushman [June] (3; UMMZ); Mount Rainier National Park [June-July, Sept.] (62; AMNH, CArm, CAS, CNC, DHKa, DJLa, ICCM, MCZ, SJSC, UASM, UBC, USNM, UWBM, WSU), Carbon River [June-July] (16; FMNH, UWBM), Fryingpan Creek [1160m-1190m] [July-Aug.] (40; CNC, DHKa, SJSC), Ipsut Creek [Aug.] (1; CAS), Kautz Creek [July] (2; UWBM), Longmire [June, Sept.] (4; DHKa, SJSC, UWBM), Narada Falls (Paradise River) [July] (1; UWBM), Nisqually River ([1160m-1420m] and Cougar Rock Campground [980m], Longmire area, below Nisqually Glacier [1220m-1520m], 0.1 mi. above Paradise River [980m], Sunshine Point Campground [610m]) [July-Sept.] (360; CAS, CUIC, DHKa, MCZ, OSUO, UASM, USNM, UWBM), North Fork Puyallup River (below toe of Puyallup Glacier [1100m-1650m]) [Aug.]

(18; CNC, DHKa), Paradise River ([1220m]) [July] (1; UWBM), South Fork Puyallup River [July] (1; UWBM), Stevens Creek ([1190m]) [July] (2; DHKa), Sunrise area (White River [1220m]) [July] (78; CAS, LRus, USNM, UWBM), White River (Silver Springs Campground [790m], White River Campground [1190m-1520m]) [June-Sept.] (96; AMNH, CAS, DHKa, FMNH, SJSC, UWBM), Yakima Park [Aug.] (3; MCZ); Olympic National Park [July-Aug.] (23; CAS, CUIC, KUSM, LACM, MCZ, UASM, USNM, UWBM), Elwha Campground [Aug.] (2; CUIC), Elwha River [July] (4; UWBM), Olympic Hot Springs [May-July] (5; CAS, UWBM); Pierce Co., Ashford (4 mi. e. on Nisqually River at Goat Creek [590m]) [July] (2; DHKa), Carbonado (Carbon River) [May] (9; DHKa, JSch), Elbe (Nisqually River [400m]) [July] (13; DHKa), Puyallup (1; WSU), White River (Silver Springs Recreation Area [760m]) [June] (6; USNM); Snohomish Co., Glacier Peak [July] (3; CAS, UWBM); Whatcom Co., Glacier (and 3 mi. e., 4 mi. e. at North Fork Nooksack River [380m]) [July-Aug.] (9; CAS, DHKa, LRus), Mount Baker [Sept.] (15; CAS, UWBM), Shuksan ([760m]) [Aug.-Sept.] (4; LRus), Shuksan Creek [Aug.] (1; UWBM), Skagit River (at Newhalem Campground) [July] (1; UWBM); Yakima Co., American River [July] (2; UWBM), Bumping Lake [June, Aug.] (9; UMM, UIMI, UMMZ, WSU), Bumping River [June, Sept.] (4; ANSP, CAS, USNM), Cliffdell (4.3 mi. se. at Naches River [730m]) [July] (125; DHKa), Naches (15.1 mi. nw. at Tieton River [720m]) [July] (8; DHKa), Naches River [July] (1; USNM), Rimrock [July] (1; USNM), Tieton River (at Naches River [560m]) [July] (1; DHKa), Wildcat Creek (at Tieton River [880m]) [July] (9; DHKa); County unknown, Mount Baker National Forest [Sept.] (1; SJSC).

Nebria piute Erwin and Ball, NEW STATUS

Map: Figure 410

Specimens examined: 158 (94♂, 64♀)

UNITED STATES OF AMERICA

UTAH: Beaver Co., Circleville Mountain (15.0 mi. w. of Junction [3140m], LaBaron Lake [2960m]) [June, Sept.] (153; CAS, DHKa, MCZ, UASM, USNM), Puffer Lake ([2510m-2560m]) [Aug.] (2; ANSP); Piute Co., Mount Belknap (14.1 mi. w. or Marysvale at Beaver Creek [2930m]) [July] (3; DHKa).

Nebria purpurata LeConte

Map: Figure 409

Specimens examined: 484 (250♂, 234♀)

UNITED STATES OF AMERICA

COLORADO: (4; ANSP, LACM, USNM); Archuleta Co., Upper San Juan River ([2130m-3200m]) [Aug.] (1; USNM); Boulder Co., Arapahoe Pass ([2740m-3350m]) [Aug.] (4; RTBe), Lake Isabelle ([3310m]) [July-Aug.] (3; CUB), Rainbow Lakes ([3350m]) [Aug.] (1; CNC), South St. Vrain Creek ([3200m]) [July] (5; CArm, CUB); Clear Creek Co., Berthoud Pass [Aug.] (5; USNM), Georgetown ([2530m-2620m]) [June] (2; CAS, MCZ), Leavenworth Valley (Argentine Road [2740m-3350m]) [June-July] (42; ANSP, CAS, DHKa, FMNH, KSUC, MCZ, ROM, UMMZ, USNM), Silver Plume ([2740m-3050m]) [June] (3; MCZ, USNM); Conejos Co., Monkhaven [June] (7; CAS); Custer Co., St. Charles River (1.9 mi. sw. of San Isabel [2710m-2830m]) [June] (9;

DHKa); Gunnison Co., Canyon of Big Blue ([2590m]) [June] (28; AMNH, ANSP, CAS, ICCM, KUSM, MCZ, UASM, UMRM, USNM); Hinsdale Co., San Juan Mountains ([3660m]) [Aug.] (4; CAS, MCZ, OSUO); Huerfano Co., near Sierra Blanca [July] (3; OSUO); Jackson Co., Agnes Lake [Aug.] (7; MSU); Lake Co., Lake Creek (7 mi. w. and 12 mi. w. of Twin Lakes) [Aug.] (14; DHKa, EAMa), North Fork Lake Creek ([3410m]) [Aug.] (6; DHKa); La Plata Co., Gold King Mill (Tirbircio Creek [2830m]) [Aug.] (4; UASM); Mineral Co., Creede ([2900m]) [July] (15; MCZ), Rio Grande River (4 mi. w. of South Fork) [Aug.] (3; DHKa), Wolf Creek Pass ([3050m-3290m] and 2 mi. w.) [July-Sept.] (17; CAS, DHKa, EAMa); Ouray Co., Ouray [June] (22; CAS, USNM); Park Co., Halfway (1; PADA), Middle Fork South Platte River (near Hoosier Pass [3510m]) [July] (9; DHKa); Rocky Mountain National Park ([3140m-3840m]) [July] (1; AMNH), Chasm Lake (on stream below [3810m]) [Aug.] (3; CArm), Fall River ([2620m]) [Aug.] (15; UASM, USNM), Fall River Road (1.7 mi. w. of Chasm Fall Trail) [Aug.] (1; UAFA), Lake Hiayaha [Aug.] (2; UAFA), Ouzel Falls ([2740m-3050m]) [July-Aug.] (12; CArm, DHKa); San Juan Co., Red Mountain Pass (and 1 mi. s. to 2 mi. s.) [July, Sept.] (3; CAS, KUSM), Silverton ([2990m-3050m]) [June, Aug.] (6; CSU, MCZ, USNM); San Miguel Co., South Fork San Miguel River ([2590m]) [July] (1; MCZ); Summit Co., Blue Lakes ([3600m]) [July] (3; DHKa), Monte Cristo Creek ([3350m]) [July] (3; DHKa), Quandary Peak (east slope [3410m-3960m]) [July-Aug.] (112; DHKa, USNM); County unknown, "Laramie Co." (1; ICCM), Mount Boullion (1; ICCM). NEW MEXICO: Rio Arriba Co., Rio Puerco (at Rio Puerco Campground [2350m-2440m]) [June] (2; DHKa); Taos Co., Red River (2.2 mi. w. of Red River P. O. at June Bug Campground [2610m], and

4.1 mi. w. of Red River P. O. [2580m]) [Jun (95; DHKa).

Doubtful Records. UNITED STATES OF AMERICA, COLORADO: Denver Co., Denver (1; ICCM).

No Data. (1; LACM).

Nebria sahlbergii Fischer

Map: Figure 391

Nebria sahlbergii sahlbergii Fischer

Specimens examined: 4125 (2200♂, 1925♀)

CANADA

ALBERTA: Banff National Park, Banff [Sept.] (1; CNC), Bow Pass [Sept.] (1; RTBe), Lake Louise [Aug.] (1; AMNH), Popes Peak (east slope [2530m]) [Aug.] (1; SJSC); Jasper National Park, Jasper [Aug.] (8; CNC, MCZ), Medicine Lake [July] (46; CAS, CUIC), Miette Hot Springs (Sulphur Creek [1370m]) [July] (51; DHKa, MCZ), Miette River (at Meadow Creek [1100m]) [July] (2; DHKa), Mount Edith Cavell ([1680m]) [July-Aug.] (2; DHKa, ROM); Other localities, Assineau River (near Lesser Slave Lake) [July] (2; DHKa), Cardinal River [May] (7; DHKa), Wildhay River (20 mi. nnw. of Entrance on Grande Cache Road [1310m], 30 mi. wnw. [1220m] and 40 mi. nnw. [1430m] of Entrance) [June] (8; DHKa, UASM). BRITISH COLUMBIA: Glacier National Park, Glacier [July-Sept.] (16; BFCa, CAS, USNM), Illecillewaet Creek [July] (29; GRNo, USNM), Rogers Pass ([1370m]) [Aug.] (1; CUIC); Yoho National Park [July] (2; CAS), Cathedral Campground [Aug.] (1; R e), Field ([1460m] and 3 mi. e. on Kicking Horse River) [June-July] (17; CAS, CUIC, UBC, USNM), Kicking

Horse River (at Amiskwi River, at Kicking Horse Campground) [July-Aug.] (10; DHKa, UBC), Yoho River ([1520m], 4 to 12 mi. e. of Field, at Takakkaw Falls [1430m]) [Aug., Oct.] (20; DHKa, UASM); Other localities, Atlin ([670m]) [Aug.] (1; CNC), Barkerville (Cunningham Creek, Grouse Creek [1280m], Williams Creek [1280m]) [Aug.-Sept.] (35; CAS, UBC, UWBM), Big Boulder Creek (e. of Pine Pass) [June] (11; CNC, UASM), CheeKye [Aug.] (1; UBC), Chetwyn (5 mi. w. at Bissett Creek) [Aug.] (1; MSU), Chilkat Pass ([1070m], at Kelsall Lake [1070m]) [July] (4; CNC, UASM), Clear Creek (Haines Highway mi. 61.3) [Aug.] (14; UASM), Contact Creek (Alaska Highway mi. 588.1) [Aug.] (4; DHKa), Cottonwood Creek [July] (1; CNC), Cultus Lake Provincial Park (Entrance Bay Campground) [June] (1; ROM), Downie Creek [Aug.] (1; CAS), Garibaldi Provincial Park (Black Tusk Meadow [1580m], Diamond Head Trail [1070m]) [July-Aug.] (20; CNC, UBC), Golden (1.9 mi. e. on Kicking Horse River [1160m]) [Aug.] (14; DHKa), Golden Ears Provincial Park (Alouette Lake) [July] (1; NMDo), Goodrich Creek (12 mi. w. of Little Prairie) [June] (1; UASM), Hope [July] (1; BFCa), Hope Mountains [Aug.] (1; INHS), Hunter Creek (at Restmore Lodge on Fraser River) [July] (4; CAS), Hyland River (Alaska Highway mi. 605) [Aug.] (1; DHKa), Indian River [Aug.] (1; CAS), Kalum Lake (n. of Terrace) [June] (3; CNC), Klehini River (Haines Highway mi. 50) [June] (20; CNC, UASM), Lake Alice Provincial Park (0.2 mi. n. of Stump Lake at CheeKye River [100m]) [Aug.] (53; CAS, DHKa), Liard River (at Trout River) [June] (1; CNC), Lillooet [June] (3; CNC), MacDonald River (Alaska Highway mi. 413 [1370m]) [July] (1; CNC), Manning Provincial Park (Coldsprings Campground, Skagit River) [July-Aug.] (13; BFCa, ROM, RTBe), Mara Lake [Aug.] (1; BFCa), Midday Valley (near Merritt) [July] (4; INHS, MCZ), Mission City [June]

(1; CNC), Mount Robson Provincial Park (at Mount Robson Campground [1830m]) [July] (20; ANSP, MCZ, UASM, UBC, USNM), Muncho Lake Provincial Park (Muncho Lake) [Aug.] (3; CNC, UASM), Nina Creek (24 mi. nw. of Manson Creek [1070m]) [Aug.] (16; RFre), Onehundredfifteen Creek (Alaska Highway mi. 403.4) [Aug.] (1; DHKa), Perow area (McEvoy Creek) [June] (1; UASM), Peterson Creek (Alaska Highway mi. 445) [June] (4; CNC), Pine Pass (Pine River) [Aug.] (1; MSU), Prince Rupert (and at Mount Hays [300m-610m]) [June-July] (4; CNC, CUIC), Quesnel Lake [Sept.] (3; CAS, KUSM), Revelstoke [Aug.] (3; BFCa), Seltat Creek (Haines Highway mi. 49) [June] (19; CNC, UASM), Seton Creek (near Lillooet) [June] (7; UASM), Skagit River (Hope Trail at Cañon Camp [760m]) [July] (6; MSU, UBC, USNM), Snass Creek ([760m]) [July] (2; MSU, UBC), Spious Creek [May, July] (9; CAS, CNC, MCZ), Stanley [June-Aug.] (44; CAS, CNC, KUSM, UBC), Summit Lake (Alaska Highway mi. 392 [1280m]) [July] (1; CNC), Terrace (7 mi. e.) [June] (1; CNC), Thornhill Mountain (near Terrace [1520m]) (1; MCZ), Tetsa River (Alaska Highway mi. 376 to 383) [June, Aug.] (6; DHKa, LRus, UASM), Thompson River (near Ashcroft) [June] (1; JVMa), Three Guardsmen Pass (Haines Highway mi. 56.7) [June] (2; CNC, UASM), Toad River (at Alaska Highway) (2; JVMa), Trout Creek (13 mi. n. of Smithers) [June] (5; CNC, UASM), Tyee (2.6 mi. w.) [June] (3; UASM), Vancouver [Mar., June, Aug.] (4; INHS, NMDo), Vernon [July-Aug.] (3; CAS, UASM), Whipsaw Creek (at Hope Trail [1220m]) [July] (3; MCZ, UBC), Wigwam Inn (Burrard Inlet) [June, Sept.] (7; CAS, CNC, UBC), Zymoetz River (ne. of Terrace) [June] (1; UASM); Vancouver Island [June] (3; JVMa), Abernathy Brook (e. of Youbou) [Aug.] (5; UASM), Alberni (9 mi. e. at West Cameron Creek, 30 mi. w.) [May, Aug.] (4; CNC, UASM), Cowichan Lake [June] (1; CNC), Duncan (Cowichan River) [Oct.] (2; UWBM),

Englishman River Falls State Park (3 mi. w. of Parksville) [Aug.] (2; UASM), Goldstream Provincial Park [May-June, Aug.] (46; DHKa, UWBM), Lockwood Creek (near Parksville) [May] (5; UASM), MacMillan Provincial Park (12 mi. e. of Alberni) [Aug.] (2; UASM), Mount Arrowsmith Trail ([300m-980m]) [Aug.] (2; UASM), Nanaimo (Chase River) [July-Sept.] (7; MCZ, USNM, UWBM), Parksville [Aug.] (1; UWBM), Port Hardy [June] (3; UWBM), Strathcona Provincial Park (8 mi. e.) [June] (1; ROM), Victoria [June-July] (32; UASM, USNM). YUKON TERRITORY: Logjam Creek (Alaska Highway mi. 751.1) [Aug.] (3; DHKa), Morley River (Alaska Highway mi. 777) [Aug.] (3; DHKa), Partridge Creek (Alaska Highway mi. 735.9) [Aug.] (3; DHKa), Quill Creek (Haines Highway mi. 150) [June] (1; UASM), Rancheria (Swift River) [Aug.] (16; CNC, UASM), Seagull Creek (Alaska Highway mi. 733) [Aug.] (5; DHKa), Swift River (Alaska Highway mi. 733 to 736.2) [June, Aug.] (38; CNC, DHKa, LRus, UASM), Upper Rancheria River (Alaska Highway mi. 721.6) [Aug.] (5; DHKa), Upper Liard River (Alaska Highway mi. 642.6) [June] (5; CNC, UASM), Whitehorse Pass [July] (2; CAS).

UNITED STATES OF AMERICA

ALASKA: Anchorage [June] (2; CNC), Big Boulder Creek (Haines Highway mi. 34) [June] (21; MCZ, UASM), Bird Creek (27 mi. se. of Anchorage [July] (17; MCZ, UASM), Cape Yakataga [June] (13; CAS), Cold Bay [July] (224; DHKa, MCZ, UASM), Chilkat River (13 to 14 mi. n. of Haines) [June] (2; MCZ, UASM), Hope [June-July] (9; CNC), Katmai [June-July] (12; CAS, DHKa, OSUC, USNM), Ketchikan [July] (4; DHKa, FMNH), Kodiak Island (Amara Lake area, Anton Larsen Bay, Bear Lake, Kalsin Bay, Kodiak and 10 mi. n. and 30 mi. s., Pasagshak Bay, Shasta Creek [240m]) [June-

Sept.] (48; CAS, MCZ, OSUC, UASM, USNM, UWBM), Glenn Highway (at Knik River) [Aug.] (2; UASM), Kuiu Island (Alvin Bay, Reid Bay) [Aug.] (13; DHKa, FMNH), Kupreanof Island (Totem Bay) [Aug.] (12; FMNH), Little Boulder Creek (Haines Highway mi. 31) [June] (11; MCZ, UASM), Muir Glacier (at toe) (9; MCZ, UWBM), Prince of Wales Island (Port Protection) [Aug.] (3; FMNH), Savonoski (Naknek Lake) [June-Aug.] (3; CAS OSUC), Seward [July] (1; CUIC), Sitka [June] (1; USNM), Skagway [July] (5; CAS), White Pass [July] (2; LACM), Worthington Glacier (Richardson Highway mi. 28) [Aug.] (5; LRus, MCZ, UASM); Aleutian Islands, Akutan [Aug.] (3; CAS), Umnak Island (Crater Creek, Okmok Caldera, Tulik Volcano, Umnak and 2 mi. and 10 mi. n.) [July] (104; CNC, MCZ, UASM), Unalaska Island (Broad Bay at mouth of Makushin River, Driftwood Bay, Dutch Harbor, Glacier River, Makushin Bay at south end, Mount Makushin on north slope [400m-460m], Nateekin Bay at mouth of Shaisinkof River, Unalaska) [July-Sept.] (542; CAS, CUIC, DHKa, MCZ, UASM, USNM, UWBM), Unimak Island (False Pass) [July] (1; CUIC). OREGON: Clackamas Co., Brightwood (Salmon River [320m]) [May, July] (59; DHKa, MSU), Clackamas River (at Austin Hot Spring) [July] (1; OSUO), Colton [Apr.] (1; CAS), Rhododendron (and 1 mi. se. on Zig Zag River [490m-600m]) [July-Aug.] (18; CAS, DHKa), Zig Zag River [Sept.] (1; UWBM); Clatsop Co., Astoria [July] (2; MSU), Cannon Beach [June] (5; CAS); Columbia City [Sept.] (1; OSUO), Mist [July] (1; CAS); Crater Lake National Park [June, Sept.] (3; JSch); Deschutes Co., Sisters (Squaw Creek [980m]) [Aug.] (15; CAS, DHKa), Soap Creek ([1750m]) [Aug.] (20; CAS, DHKa); Douglas Co., North Umpqua River (at Toketee Lake [730m]) [July] (61; DHKa), Steamboat Creek (at Steamboat Falls [410m]) [July] (1; DHKa); Hood River Co., East Fork Hood River (4.2 mi. s. of Mount

Hood Post Office [730m]) [July] (3; DHKa), Hood River (and 0.2 mi. s. on Hood River [60m]) [May, July] (12; DHKa, UWBM), Mount Hood (east slope, south slope, Cloud Cap, Robin Hood Campground, Sand Creek) [July] (44; CAS, DHKa, MCZ, MSU, NMDo, UCR, UIMI, UWBM), Parkdale (Hood River Rapids) [July] (2; CAS), Perham Creek [June] (1; DHKa), Polallie Campground [May] (1; JSch); Jackson Co., Butte Falls (0.3 mi. e. on South Fork Big Butte Creek [730m]) [July] (7; DHKa), Castle Creek [July] (1; UIMI); Lane Co., Jordan Creek [May] (1; DHKa), McKenzie River [June] (5; UWBM), Nimrod (0.9 mi. w. on McKenzie River [270m]) [July] (14; DHKa), North Fork McKenzie River (at Boulder Creek [520m]) [July] (10; DHKa), Oakridge (4.6 mi. nw. at Willamette River) [June] (5; USNM), Salt Creek (17 mi. e. and 22.6 mi. se. of Oakridge) [July, Sept.] (6; DHKa, LRus); Linn Co., Lost Prairie (40 mi. e. of Sweet Home [910m]) [Sept.] (4; LRus), Marion Forks (3.2 mi. s. at Downing Creek [930m], 6 mi. s. at North Santiam River [910m]) [July-Aug.] (11; CAS, DHKa), North Fork McKenzie River (5.2 mi. s. of Highway 20 on Highway 126 [910m]) [July] (3; DHKa); Marion Co., Abiqua Creek (12.5 mi. sw. of Molalla [80m]) [July] (2; DHKa), Cheat Creek (at Whitewater Road [910m]) [July] (16; DHKa), Detroit ([460m], 2.5 mi. e. at North Santiam River [490m], 5 mi. n.) [June-Sept.] (21; CAS, DHKa, LRus, UWBM), Mount Jefferson (northwest slope at Russell Creek [1680m-1740m]) [Aug.] (1; DHKa), North Santiam River (and 13 mi. se. of Detroit) [July-Aug.] (3; FMNH, OSUO), Silver Falls State Park (North Falls) [June, Aug.] (24; LRus, RTBe, UWBM); Multnomah Co., Horsetail Falls State Park (Horsetail Falls [120m]) [May-July] (57; DHKa, JSch, ODA, OSUO, USNM), Oneonta Gorge (Columbia River) [June] (1; DHKa); Umatilla Co., south of Kooskooskie (Washington) [June] (2; UWBM). WASHINGTON: (11; AMNH, ANSP,

INHS, LACM, USNM); Chelan Co., Tumwater Canyon ([610m]) [May] (1; LRus); Clallam Co., [Sept.] (1; CAS), Elwha River [July] (11; UWBM), Forks [July] (5; CAS), Klahowya State Park (Soleduck River) [June] (3; CAS), La Push [May] (5; CNC), Port Angeles (and 4 mi. w.) [May-July] (8; CAS, CDA, DHKa, UASM), Soleduck River [Sept.] (1; SJSC), Ozette River [May] (1; UWBM); Clark Co., Battle Ground (1 mi. s. at East Fork Lewis River [80m]) [May] (20; DHKa), Lewisville Park [June] (1; MSU); Cowlitz Co., Cougar [Sept.] (1; OSUO), North Fork Toutle River (14 mi. e. of Toutle [300m]) [Aug.] (32; CAS, DHKa); Grays Harbor Co., Lake Quinault [May] (2; CAS), Satsop River [Sept.] (1; UWBM); Jefferson Co., Port Townsend [July] (2; MCZ); King Co., Carnation [May] (5; LRus, UWBM), Cedar Mountain [May] (3; UWBM), Cedar River [May] (1; UWBM), Enumclaw [July] (2; UWBM), Fall City [May] (2; LRus), Green River Gorge [May] (1; LRus), Greenwater (Greenwater Campground, 5 mi. w. on White River [490m]) [June, Aug.] (31; DHKa, UWBM), North Bend (and at Maloneys Grove) [May-Aug.] (18; CAS, FMNH, UIMI, UWBM), Renton (Cedar River) [May] (3; UWBM), Skykomish area [July] (2; UASM), Snoqualmie River (at Snoqualmie Falls) [July, Sept.] (3; UWBM), Snoqualmie Pass [July] (1; CAS), Stevens Pass area (White Rock Springs) [July] (2; CAS); Kittitas Co., Cle Elum [June-July] (6; UWBM), Easton (15; CAS, USNM), Ellensburg [May, Sept.] (48; DHKa, FMNH, UWBM), Teanaway Ridge ([910m]) [July] (4; LRus), Thorp [May] (4; LRus, UWBM); Klickitat Co., White Salmon [Sept.] (2; UWBM); Lewis Co., Carlson (8.4 mi. s. at East Fork Tilton River [350m]) [July] (7; DHKa), Cinebar [June] (1; CDA), Curtis (1 mi. n. at Chehalis River [140m]) [May] (2; DHKa), Packwood (3 mi. ne. at Lake Creek [370m]) [July] (4; DHKa), White Pass (1.5 mi. w. at Millridge

Creek [1280m]) [July] (1; DHKa); Mason Co., Shelton [Aug.] (2; UWBM), South Fork Skokomish River [July] (1; UWBM); Mount Rainier National Park [June-Sept.] (106; CAS, CUIC, DHKa, KUSM, LACM, MCZ, SJSC, UBC, USNM, UWBM), Carbon River [June-July] (7; FMNH, UWBM), Fryingpan Creek ([1160m]) [July-Aug.] (126; CNC, DHKa, SJSC), Kautz Creek [July, Sept.] (24; UWBM), Longmire ([910m] and at Nisqually River) [May, July-Sept.] (66; CAS, CNC, SDSU, UWBM), Nisqually River ([1170m-1420m], at Cougar Rock Campground [960m], near Longmire, at toe of Nisqually Glacier, 0.1 mi. above Paradise River [980m], at Sunshine Point Campground [610m]) [July-Aug.] (71; CAS, DHKa, UWBM), North Fork Puyallup River (at toe of Puyallup Glacier [1100m-1650m]) [Aug.] (2; CNC, DHKa), Ohanapecosh [June, Aug.] (4; SJSC, USNM), Paradise area (Paradise Park, Paradise Valley) [July-Aug.] (2; CAS, UWBM), Silver Creek [Aug.] (1; UWBM), Sunrise area [July] (31; CAS), West End Road [July] (1; CAS), White River (at White River Campground [1190m-1520m]) [June-Sept.] (112; CAS, CUB, DHKa, FMNH, SDSU, USNM, UWBM); Olympic National Park [Aug.] (15; CAS, CUIC, LACM, MCZ), Dosewallips River (at Mascot Campground) [July] (3; UWBM), Elwha River ([300m] and at Elwha Campground) [May, Aug.] (27; ALar, CUIC, LRus), Lake Crescent [June, Aug.-Sept.] (34; CAS, CUIC, LRus, UWBM), Olympic Hot Springs (Boulder Creek [610m-780m]) [May-Aug.] (64; CAS, CNC, DHKa, UIMI, UWBM), Sol Duc Hot Springs [June-July, Sept.] (8; CAS, UWBM); Pierce Co., Ashford (4 mi. e. on Nisqually River at Goat Creek [590m-610m]) [July] (62; DHKa), Elbe (Nisqually River [400m]) [July-Aug.] (96; DHKa), Fairfax [Oct.] (4; FMNH), Kapowsin [Oct.] (1; FMNH), South Prairie [Oct.] (1; FMNH), White River (at Silver Springs Campground [760m-790m]) [June, Aug.] (312; DHKa, UASM); Skagit Co., Van Horn [Apr.] (2; UWBM), Skamania Co., Carson (8 mi. n. at Wind River

[340m]) [May, July] (6; DHKa), Columbia River (15 mi. w. of Underwood) [May] (10; DHKa), Cook [Aug.] (1; UWBM), Mount St. Helens (north slope at Leschi Creek [980m]) [Aug.] (1; DHKa), North Bonneville (1 mi. w. at Hamilton Creek [50m]) [May] (5; DHKa), North Fork Toutle River (at Spirit Lake Lodge [940m]) [Aug.] (1; DHKa); Arlington (North Fork Stillaguamish River) [Aug.] (2; UWBM), Darrington [May] (1; UWBM), Glacier Peak [Aug.] (2; UWBM), North Fork Sauk River [June] (1; UWBM), Stillaguamish [Aug.] (2; UWBM), Sultan [May] (2; UWBM); Thurston Co., Deschutes River [May] (2; UWBM); Walla Walla Co., Kooskooskie [May, Aug.] (24; UWBM), Walla Walla (and at Mill Creek, 2 mi. s. at Walla Walla River [320m]) [May-Sept.] (60; CAS, DHKa, JSch, MCZ, OSUO, UIMI, UWBM, WSU); Whatcom Co., Glacier (and 3 and 4 mi. e. on North Fork Nooksack River [380m]) [July-Aug.] (29; CAS, DHKa, LRus), Mount Baker (1 mi. e. of Picture Lake at Razor Hone Creek [1040m]) [Aug.-Sept.] (7; DHKa, UWBM), North Fork Nooksack River (19 mi. w. of Glacier [270m], at Silver Fir Campground [610m]) [Aug.] (39; CAS, DHKa), Shuksan ([760m]) [Aug.-Sept.] (14; LRus), Shuksan Creek [Aug.] (30; UWBM); Whitman Co., Pullman [June] (1; ICCM); Yakima Co., American River (at Hell's Crossing Campground [1040m]) [July-Aug.] (27; DHKa, KUSM, UIMI, USNM, UWBM), Bumping River (8 mi. sw. of Highway 410 [1010m]) [July-Aug.] (7; DHKa, JSch, USNM), Cliffdell (4.3 mi. se. on Naches River [730m]) [July] (1; DHKa), Mount Adams (Chaparral Creek [880m]) [Sept.] (10; FMNH, UWBM), Naches River (at Tieton River [560m]) [July-Aug.] (3; DHKa, USNM), Tieton Dam [Aug.] (4; CAS, PURC, WSU), Tieton River (15.1 mi. nw. of Naches [720m]) [July] (1; DHKa); County unknown, Pack Forest [Aug.] (1; UWBM).

Doubtful Records. UNITED STATES OF AMERICA, CALIFORNIA: (2; ANSP).

No Data. (1; MCZ).

Nebria sahlbergii modoc Kavanaugh, NEW SUBSPECIES

Specimens examined: 13 (9♂, 4♀)

UNITED STATES OF AMERICA

CALIFORNIA: Modoc Co., Cedar Pass [June] (2; USNM), New Pine Creek (4 mi. e. at Pine Creek [1740m]) [May] (11; DHKa).

Nebria sahlbergii triad Kavanaugh, NEW SUBSPECIES

Specimens examined: 214 (99♂, 115♀)

UNITED STATES OF AMERICA

CALIFORNIA: Siskiyou Co., Gulick Creek (at road to Josephine Lake [1550m]) [Aug.] (1; CAS); Trinity Co., Boulder Creek (at Goldfield Campground [1070m]) [July] (56; CAS, DHKa), Coffee Creek (at Coffee Creek Ranch [1070m]) [July] (32; CAS, DHKa), Morris Meadows ([1340m]) [Aug.] (1; PUCA), South Fork Salmon River (at Big Flat Campground [1490m]) [June-Aug.] (124; CAS, DHKa, FMNH).

Nebria schwarzi Van Dyke

Map: Figure 409

Nebria schwarzi schwarzi Van Dyke

Specimens examined: 243 (147♂, 96♀)

CANADA

ALBERTA: [July-Aug.] (9; BFCa, DBUM); Banff National Park, Banff

[June-Sept.] (60; AMNH, CAS, DHKa, KSUC, KUSM, MCZ, UASM, UCD, USNM), Bow River (at Spray River) [June, Aug.] (28; CAS, UASM), Cascade River [Aug.] (19; AMNH, CAS, MCZ, UASM), Lake Louise [June-Sept.] (31; AMNH, FMNH), Lake Minnewanka [July] (1; BFCa), North Saskatchewan River (at Highway 93) [July] (3; DHKa), Spray River [Aug.] (2; CAS); Jasper National Park, Jasper [Aug.] (1; CNC), Miette River (at Meadow Creek) [July] (1; HGou); Other localities, Athabasca River (at Grande Cache Road [1100m]) [June] (1; DHKa), Cline River (at Highway 11) [Aug.] (9; DHKa), Ghost Dam [July] (11; BFCa), North Fork Wildhay River (40 mi. wnw. of Entrance [1430m]) [June] (2; DHKa). BRITISH COLUMBIA: Yoho National Park [June-July] (4; DHKa, UWBM), Field (and 3 mi. e. at Kicking Horse River) [June-Sept.] (37; CAS, CNC, DHKa, DJLa, MCZ, USNM), Yoho River (4 to 12 mi. ne. of Field, at Takakkaw Falls) [Aug.] (17; DHKa, JBel, UASM); Other localities, Golden (1.9 mi. e. at Kicking Horse River [1160m]) [Aug.] (8; DHKa).

No Data. (1; RCM).

bria schwarzi beverlianna Kavanaugh, NEW SUBSPECIES

Specimens examined: 255 (133♂, 122♀)

UNITED STATES OF AMERICA

WYOMING: Sublette Co., Bondurant (8 mi. nw. at Hoback River [2100m]) [July-Aug.] (255; DHKa).

Nebria spatulata Van Dyke

Map: Figure 403

Nebria spatulata spatulata Van Dyke

Specimens examined: 70 (27♂, 43♀)

UNITED STATES OF AMERICA

CALIFORNIA: Kings Canyon National Park, Brewer Lake [Sept.] (3; CAS, CNC); Sequoia National Park, Mount Sillman ([3050m]) [Aug.] (4; CAS, CNC), Rattlesnake Creek (1; CNC); Tulare Co., Franklin Lakes ([3050m-3140m]) [July-Sept.] (62; CAS, CNC, DHKa, KSUC, MCZ).

Nebria spatulata sierrae Kavanaugh, NEW SUBSPECIES

Specimens examined: 60 (29♂, 31♀)

UNITED STATES OF AMERICA

CALIFORNIA: Inyo Co., Big Pine Creek (at Finger Lake [3290m]) [Aug.] (4; CAS); Mono Co., H. M. Hall Natural Area ([3350m]) [July-Sept.] (9; RPPa), Saddlebag Lake [Sept.] (3; CAS), White Mountain (northeast slope in cirque above Big Horn Lake [3290m-3480m]) [July] (13; DHKa); Tuolumne Co., Sonora Pass ([2740m-3350m]) [July] (3; UCB, USNM); Yosemite National Park, Maclure Creek Basin ([3290m-3380m]) [Sept.] (1; DHKa), Mount Lyell ([3350m]) [July-Aug.] (23; CAS), Tioga Pass ([3050m]) [Aug.] (2; CAS).

Doubtful Records. UNITED STATES OF AMERICA, CALIFORNIA: San Bernardino Co., [July] (2; CAS).

Nebria suturalis LeConte

Map: Figure 398

Specimens examined: 304 (155♂, 149♀).

CANADA

ALBERTA: Jasper National Park, Athabasca Glacier (at toe [2040m]) [July] (10; DHKa). NEWFOUNDLAND: Labrador, Emily Harbour [July] (1; CUIC), Voisey Bay (1; CNC). ONTARIO: Thunder Bay District, Black Bay (on islands at bay mouth) (3; MCZ). QUÉBEC: Territoire du Nouveau-Québec, Inoucdjouac [July] (2; ALar), Rivière Koroc [July] (1; DBUM).

UNITED STATES OF AMERICA

COLORADO: (1; MCZ); Boulder Co., Ward (w. of [3810m]) [July] (2; CArm); Clear Creek Co., Loveland Pass ([3660m]) [July] (1; CAS), Mount Evans ([4270m] and Summit Lake [3900m]) [June-July] (2; CNC); Laramie Co., Fort Collins (w. of) (2; ICCM); Rocky Mountain National Park, Hagues Peak ([3960m]) [Aug.] (2; RTBe), Longs Peak [July] (2; CArm, CUB); Summit Co., Grays Peak ([4220m] and summit [4350m]) [July, Sept.] (2; DHKa), Quandary Peak (east slope [3570m-3960m]) [July-Aug.] (19; DHKa, USNM). NEW HAMPSHIRE: (28; AMNH, ANSP, CAS, DHKa, INHS, KUSM, MCZ, USNM); Coos Co., Mount Adams [July] (1; MCZ), Mount Jefferson (Monticello Lawn [1650m]) [July] (5; PMCh), Mount Madison (1; CUIC), Mount Monroe (and Red Lake [1520m]) [June-July] (4; CAS, MCZ), Mount Quincy Adams (Starr Lake) [June] (1; MCZ), Mount Washington ([1520m-2190m] and Lake of the Clouds [1520m], summit area [1890m], Tuckerman Ravine [1550m-1650m]) [May-Sept.] (160; ALar, AMNH, ANSP, CAS, CNC, DHKa, ICCM, KUSM, MCZ, PADA, PMCh, PMNH, RDav, UASM, USNM, UWEM); Grafton Co., Franconia area [July] (1; MCZ); County unknown, White Mountains ([above 460m]) [July-Aug.] (11; ICCM, MCZ, MSU, USNM). NEW YORK: (1; AMNH); Essex Co., Haystack Mountain [Aug.] (1; RTBe).

VERMONT: C ttenden Co., Mount Mansfield ([1250m], Chin, Nose, Subway [1190m-1220m], summit [1310m]) [June-Aug.] (36; CAS, DHKa, RTBe, UASM, USNM). WYOMING: Grand Teton National Park, North Fork Garnet Canyon (below headwall [3510m]) [Aug.] (1; SJSC).

Doubtful Records. CANADA, ONTARIO: Middlesex Co., London (1; CNC). UNITED STATES OF AMERICA, MASSACHUSETTS: (1; MCZ).

No Data. (1; AMNH).

Nebria trifaria LeConte

Map: Figure 411

Nebria trifaria trifaria LeConte

Specimens examined: 1219 (617♂, 602♀)

UNITED STATES OF AMERICA

COLORADO: (2; ANSP, LACM); Boulder Co. [Aug.] (1; CUB), Arapahoe Pass ([2740m-3050m]) [Aug.] (5; RTBe), Jenney Lake ([3200m]) [July] (1; CArm), Lake Isabelle ([3170m]) [July] (7; CArm), Jasper Lake ([3260m]) [Aug.] (1; CArm), Lefthand Creek (5 mi. e. of Ward [2530m]) [July-Aug.] (80; CArm, DHKa), Little Royal Gorge [Aug.] (1; CUB), Long Lake ([3140m]) [July, Sept.] (6; CArm), Mitchell Lake ([3290m]) [July] (7; CArm, CUB), Rainbow Lakes (10 mi. sw. of Ward [3350m]) [Aug.] (1; CNC), Red Rock Lake ([2900m]) [Aug.] (6; CArm), South St. Vrain Creek ([3050m]) [July] (1; CUB), Yankee Doodle Lake ([3140m]) [July] (1; CArm); Clear Creek Co Leavenworth Valley (Argentine Road [2740m-3350m], Waldorf Mine [3540m]) [ne-July] (19; ANSP, CAS, CNC, DEUN, DHKa, FMNH, MCZ, ROM, UMMZ, USN), Mount Evans (Echo Lake [3230m],

Summit Lake [3960m]) [July] (3; CAS, CNC), Silver Plume ([2740m-3050m]) [June] (6; ANSP, CAS, MCZ, UWEM); El Paso Co., Gold Camp Road (9 mi. w. of Broadmoor at South Cheyenne Creek [2650m-2740m]) [July-Aug.] (50; DHKa, EAMa); Gilpin Co., Rollinsville area [July] (1; CArm); Jackson Co., Cameron Pass ([3140m]) [Aug.] (1; UASM); Larimer Co., Bennett Creek [May-July] (18; RTBe), Browns Lake Trail [Aug.] (1; RTBe), Buckhorn Creek [July] (2; RTBe), Cameron Pass ([3050m]) [June, Aug.] (6; MSU, RTBe, UASM, USNM), Crown Point Road (at Bennett Springs [2290m-2350m], at Crown Point Trail [3140m-3200m], 40 mi. w. of Bellevue [2740m]) [June-Aug.] (20; DHKa, RTBe, UASM, USNM), Monument Gulch [July] (18; RTBe), North Fork Cache la Poudre River [June] (2; RTBe), Zimmerman Lake [Aug.] (5; RTBe); Park Co., Kenosha Pass [July] (1; CAS); Rocky Mountain National Park, Blue Lake [July] (3; RTBe), Chasm Lake (stream below) [Aug.] (3; CArm), Endovalley Campground [Aug.] (4; RTBe), Fall River ([2620m]) [Aug.] (1; UASM), Hang Lake [Aug.] (1; RTBe), Lake Hiayaha [Aug.] (3; UAFA), Longs Peak ([3050m-3350m] and Boulder Field [3840m], Larkspur Creek) [July-Aug.] (27; CArm, CAS), Thunder Lake ([3080m] and Thunder Lake Trail [2500m-3350m]) [June] (2; CArm); Routt Co., Walton Creek (above Dumont Lake [2900m-2960m]) [Aug.] (3; DHKa). IDAHO: Bear Lake Co., Bloomington Lake (12.1 mi. sw. of Bloomington [2500m-2560m]) [July-Aug.] (27; DHKa, FMNH, UWEM). MONTANA: Carbon Co., Quad Creek (17 mi. sw. of Red Lodge [3050m]) [July] (42; DHKa). NEVADA: Elko Co., Jarbridge [Sept.] (6; NSDA), Lamoille Canyon [June] (1; GRNo), Thomas Creek (at Thomas Creek Campground [2320m-2380m]) [Aug.] (20; DHKa). UTAH: Cache Co., Logan River (13.7 mi. e. of Logan at Cottonwood Creek [1740m]) [Aug.] (22; DHKa), White Pine Lake

([2440m]) [July] (2; CAS); Garfield Co., Cottonwood Peak (38.5 mi. sw. of Antimony at Cottonwood Creek [2440m]) [July] (72; DHKa), Mount Dutton (23.4 mi. sw. of Antimony at North Fork Deep Creek [3120m]) [July] (18; DHKa); Iron Co., Cedar Breaks National Monument ([3200m]) [June-Aug.] (36; CAS, OSUC), Cedar Canyon (Coal Creek [2650m]) [June] (6; DHKa), The Mammoth ([3050m]) [July] (12; ANSP, KSUC, MCZ, UASM, USNM), Parowan Creek (13.5 mi. s. of Parowan [2800m]) [June] (10; DHKa); Kane Co., Long Valley Junction [Aug.] (11; CAS); Salt Lake Co., Alta [June] (68; AMNH, ANSP, CAS, CNC, KSUC, USNM), City Creek Canyon (1; USNM), Lake Catherine ([3020m-3080m]) [Aug.] (1; ANSP); Sevier Co., Monroe Peak (8.6 [2640m] and 12.4 mi. se. of Monroe [2990m]) [July] (3; DHKa), Mount Marvine (0.1 mi. n. of Johnson Valley Reservoir at Sevenmile Creek [2590m]) [Aug.] (10; DHKa); Tooele Co.,Grantsville (12 mi. sw.) [May] (3; MSU); Uintah Co., (5; USNM), Big Brush Creek (7 mi. wnw. of Highway 44 [2620m]) [Aug.] (12; DHKa); Utah Co., American Fork Canyon ([2900m] and 5.1 mi. e. of Highway 146 [1860m], 7 mi. e. of Alpine at Little Mill Campground [1830m]) [Aug.] (27; DHKa, MCZ), Aspen Grove (Provo Canyon [2130m]) [May, Aug.] (3; CAS), Mount Timpanogos (and at Glacier Lake) [July] (44; CAS, MCZ, USNM), North Fork Provo Canyon (1.5 mi. n. of Highway 189 [1680m], Sundance Ski Area [1890m]) [Aug.] (129; DHKa, USNM), Provo Canyon [Apr., June] (12; CAS, CDA, USNM), South Fork American Fork Canyon (6.4 mi. e. of Highway 146 [1980m]) [Aug.] (27; DHKa); Wayne Co., Bluebell Knoll (31 mi. s. of Torrey [2440m-3050m]) [July] (46; DHKa, USNM); County unknown, Wasatch Mountains [June-July] (15; CAS). WYOMING: Albany Co., Brooklyn Lake ([3200m]) [July] (18; DHKa), Centennial [Aug.] (1; MSU), Douglas Creek (1 mi. sse. of Keystone [2440m]) [July] (16; DHKa), Laramie Peak (south slope at Friend Creek

[2440m]) [July] (20; DHKa), Little Brooklyn Lake ([3120m]) [July] (8; DHKa), Snowy Range Pass ([3200m]) [June] (8; UASM); Carbon Co., South Brush Creek (20 mi. se. of Saratoga [2470m]) [July] (1; DHKa), Hidden Treasure Gulch (11.5 mi. wsw of Encampment [2870m]) [July] (2; DHKa), Silver Lake ([3170m]) [July] (2; USNM), Slaughterhouse Gulch (11 mi. sw. of Encampment [2870m]) [July] (6; DHKa); Grand Teton National Park [July] (7; CAS), Death Canyon ([3050m]) [Aug.] (1; ANSP), Mount Teewinot (southeast slope [2160m-2740m]) [Aug.] (27; DHKa), South Fork Cascade Canyon ([3050m-3110m]) [July] (9; CAS, DHKa, DJLa, UASM, USNM); Lincoln Co., White Creek (20 mi. se. of Alpine Junction [1950m-2190m]) [July] (3; DHKa), Wolf Creek (16.1 mi. sw. of Hoback Junction [1770m-1780m]) [July-Aug.] (5; DHKa); Sublette Co., Fremont Lake [July] (1; CAS), Green River Lakes (west shore [2440m-2590m]) [July] (24; DHKa), Hoback River (14 mi. sw. of Highway 187/189 [2440m]) [July] (10; DHKa); Teton Co., Granite Creek (at Little Granite Creek [2150m]) [Aug.] (20; DHKa), Togwotee Pass ([2960m]) [Aug.] (11; DHKa, KUSM); Yellowstone National Park ([2130m-3050m]) [Sept.] (1; MCZ).

Doubtful Records. UNITED STATES OF AMERICA, ARIZONA: Navajo Co., Clay Springs [Sept.] (1; CAS); Pima Co., Hendrichs Canyon (Baboquivari Mountains [980m]) [Sept.] (2; ANSP). COLORADO: La Plata Co., Durango (22 mi. w.) [May] (3; MSU).

No Data. (7; EMUS, USNM).

Nebria trifaria catenata Casey

Specimens examined: 340 (176♂, 164♀)

UNITED STATES OF AMERICA

COLORADO: (12; CAS, ICCM, KSUC, MCZ, USNM); Archuleta Co., Upper San Juan Valley ([2130m-3200m]) [Aug.] (3; MCZ); Chaffee Co., St. Elmo [July] (1; ICCM); Dolores Co., Rico area ([2590m-3050m]) [July] (11; AMNH, ANSP, KUSM, MCZ, OSUC, UMRM); Gunnison Co., Canyon of Big Blue ([2590m]) [July] (1; MCZ); La Plata Co., Durango area ([1680m-2130m]) [July] (1; MSU), Gold King Mill (Tirbircio Creek [2830m]) [Aug.] (1; UASM), Hermosa Creek Trail (nw. of Hermosa [2960m]) [Aug.] (1; UASM); Mineral Co., Wolf Creek Pass ([3510m] and 2 mi. w.) [June, Aug.] (34; CAS, DHKa, EAMa); Montezuma Co., Dolores River (at Highway 145) [Sept.] (1; CAS); Montrose Co., Montrose (and Uncompahgre Plateau [2740m-3050m]) [July] (16; ANSP, KUSM, MCZ, OSUC, UMRM, USNM); Ouray Co., Ouray (and vicinity [2740m-3050m], Box Canyon [2290m-2440m], Toll Road) [July] (3; CAS, USNM); San Juan Co., Silverton area [3050m] [Aug.] (1; MCZ); San Miguel Co., South Fork San Miguel River ([2590m]) [July] (6; ANSP, KUSM, MCZ, OSUC, USNM); County unknown, La Plata Mountains ([2740m-3660m]) [July] (3; CSU, USNM). NEW MEXICO: Lincoln Co., Capitan (1; CUIC). UTAH: Grand Co., Mill Creek (at Oowah Lake [2680m]) [Aug.] (12; DHKa), Moab area [July] (1; BFCa); San Juan Co., Abajo Peak (13.5 mi. sw. of Monticello [3350m]) [Aug.] (17; UASM), Blue Lake (Geyser Pass) [Aug.] (1; AMNH), Mill Creek Valley ([2900m]) [Aug.] (4; UASM), Monticello (vicinity and 5 mi. w. [2500m], 8.7 mi. w. [3050m], 12.3 mi. w. [2740m]) [July-Aug.] (41; DHKa, MCZ, UASM), Mount Linnaeus (east slope [3050m]) [July] (122; DHKa, USNM), North Creek (7.1 mi. w. of Monticello [2560m-2830m]) [July-Aug.] (38; DHKa, UASM, USNM), Spring Creek ([2590m]) [July] (3; DHKa, USNM).

No Data. (3; ICCM, PURC, USNM).

Nebria trifaria utahensis Kavanaugh, NEW SUBSPECIES

Specimens examined: 15 (10♂, 5♀)

UNITED STATES OF AMERICA

UTAH: Garfield Co., Hanksville (24 mi. s. [2290m]) [July] (3; CNC), Lonesome Beaver ([2290m]) [July] (12; CAS, CNC).

Nebria vandykei Bänninger

Map: Figure 408

Nebria vandykei vandykei Bänninger

Specimens examined: 161 (70♂, 91♀)

UNITED STATES OF AMERICA

WASHINGTON: Mount Rainier National Park ([1830m]) [Aug.] (4; CUIC, UWBM), Fryingpan Creek ([1160m]) [July] (1; CNC), Nisqually River ([1160m-1420m]) [July] (4; DHKa), North Fork Puyallup River (below toe of Puyallup Glacier [1100m-1650m]) [Aug.] (1; DHKa), Paradise area (Edith Creek Basin [1710m-1920m], Golden Gate [1920m-2000m], Paradise Glacier, Paradise Park [1680m-1830m], Paradise Valley) [July-Aug.] (109; AMNH, CAS, CNC, DHKa, MCZ, UASM, UCD, USNM, UWBM), Sunrise area (east slope of Burroughs Mountain [1890m-1980m]) [Aug.] (3; DHKa), Yakima Park ([2040m]) [July] (1; UIMI); Olympic National Park, Olympic Mountains (1; UWBM); Skamania Co., Mount St. Helens (northeast slope [1520m-1620m], north slope at snowfield below Leschi Glacier [1580m-1680m], north slope at toe of Forsyth Glacier [1620m-1650m]) [Aug.] (27; CAS, DHKa); Whatcom Co., Mount Baker (northeast slope near Heather Meadows area at Austin Pass [1190m-1310m]) [Aug.] (10; CAS, DHKa).

Nebria vandykei wyeast Kavanaugh, NEW SUBSPECIES

Specimens examined: 188 (105♂, 83♀)

UNITED STATES OF AMERICA

OREGON: Deschutes Co., Middle Sister Peak (east slope at North Fork Squaw Creek [1950m-2190m]) [Aug.] (19; CAS, DHKa); Hood River Co., Mount Hood ([1740m] and Hood River Meadows Ski Area [1920m-1950m], Timberline Lodge area [1830m-1950m], Sand Creek) [June-Aug.] (130; CAS, DHKa, UWBM); Marion Co., Mount Jefferson (north slope [1860m-1920m], south end of Jefferson Park [1830m], Russell Creek [1680m-1740m], West Branch Whitewater River [1830m-1890m]) [Aug.] (39; CAS, DHKa, OSUO).

Nebria virescens Horn

Map: Figure 381

Specimens examined: 373 (175♂, 198♀)

CANADA

BRITISH COLUMBIA: (1; MCZ); Vancouver (Stanley Park, Second Beach) [May-July, Sept.-Oct.] (31; DHKa, MCZ, UBC); Vancouver Island (3; AMNH, CNC), Goldenstream Provincial Park [Sept.] (2; USNM), Long Beach (12 mi. s. of Tofino) [May] (2; CNC), Nanaimo [Oct.] (1; USNM), Victoria (and John Dean Park [240m], Mt. Douglas [230m]) [Aug.-Oct.] (8; CNC, DHKa, UASM).

UNITED STATES OF AMERICA

CALIFORNIA: (1; ANSP); Modoc Co., [May] (2; CAS), Devil's Garden District (Modoc National Forest) [June] (9; DHKa, UCB, UWEM), Hilton Spike [June] (1; USNM), Snell Spring (20 mi. ssw. of Alturas) [July] (4; EISc), Willow Ranch (1; USNM); Sequoia National Park, Alta Meadow ([2740m]) [Aug.] (2; CAS); Yosemite National Park, Olmsted Point (1.5 mi. sw. Tenaya Lake on Tioga Road [2560m]) [Nov.] (3; DHKa). IDAHO: Bonner Co., Sagle [Apr.] (1; NMDo), Sandpoint [Apr.] (3; MCZ); Nez Perce Co., Waha [Aug.] (1; UWBM). OREGON: (37; ANSP, CAS, FMNH, ICCM, KUSM, MCZ, OSUC, PADA, UMRM, USNM); Baker Co., Baker Creek [Oct.] (1; UWBM), Dixie area ([1370m]) [June] (1; USNM); Benton Co., Corvallis [Feb., May-June, Oct.-Nov.] (20; CAS, FMNH, OSUO, USNM), Marys Peak [Oct.] (1; OSUO), Philomath (1; USNM), Winkle Lake (10 mi.s. of Corvallis) [Oct.] (1; OSUO); Clatsop Co., Saddle Mountain [June, Oct.] (2; ODA, UWBM); Douglas Co., Drain [June] (1; CAS); Jackson Co., Lake Creek [Mar.] (5; UCD), Medford [Apr.] (1; FMNH), Pinehurst [May] (2; DHKa, JSch); Josephine Co., [June] (1; FMNH); Klamath Co., Bly (11 mi. ne.) [June] (1; JSch), Chiloquin [July] (1; CAS), Gearhart Mountain (at base) [June] (1; JSch), Keno [Apr.] (5; UCD), Linn Co., (1; OSUO), Albany [June-July] (3; MCZ, USNM); Marion Co., Salem [Feb.] (1; USNM); Multnomah Co., Portland [May, Sept.-Oct.] (8; CAS, DHKa, USNM); Umatilla Co., Binghams Springs [May] (1; UIMI), Meacham [May-June] (17; CAS, MCZ, UIMI, UWBM), Langdon Lake [Aug.] (2; UWBM), Tollgate Road ([910m-1220m]) [June, Oct.] (14; CAS, UIMI, USNM, UWBM), Weston [May] (1; UIMI); Union Co., Lookout Creek Trail [Nov.] (4; JSch); Washington Co., Dilley (6; CAS, USNM), Forest Grove [Oct.] (2; ANSP), Gaston (1; CUIC); Yamhill Co.,

McMinnville (2 mi. sw.) [Feb.] (4; CAS). WASHINGTON: (25; ANSP, CAS, DEUN, DHKa, INHS, MCZ, USNM, WSU); Grays Harbor Co., Hoquiam [May] (2; CAS); Island Co., Coupeville [Mar.] (1; JSch); King Co., Kent [Sept.] (2; WSU), Seattle (and Innis Arden) [Mar.-May, July] (24; ICCM, KSUC, MCZ, USNM, UWBM, WSU); Kittitas Co., Ellensburg [May] (1; LRus); Klickitat Co., Bickelton (1 mi. w. at Pine Creek [1010m]) [May] (1; DHKa); Okanogan Co., Bunker Hill Lookout (Pasayten Wilderness [2120m]) (1; JSUC); Pierce Co., Steilacoom (6; UWBM), Tacoma [Sept.] (2; CAS); San Juan Co., San Juan Island [May, July] (4; CAS, UWBM); Skamania Co., Carson (8 mi. n. on Wind River [340m]) [May] (3; DHKa); Spokane Co., Spokane (Spokane Falls) [May] (1; MCZ); Thurston Co., Olympia [Mar., Dec.] (18; CAS, CUIC, MCZ, SDSU, UMMZ, USNM), Tenino [May] (2; USNM); Walla Walla Co., Walla Walla [Sept.] (1; MCZ); Whatcom Co., Kulshan Ridge (ne. slope Mount Baker [1460m-1520m]) [Aug.] (1; DHKa); Whitman Co., Almota (1; JSch), Kamiak Butte State Park ([1040m-1100m]) [Feb.-May, July, Oct.] (14; JSch, NMDo, UCR, UWBM, WSU), Wawawai (and 0.9 mi. e. in Wawawai Canyon) [Apr.-May] (15; CAS, DHKa, JSch, MCZ, USNM, WSU); Yakima Co., Naches [May] (1; UWBM).

No Data. (2; CAS, LEMC).

Nebria zioni Van Dyke

Map: Figure 394

Nebria zioni zioni Van Dyke

Specimens examined: 591 (296♂, 295♀)

UNITED STATES OF AMERICA

UTAH: (1; USNM); Garfield Co., Clay Creek (5.9 mi. se. of Highway 22 [2410m]) [July] (83; DHKa), Mount Dutton (24.3 mi. sw. of Antimony at North Fork Deep Creek [3120m]) [July] (23; DHKa); Iron Co., Cedar Canyon (Highway 14 at Coal Creek [2650m], 28 mi. w. of Long Valley Junction) [June-July] (185; DHKa, USNM), Parowan (2.7 mi. [1920m], 8.3 mi. [2360m], and 13.5 mi. [2800m] s. on Parowan Creek) [June] (56; DHKa), Vermillion Castle Campground [Aug.] (14; UIMI); Piute Co., Mount Belknap (14.1 mi. w. of Marysvale at Beaver Creek [2930m]) [July] (71; DHKa); Sevier Co., Monroe (1.8 mi. [1740m] and 3.3 mi. [1870m] se. on Monroe Creek) [July] (116; DHKa); Zion National Park [May] (21; CAS), Zion Canyon (North Fork Virgin River near The Pulpit [1360m]) [June] (22; DHKa).

Nebria zioni oasis Kavanaugh, NEW SUBSPECIES

Specimens examined: 46 (18♂, 28♀)

UNITED STATES OF AMERICA

UTAH: Washington Co., Leeds Creek (at Oak Grove Campground [1920m-1980m]). [June] (46; DHKa).

APPENDIX C: MATERIAL STUDIED FOR EX-GROUP COMPARISONS

Representatives of the following taxa were studied as part of the cladistic analysis of Nearctic Nebria (see section 4.1).

AMPHIZOIDAE

Amphizoa lecontei Matthew

HYGROBIIDAE

Hygrobia tarda (Herbst)

DYTISCIDAE

Hydroporus clypealis Sharp

HALIPLIDAE

Peltodytes simplex (LeConte)

GYRINIDAE

Dineustus nigrior Roberts

CARABIDAE

Trachypachus gibbsi LeConte (Trachypachini)

Systolosomus brevis Solier (Trachypachini)

Gehringia olympica Darlington (Gehringiini)

Rhysodes hamatus LeConte (Rhysodini)

Pseudomorpha angustata Horn (Pseudomorphini)

Metrius contractus Eschscholtz (Metriini)

Mystropomus subcostatus Solier (Ozaenini)

Pachyteles marginicollis Solier (Ozaenini)

Crepidogaster sp. (Crepidogastrini)

Pheropsophus sp. (Brachinini)

Brachinus pallidus Erwin (Brachinini)

Amblycheila cylindriformis (Say) (Cicindelini)

Omus californicus Eschscholtz (Cicindelini)

Megacephala carolina (Linnaeus)

Pogonostoma chalybaeum Klug (Cicindelini)

Oxychila femoralis Laporte (Cicindelini)

Cicindela hirticollis Say (Cicindelini)

Calosoma scrutator Fabricius (Carabini)

Carabus chamissonis Fischer von Waldheim (Carabini)

Ceroglossus sp. (Carabini)

Cychrus hemphili Horn (Cychrini)

Sphaeroderus canadensis Chaudoir (Cychrini)

Scaphinotus vandykei Roeschke (Cychrini)

Scaphinotus interruptus Menetries (Cychrini)

Pamborus guerini Gory (Pamborini)

Enceladus gigas Bonelli (Siagonini)

Luperca laevigata (Fabricius) (Siagonini)

Siagona depressa (Fabricius) (Siagonini)

Opisthius richardsoni Kirby (Opisthiini)

Paropisthius indicus (Chaudoir) (Opisthiini)

Notiophilus borealis Harris (Notiophilini)

Pelophila borealis (Paykull) (Nebriini)

Pelophila rudis (LeConte) (Nebriini)

Leistus nubivagus Wollaston (Nebriini)

Leistus spinibarbis (Fabricius) (Nebriini)

Leistus ferruginosus Mannerheim (Nebriini)

Leistus gracilis Fuss (Nebriini)

Leistus nitidus Duftschmid (Nebriini)

Leistus depressus Breit (Nebriini)

Leistus juldusianus Reitter (Nebriini)

Leistus rufescens (Fabricius) (Nebriini)

Leistus piceus Frölich (Nebriini)

Nebria fuscipes Fuss (Nebriini)

Nebria hellwigi (Panzer) (Nebriini)

Nebria komarovi Semenov and Znojko (Nebriini)

Nebria djakonovi Semenov and Znojko (Nebriini)

Nebria nakanei Ueno (Nebriini)

Nebria oxyptera Daniel (Nebriini)

Nebria psammodes Rossi (Nebriini)

Nebria complanata (Linnaeus) (Nebriini)

Nebria brevicollis (Fabricius) (Nebriini)

Nebria laticollis Dejean (Nebriini)

Nebria livida (Linnaeus) (Nebriini)

Nebria castanea Bonelli (Nebriini)

Nebria coreica Solsky (Nebriini)

Nebria desgodinsi Oberthür (Nebriini)

Nebria elegans Andrewes (Nebriini)

Nebria superna Andrewes (Nebriini)

Nebria nudicollis Peyerimhoff (Nebriini)

Omophron obliteratum Horn (Omophronini)

Hiletus fissipennis Ancey (Hiletini)

Hiletus versutus Schiödte (Hilitini)

Diachila arctica (Gyllenhal) (Elaphrini)

Blethisa multipunctata (Linnaeus) (Elaphrini)

Elaphrus californicus Mannerheim (Elaphrini)

Migadops bimaculata Reed (Migadopini)

Monolobus testaceus Solier (Migadopini)

Loricera pilicornis (Fabricius) (Loricerini)

Bembidion planatum LeConte (Bembidiini)

Patrobus longicornis Say (Patrobini)

Agonum maculicolle Dejean (Pterostichini)

Pterostichus adstrictus Eschscholtz (Pterostichini)

Calathus advena LeConte (Pterostichini)

AUTOBIOGRAPHY

I was born April 7, 1945 in San Francisco, California. The oldest of four boys, my childhood years were spent in Alameda and Redwood City, California where I received my elementary education. During this period, my interest in biology and the outdoors began and was encouraged by my parents who provided me with stimulating experiences on family vacations and outings and contact with others with common interests through the Cub and Boy Scouts. Perhaps most important was their tolerance of my sudden and prolonged disappearances from family outings--times when I would wander off fully absorbed by the beauty and detail of the living natural world. With but mild complaints, they also accepted the assorted reptilian, amphibian and invertebrate house guests I would bring back as "pets."

Our family moved to San Jose, California in 1959 where I completed my secondary education. I entered San Jose State University in 1963 as a pre-med student, majored in biological sciences and received a Bachelor of Arts degree in May, 1967. My interests were focused on entomology during a required course in general entomology taught by J. Gordon Edwards and William E. Ferguson. Their intense enthusiasm proved contagious and I subsequently enrolled in several elective entomology courses. I later became a student assistant with the insect collection where I met Terry L. Erwin, then completing his Master's thesis, who further channeled my interest toward the study of carabid beetles.

Following acceptance by the University of Colorado School of Medicine, I moved to Denver in 1967. I completed two years in

medicine before deciding to pursue a career in systematic entomology. I transferred to the Graduate School at the Denver Center of the University in September, 1969 and received a Master of Arts degree in May, 1970. I entered a Ph.D. program at the University of Alberta in July, 1970, with Dr. George E. Ball as my sponsor and program advisor. Based initially on my collecting experiences in the Rocky Mountains of Colorado, I decided to attempt systematic studies on the carabid genus Nebria for my doctoral dissertation project.

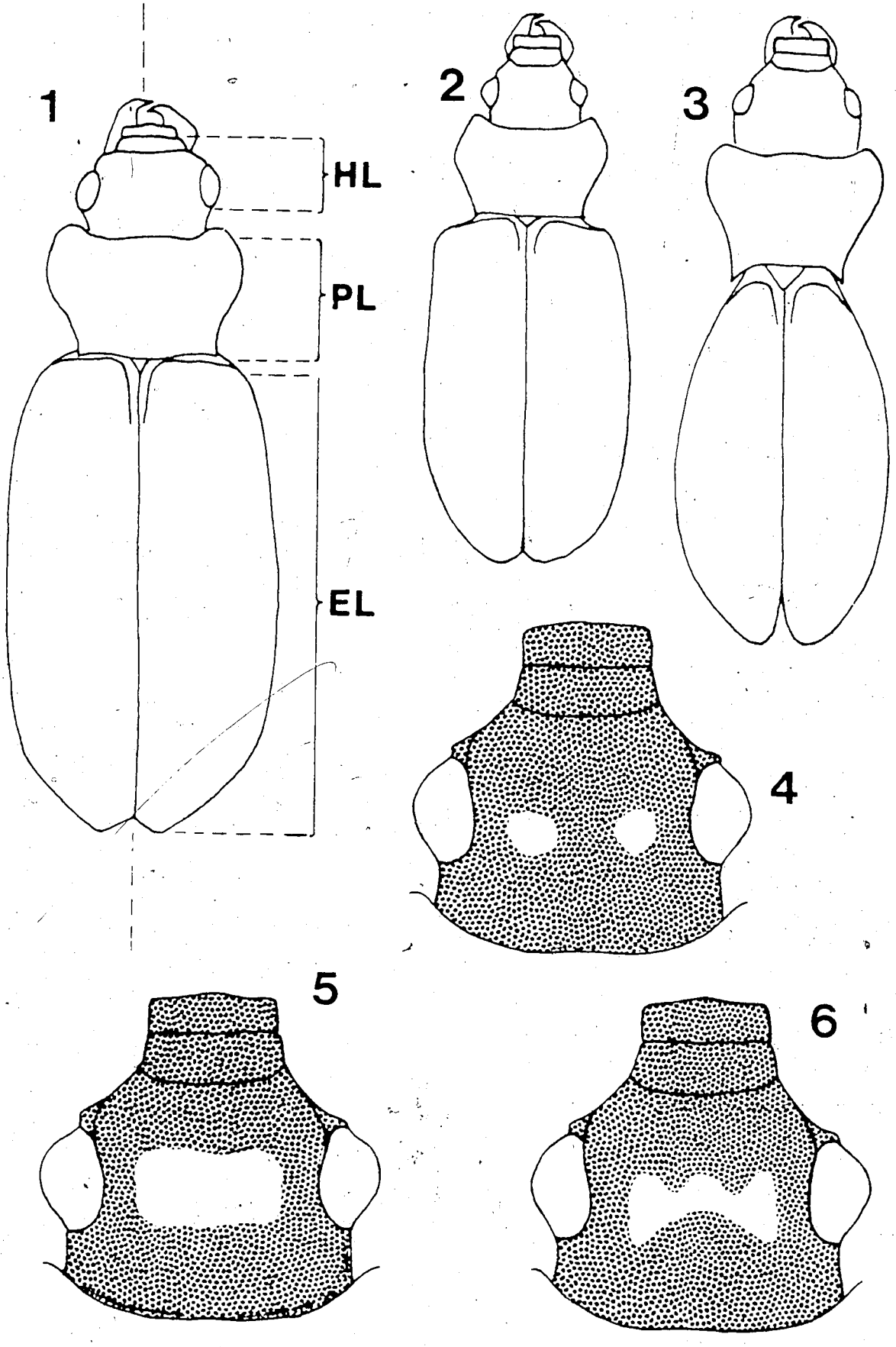
In April, 1974, prior to completion of my doctoral program, I accepted a position at the California Academy of Sciences, San Francisco, as Acting Assistant Curator of Entomology, the position I hold at present.

I met my wife, Beverly, in 1963 during our senior year of high school. We were married in September, 1965, following our second year in college, and now have five children who share our life together.

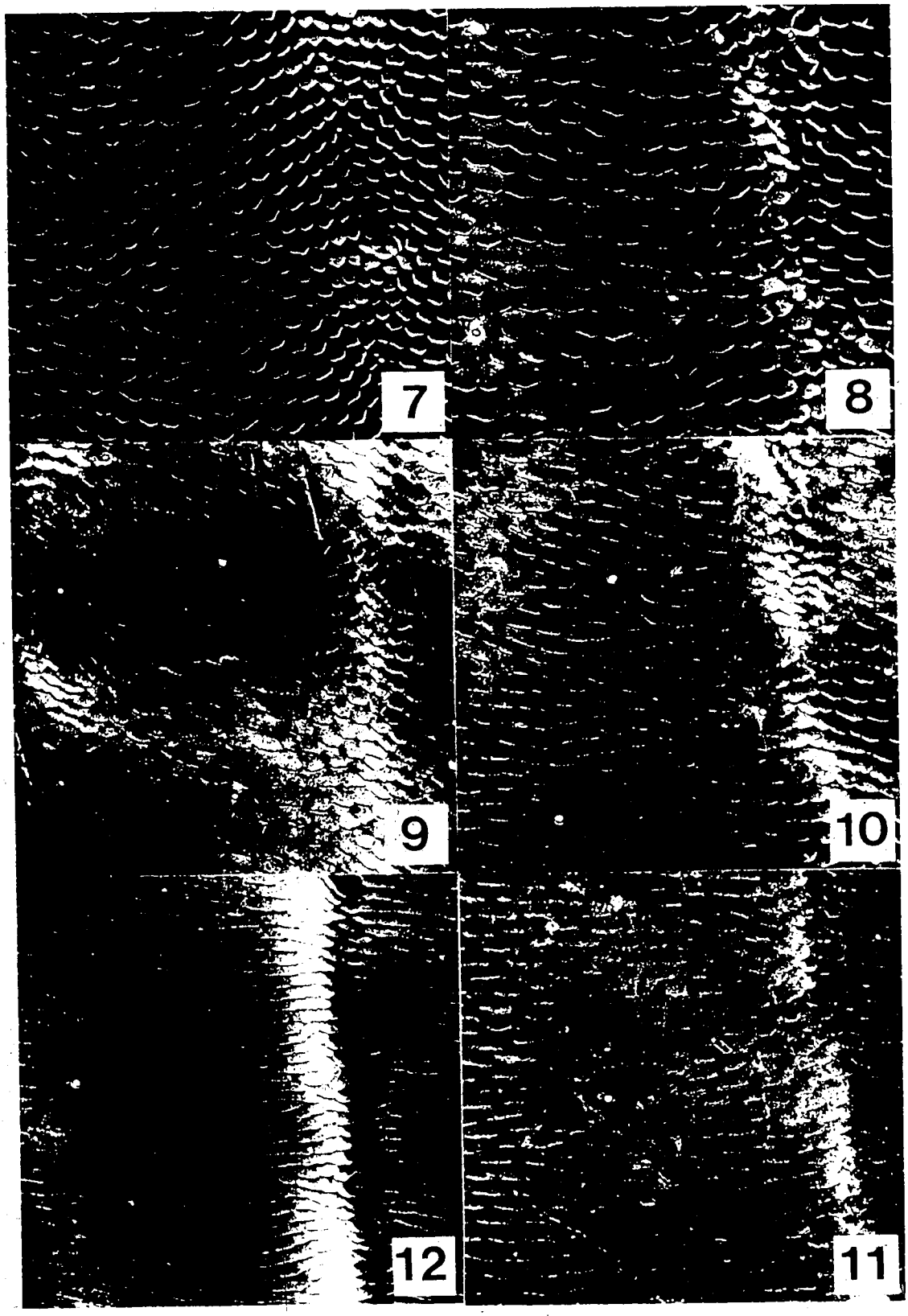
Following completion of the dissertation, I plan to continue systematic studies on the World nebriine fauna and expand my studies on the evolution and biogeography of high altitude faunas, with emphasis on Carabidae, Amphizoidae and certain silphoid and staphylinoid genera.

FIGURES

Fig. 1. Components of standardized body length; HL = head length; PL = pronotal length; EL = elytral length. Figs. 2 - 3. Habitus: general body form. 2. Type ailé. 3. Type aptère. Figs. 4 - 6. Generalized head, illustrating frontal pale spot(s). 4. Spots separate, distinct. 5. Spots broadly fused. 6. Spots narrowly fused to form M-shape.


1
HL
PL
EL
2
3
4
5
6

Figs. 7 - 12. Elytral microsculpture. 7. Nebria darlingtoni new species (Kyburz, California). 8. Nebria diversa LeConte (Waldport, Oregon). 9. Nebria appalachia Darlington (Soco Gap, North Carolina). 10. Nebria hudsonica LeConte (Penticton, British Columbia). 11. Nebria gregaria Fischer von Waldheim (Dutch Harbor, Unalaska Island, Alaska). 12. Nebria lacustris lacustris Casey (Ithaca, New York). Scale: 1.0 cm = 22.2 μ .


7
8
9
10
12
11

Figs. 13 – 21. Head, dorsal aspect. 13. Nebria crassicornis crassicornis Van Dyke (Mount Rainier, Washington). 14. Nebria crassicornis intermedia Van Dyke (Terrace, British Columbia). 14A. Nebria gyllenhali castanipes (Kirby) (Dry Wolf Creek, Montana). 15. Nebria gregaria Fischer von Waldheim (Dutch Harbor, Unalaska Island, Alaska). 16. Nebria charlottae Lindroth (Massett, Queen Charlotte Islands, British Columbia). 17. Nebria appalachia Darlington (Newfound Gap, North Carolina). 18. Nebria gebleri gebleri Dejean (Dry Wolf Creek, Montana). 19. Nebria ovipennis LeConte (Mount Conness, California). 20. Nebria spatulata spatulata Van Dyke (Franklin Lakes, California). 21. Nebria metallica Fischer von Waldheim (Manning Provincial Park, British Columbia). Scale line = 1.0 mm.

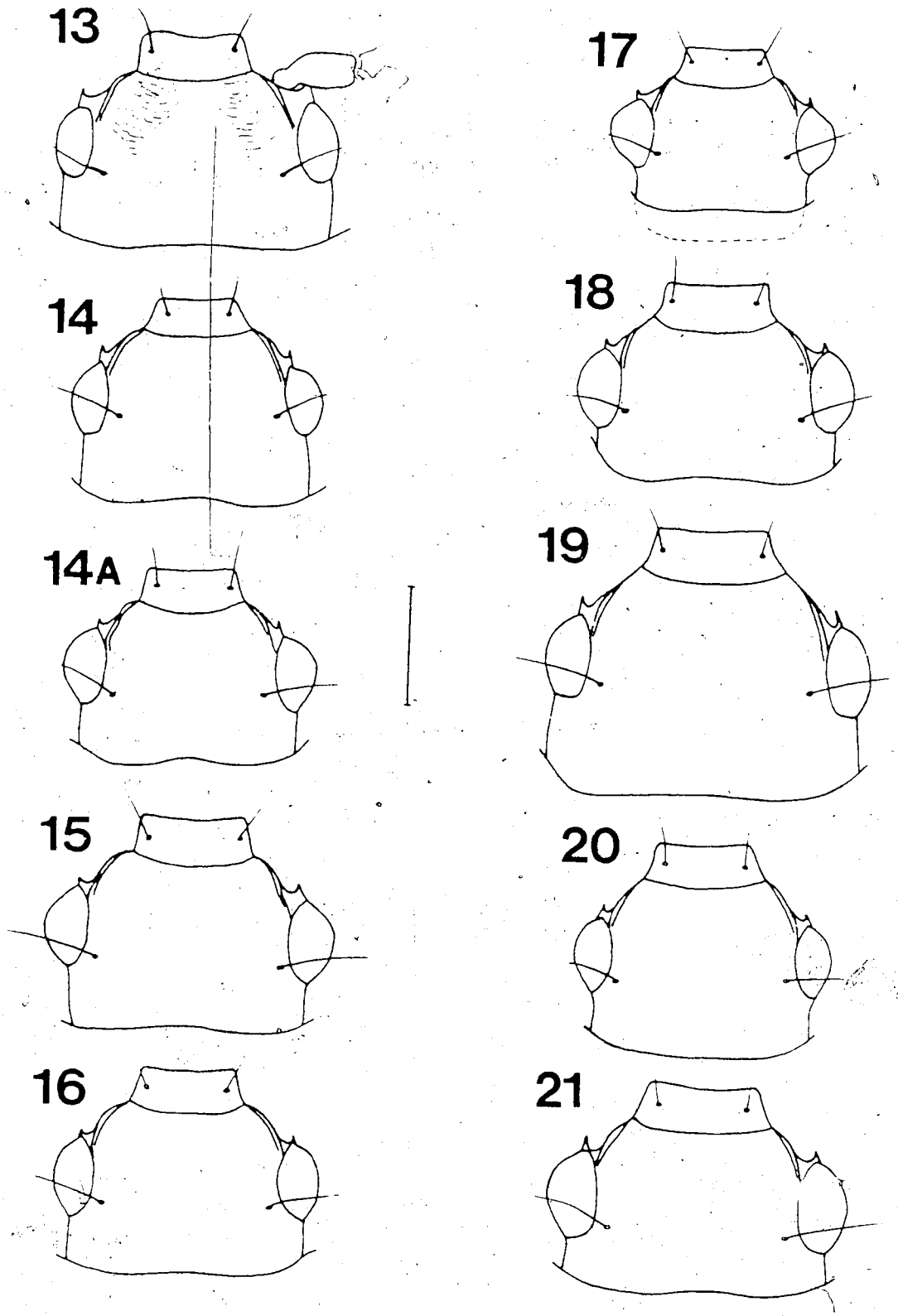
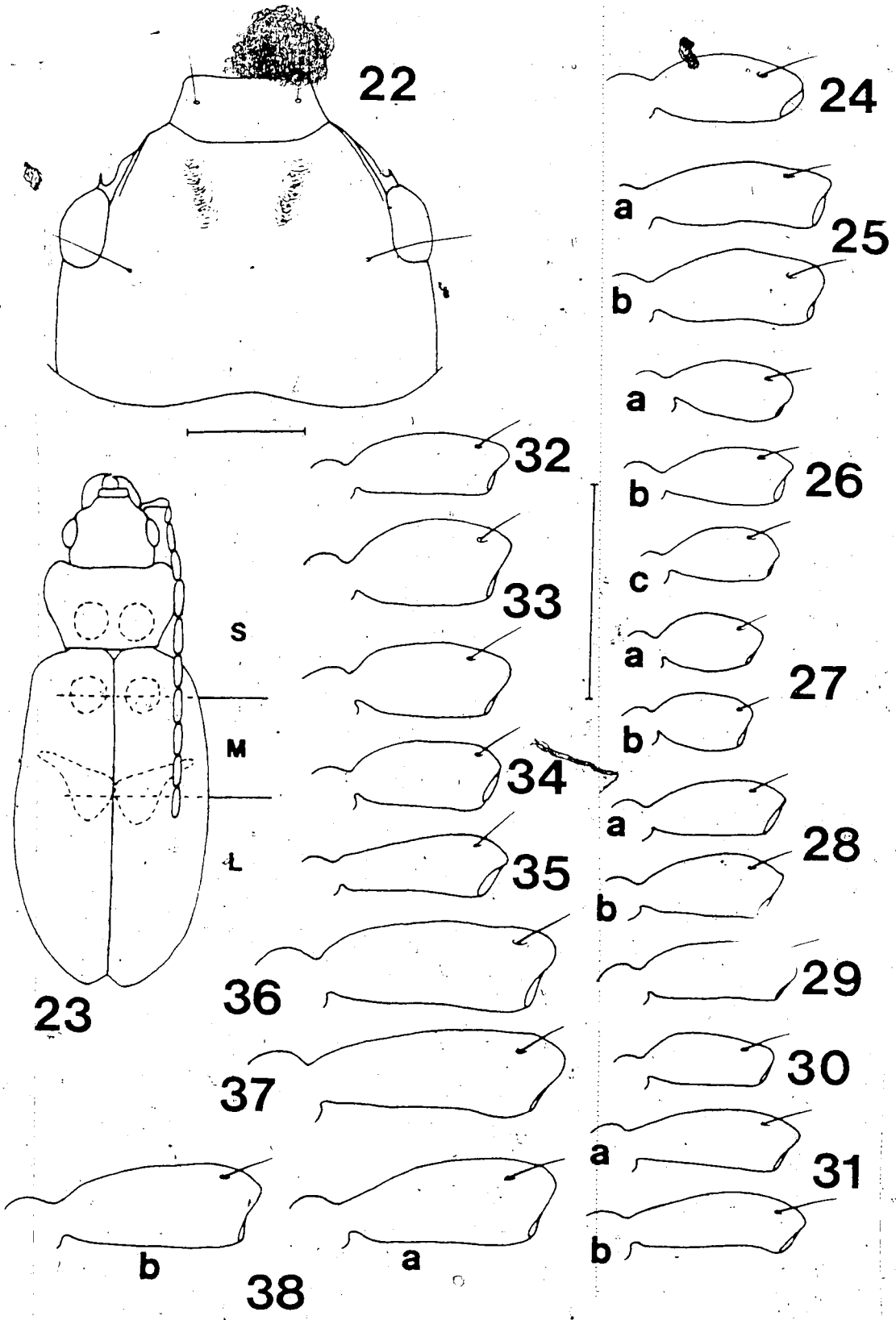
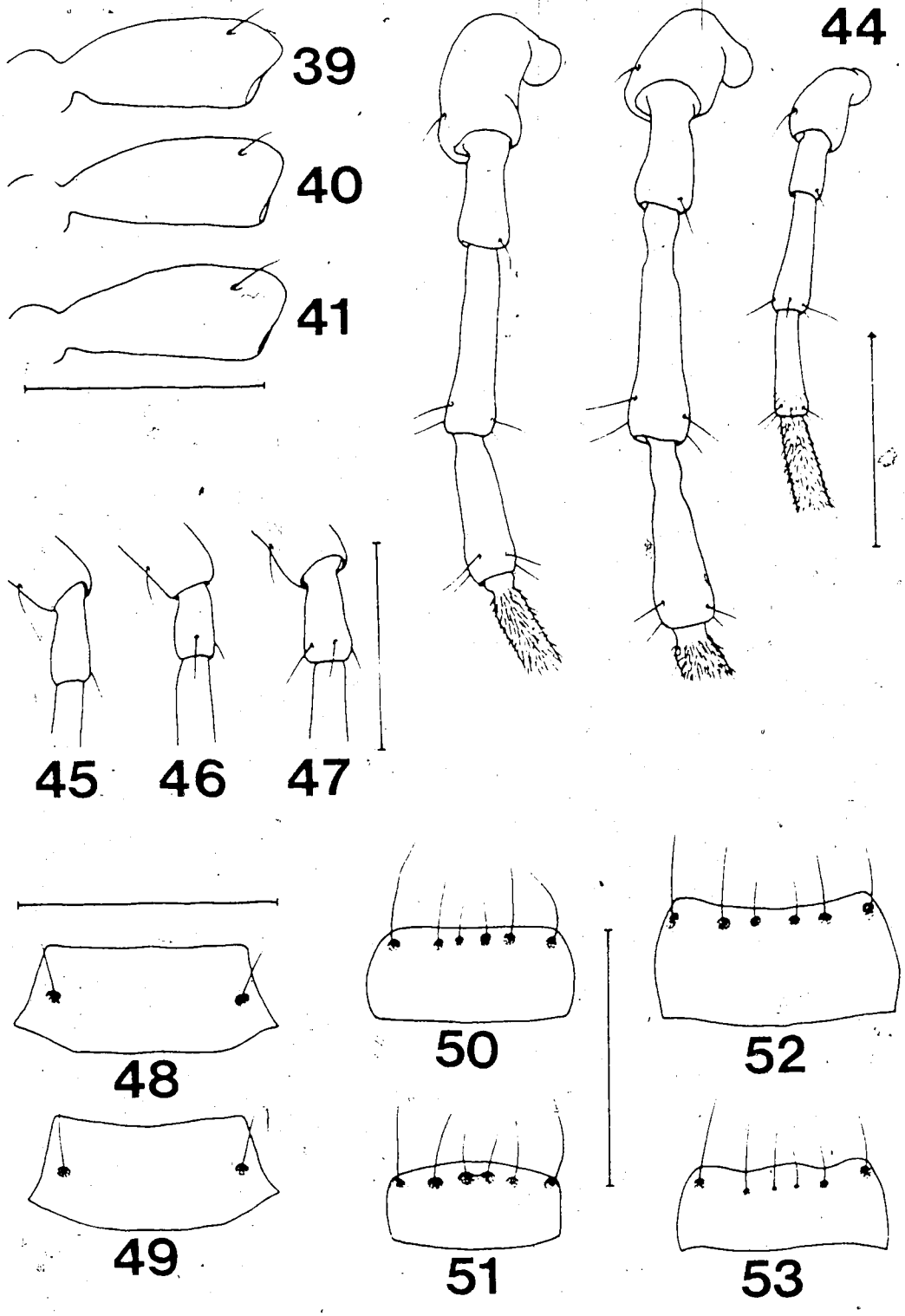
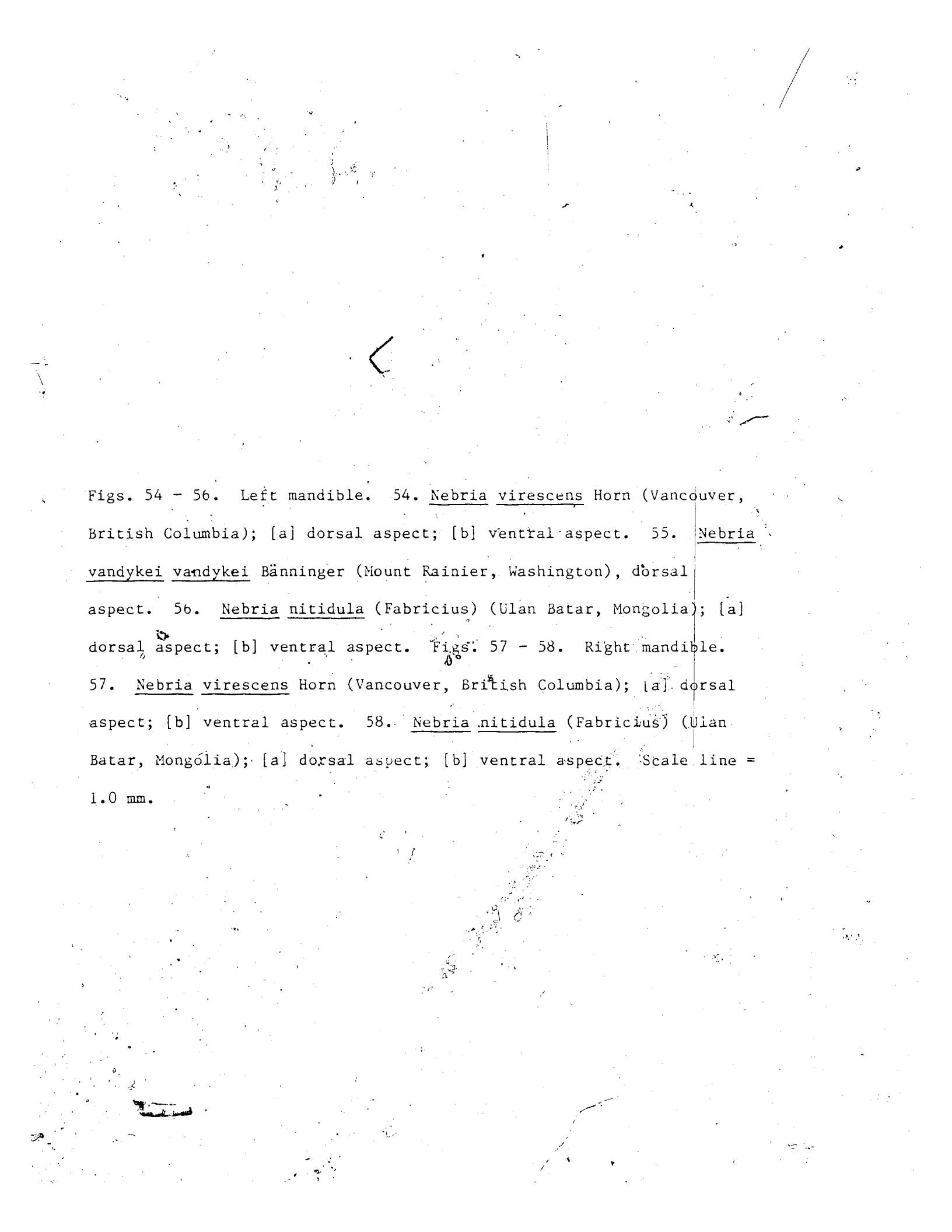

13
14
14A
15
16
17
18
19
20
21

Fig. 22. Head, dorsal aspect, Nebria ingens ingens Horn (Mount Whitney, California). Fig. 23. Relative measure of antennal length (dorsal aspect); S = range of lengths termed "short", M = range of lengths termed "medium"; L = range of lengths termed long; outlines of coxa represented by broken lines. Figs. 24 - 38. Right antennal scape, dorsal aspect. 24. Nebria gouleti new species (Underwood, Washington). 25. Nebria hudsonica LeConte ([a] Thunder Bay, Ontario; [b] Ellensburg, Washington). 26. Nebria gyllenhali castanipes (Kirby) ([a] Calling Lake, Alberta; [b] Mount Washington, New Hampshire; [c] Bumping River, Washington). 27. Nebria gyllenhali lassenensis new subspecies ([a] Mount Lassen, California; [b] Todd Lake, Oregon). 28. Nebria gyllenhali lindrothi new subspecies ([a] Brooklyn Lake, Wyoming; [b] Rio Puerco, New Mexico). 29. Nebria lyelli Van Dyke (Mount Lyell, California). 30. Nebria arkansana uinta new subspecies (Lost Lake, Utah). 31. Nebria zioni zioni Van Dyke ([a] Zion National Park, Utah; [b] Tushar Mountains, Utah). 32. Nebria zioni oasis new subspecies (Pine Valley Mountains). 33. Nebria [illegible]ipennis LeConte ([a] Yuba Pass, California; [b] Franklin Lakes, California). 34. Nebria spatulata spatulata Van Dyke (Franklin Lakes, California). 35. Nebria spatulata sierrae new subspecies (Big Horn Lake, California). 36. Nebria vandykei vandykei Bänninger (Mount St. Helens, Washington). 37. Nebria vandykei wyeast new subspecies (Mount Hood, Oregon). 38. Nebria trifaria trifaria LeConte ([a] Ward, Colorado; [b] Cedar Canyon, Utah). All scale lines = 1.0 mm.


22
24
a
25
b
a
32
b
26
33
c
S
a
27
M
34
b
a
28
L
35
b
29
36
30
37
a
31
b
23
b
38
a

Figs. 39 - 41. Right antennal scape, dorsal aspect. 39. Nebria trifaria catenata Casey (Wolf Creek Pass, Colorado). 40. Nebria coloradensis Van Dyke (Hoosier Pass, Colorado). 41. Nebria piute Ball and Erwin (Circleville Mountain, Utah). Figs. 42 - 44. Basal antennomeres, right antenna, lateral aspect. 42. Nebria purpurata LeConte (Rio Puerco, New Mexico). 43. Nebria ingens ingens Horn (Mount Whitney, California). 44. Nebria virescens Horn (Mount Baker, Washington). Figs. 45 - 47. Right antennal pedicel, anteriodorsal oblique aspect. 45. Nebria virescens Horn (Vancouver, British Columbia). 46. Nebria nivalis nivalis (Paykull) (Lake Harbour, Baffin Island). 47. Nebria nivalis nivalis (Paykull) (Lake Harbour, Baffin Island). Figs. 48 - 49. Clypeus, dorsal aspect. 48. Nebria desolata Kavanaugh (11 mi. se. of Boulder, Utah). 49. Nebria hudsonica LeConte (Woods Landing, Wyoming). Figs. 50 - 53. Labrum, dorsal aspect. 50. Nebria pallipes Say (Ithaca, New York). 51. Nebria hudsonica LeConte (Woods Landing, Wyoming). 52. Nebria ingens ingens Horn (Mount Whitney, Calfiornia). 53. Nebria gregaria Fischer von Waldheim (Dutch Harbor, Unalaska Island, Alaska). All scale lines = 1.0 mm.


39
40
41
42
43
44
45
46
47
48
49
50
51
52
53



Figs. 54 - 56. Left mandible. 54. Nebria virescens Horn (Vancouver, British Columbia); [a] dorsal aspect; [b] ventral aspect. 55. Nebria vandykei vandykei Bänninger (Mount Rainier, Washington), dorsal aspect. 56. Nebria nitidula (Fabricius) (Ulan Batar, Mongolia); [a] dorsal aspect; [b] ventral aspect. Figs. 57 - 58. Right mandible. 57. Nebria virescens Horn (Vancouver, British Columbia); [a] dorsal aspect; [b] ventral aspect. 58. Nebria nitidula (Fabricius) (Ulan Batar, Mongolia); [a] dorsal aspect; [b] ventral aspect. Scale line = 1.0 mm.

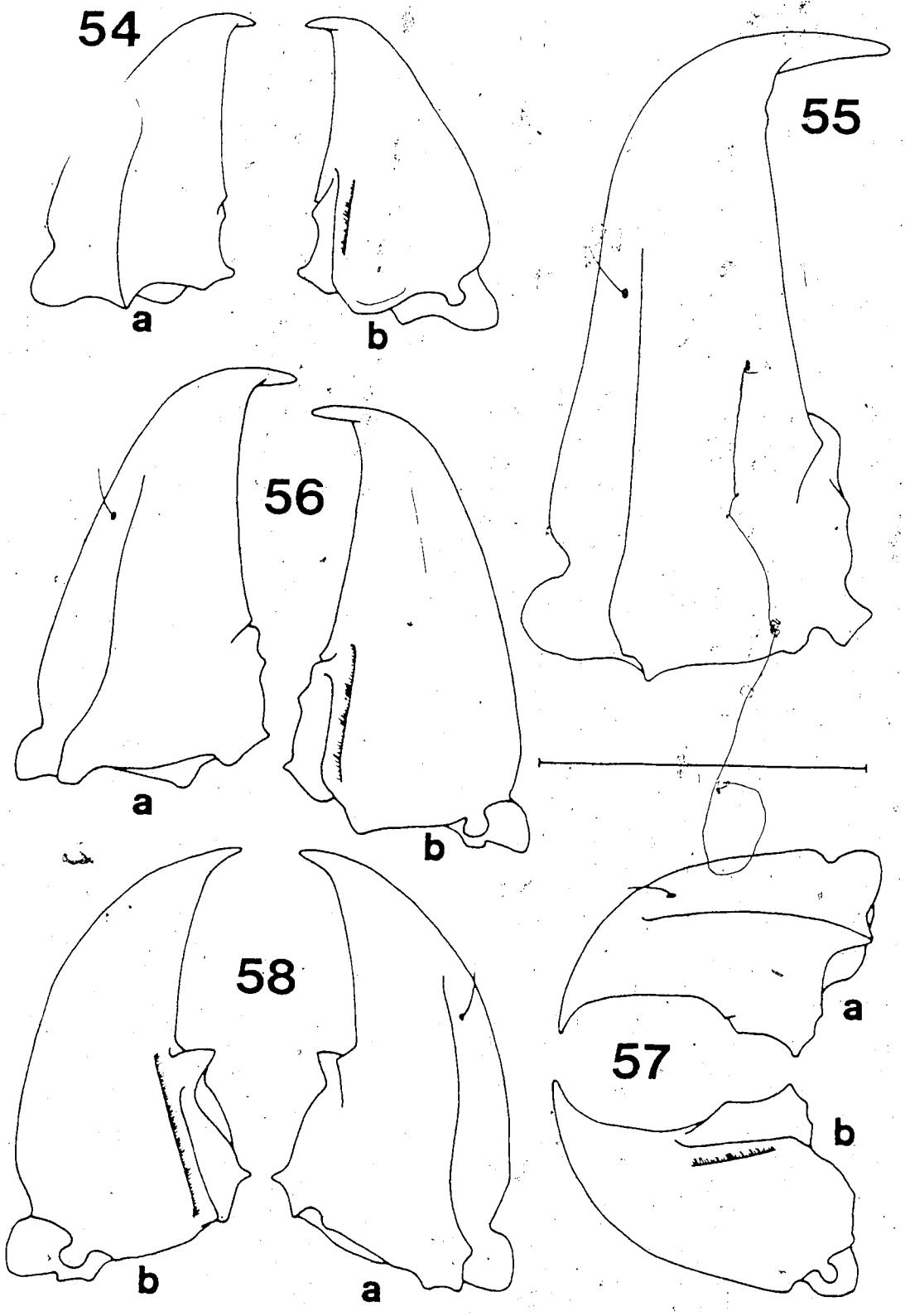
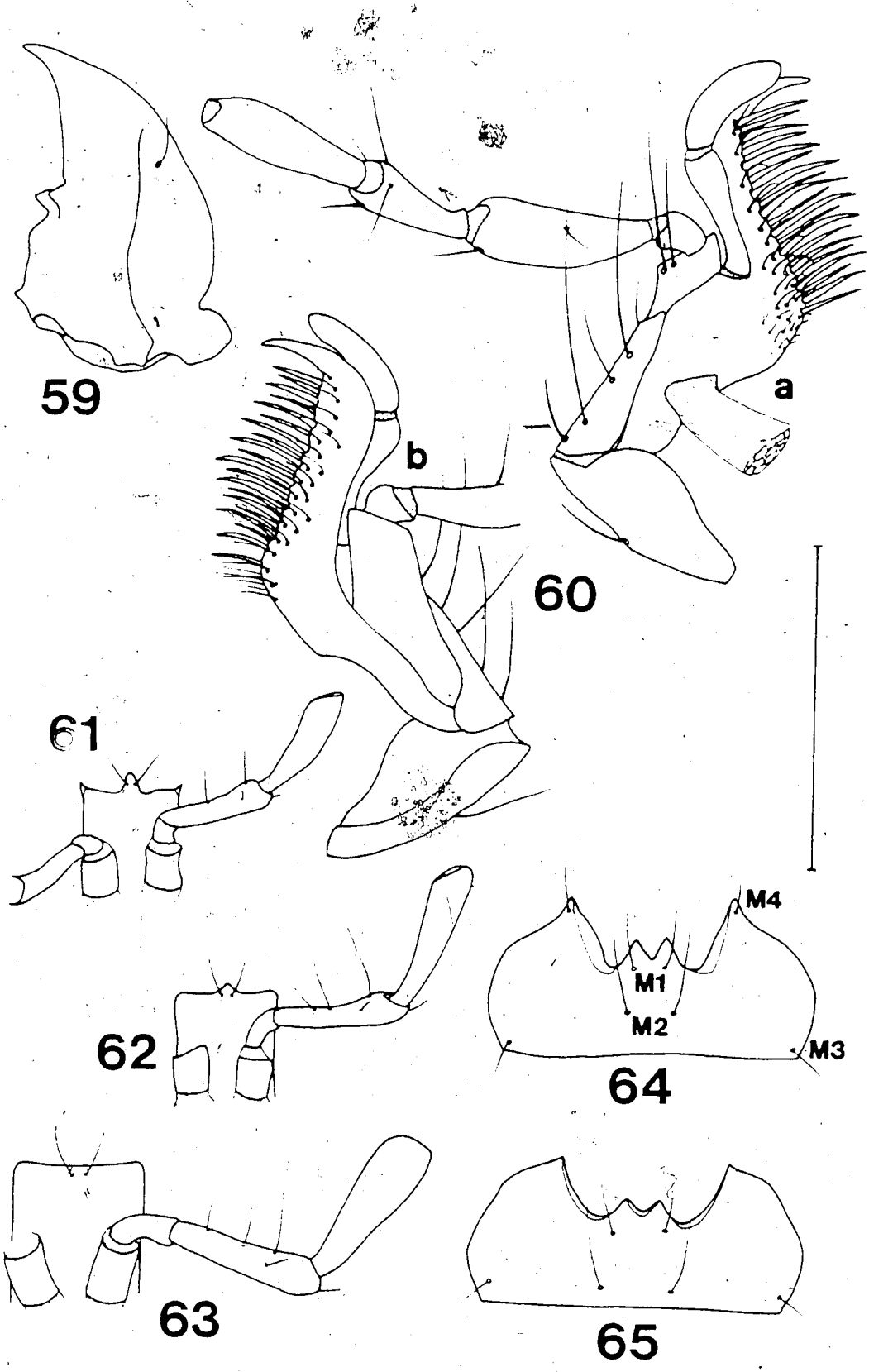
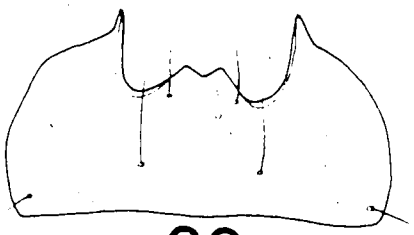

54
a
b
55
56
a
b
58
b
a
a
57
b

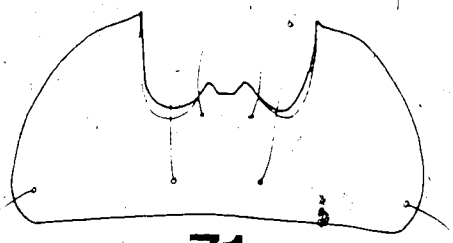
Fig. 59. Right mandible, dorsal aspect, Nebria appalachia Darlington (Soco Gap, North Carolina). Fig. 60. Right maxilla, Nebria brevicollis (Fabricius) (Hexampshire, England); [a] ventral aspect; [b] dorsal aspect. Figs. 61 - 63. Labium, ventral aspect. 61. Nebria virescens Horn (Vancouver, British Columbia). 62. Nebria hudsonica LeConte (Green River Lakes, Wyoming). 63. Nebria ingens ingens Horn (Mount Whitney, California). Figs. 64 - 65. Mentum, ventral aspect. 64. General form and chaetotaxy; setae described in text. 65. Nebria hudsonica LeConte (Green River Lakes, Wyoming). All scale lines = 1.0 mm.


59
a
b
60
61
62
M4
M1
M2
M3
64
63
65

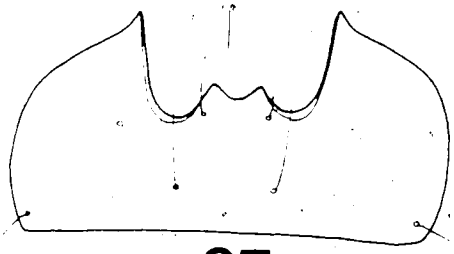
Figs. 66 - 75. Mentum, ventral aspect. 66. Nebria lyelli Van Dyke (Mount Lyell, California). 67. Nebria gregaria Fischer von Waldheim (Dutch Harbor, Unalaska Island, Alaska). 68. Nebria charlottae Lindroth (Massett, Queen Charlotte Islands, British Columbia). 69. Nebria obliqua LeConte (Hardin, Wyoming). 70. Nebria mannerheimii Fischer von Waldheim (Oakridge, Oregon). 71. Nebria desolata Kavanaugh (11 mi. se. of Boulder, Utah). 72. Nebria carri new species (Dollarhide Summit, Idaho). 73. Nebria kincaidi kincaidi Schwarz (Prince Rupert, British Columbia). 74. Nebria spatulata spatulata Vas Dyke (Franklin Lakes, California). 75. Nebria ovipennis LeConte (Mount Rose Pass, Nevada). Scale line = 1.0 mm.



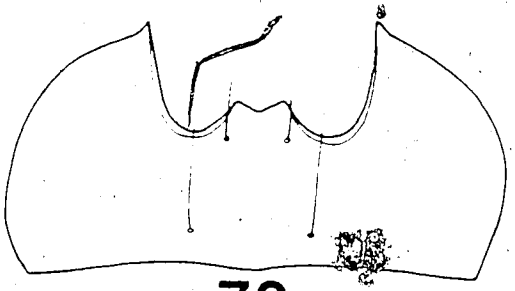
66



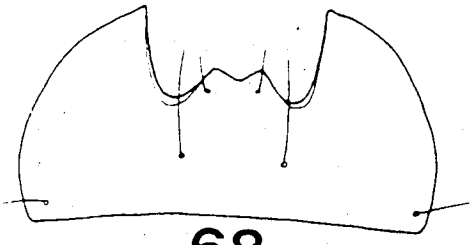
71



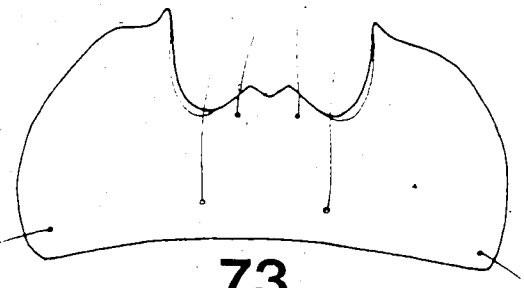
67



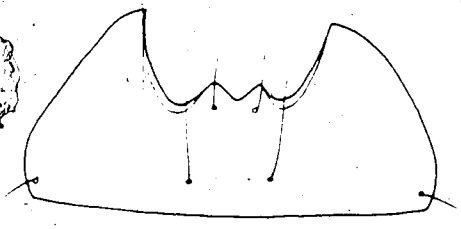
72



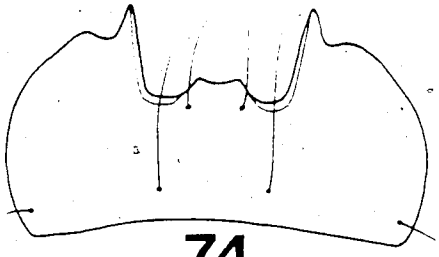
68



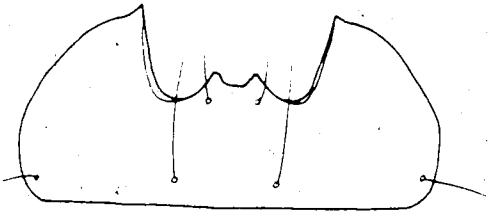
73



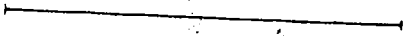
69

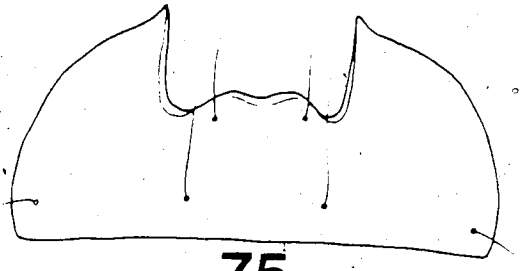


74

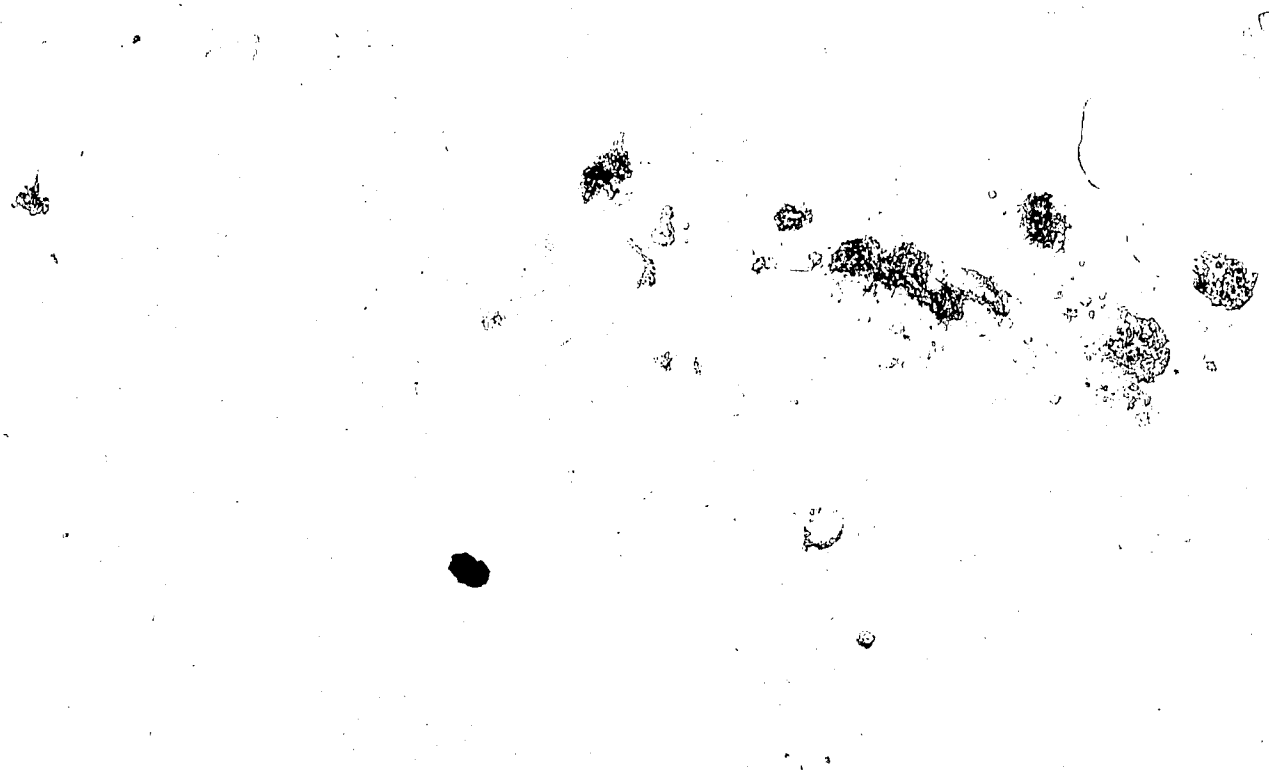


70

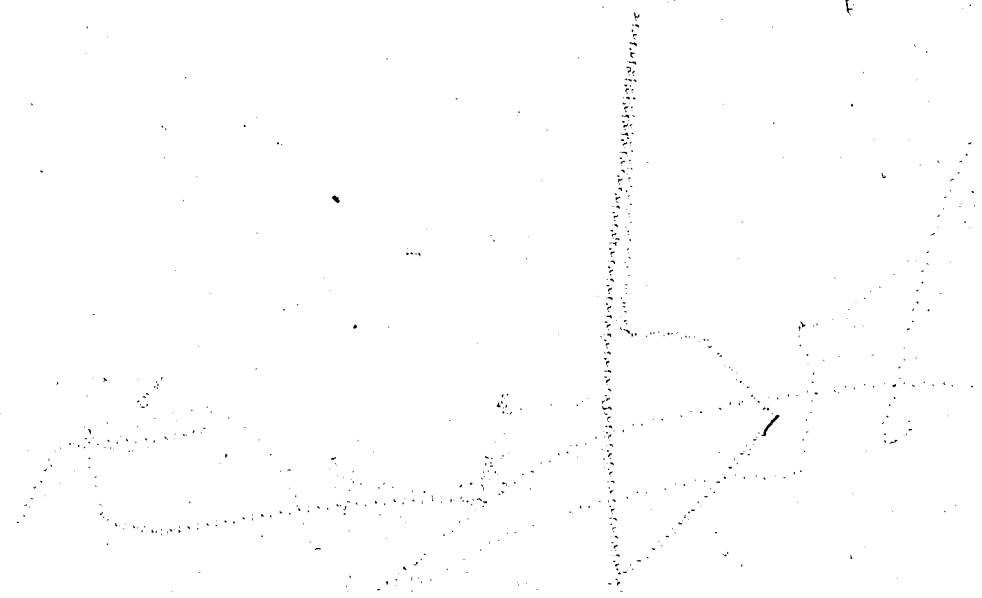


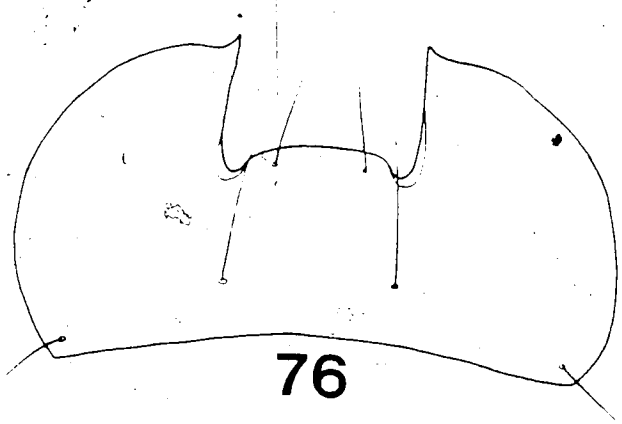


75

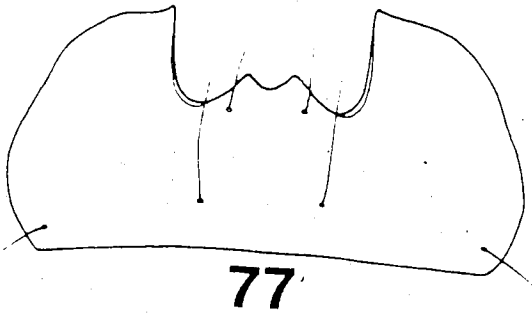


Figs. 76 - 78. Mentum, ventral aspect. 76. Nebria ingens ingens Horn (Mount Whitney, California). 77. Nebria trifaria trifaria LeConte (Laramie Peak, Wyoming). 78. Nebria trifaria catenata Casey (Wolf Creek Pass, Colorado). Figs. 79 - 81. Gula, ventral aspect. 79. General form and chaetotaxy; l = lateral setae; m = medial setae. 80. Nebria zioni zioni Van Dyke (Zion National Park, Utah). 81. Nebria purpurata LeConte (Rio Puerco, New Mexico). Scale line = 1.0 mm.

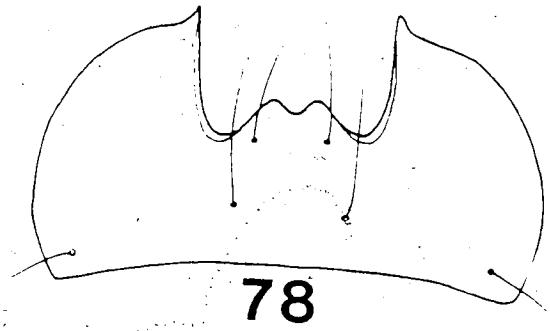




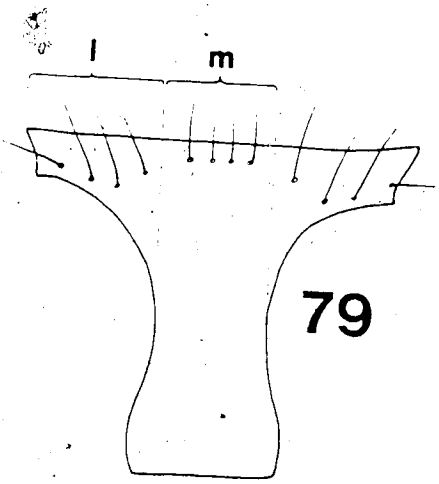
76



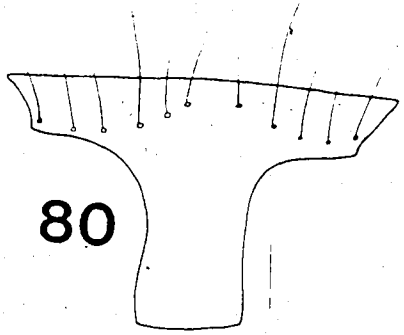
77



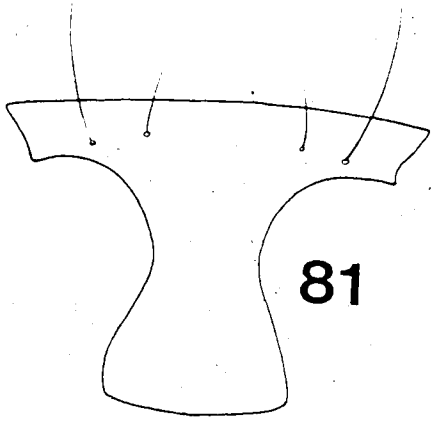
78



79

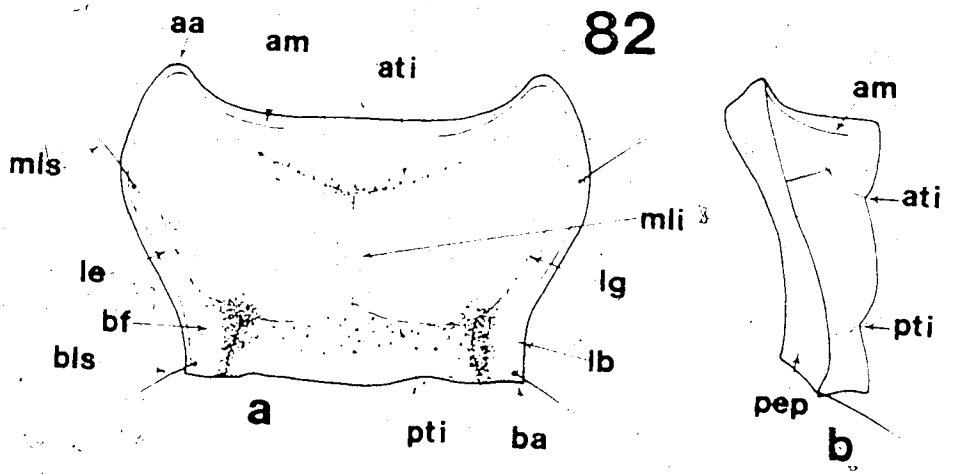


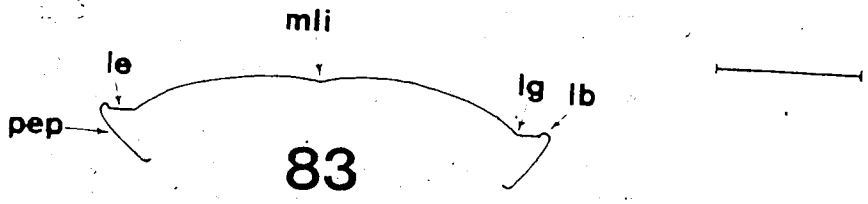
80

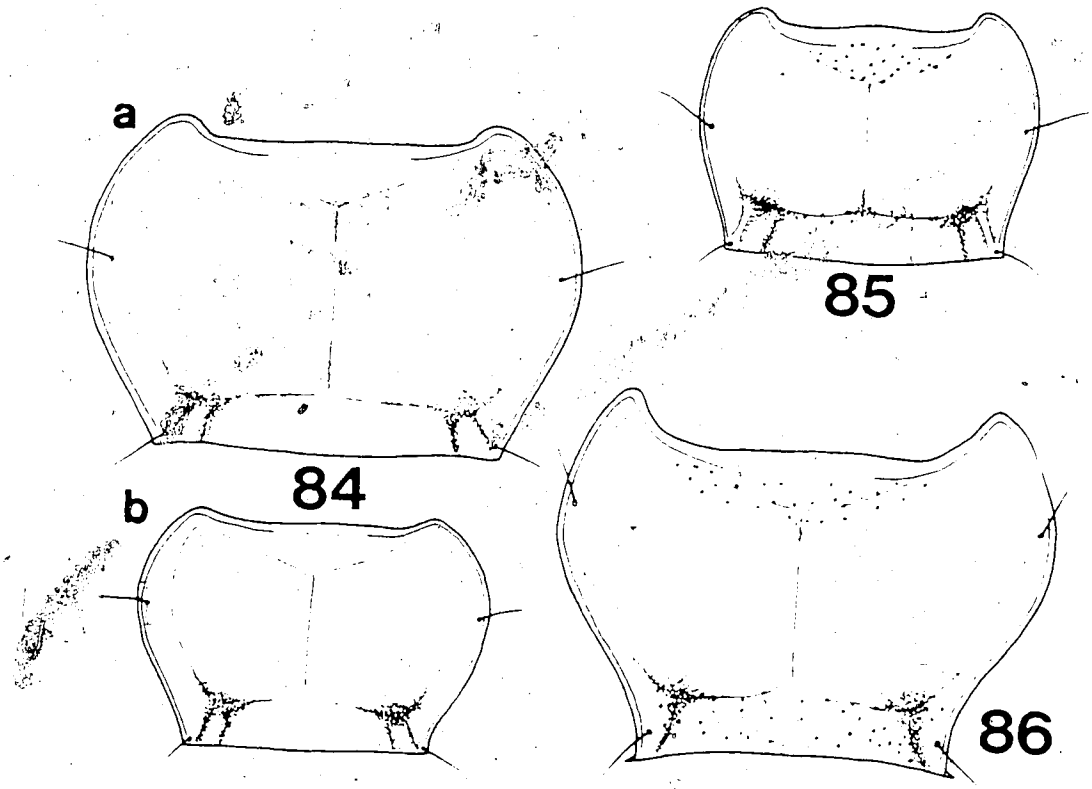


81

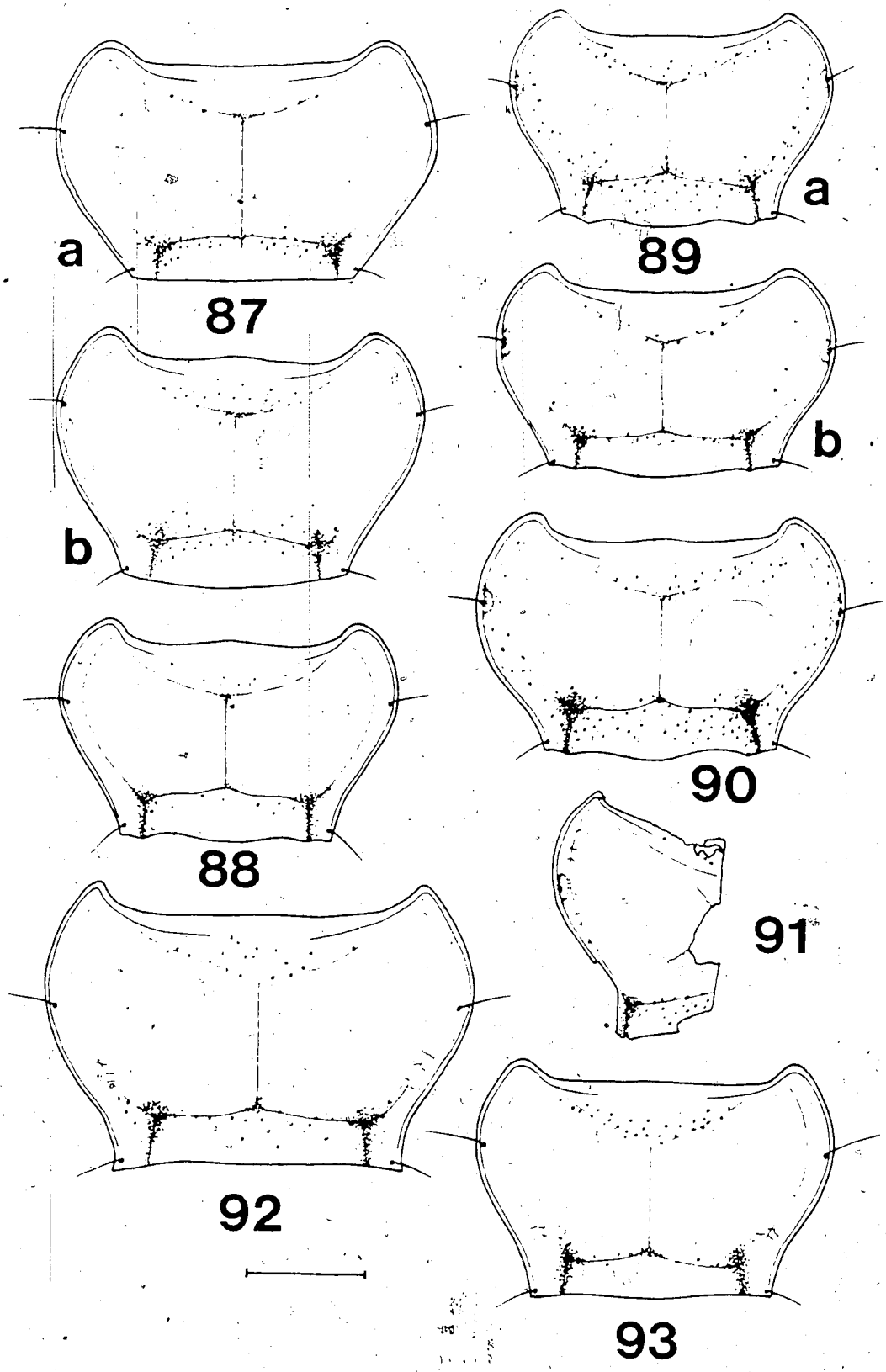
Figs. 82 - 83. Pronotum, general form and associated terms. 82. [a] dorsal aspect; [b] lateral aspect. 83. Transverse cross-section. Abbreviation code: aa = apical angle; am = apical margination; ati = anterior transverse impression; ba = basal angle; bf = basal fovea; bls = basolateral seta; lb = lateral bead (=lateral margination); le = lateral explanation; lg = lateral groove; mli = median longitudinal impression; mls = midlateral seta; pep = proepipleuron; pti = nsverse impression. Figs. 84 - 86. Pronotum, dorsal asp 84 bria virescens Horn ([a] Vancouver, British Columbia; [b] Bunker Hill kout, Washington). 85. Nebria chalceola Bates jiyama, Honsh apan). 86. Nebria paradisi Darlington (Mount Rainier, Washing). Scale line = 1.0 mm.


aa
am
ati
82
mls
mli
le
lg
bf
lb
bls
a
pti
ba
am
ati
pti
pep
b

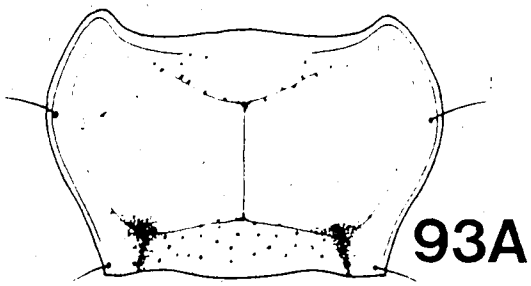

mli
le
lg
lb
pep
83

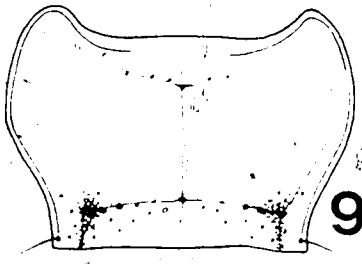

a
84
b
85
86

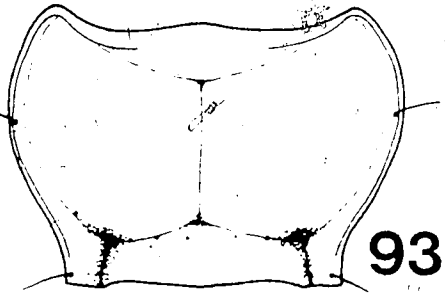
Figs. 87–93. Pronotum, dorsal aspect. 87. Nebria lacustris lacustris Casey ([a] Bayfield, Wisconsin; [b] Stowe, Vermont). 88. Nebria lacustris bellorum new subspecies (Great Balsam Mountains, North Carolina). 89. Nebria nivalis nivalis Paykull ([a] Aklavik, Northwest Territories; [b] Lake Harbour, Baffin Island). 90. Nebria nivalis gaspesiana new subspecies (Mont Albert, Québec). 91. Fossil specimen, nivalis subgroup (Lava Camp, Seward Peninsula, Alaska; ca. 5.7 million years B.P. [J. V. Matthews, personal communication]). 92. Nebria crassicornis crassicornis Van Dyke (Mount Rainier, Washington). 93. Nebria crassicornis intermedia Van Dyke (Glacier National Park, Montana). Scale line = 1.0 mm.

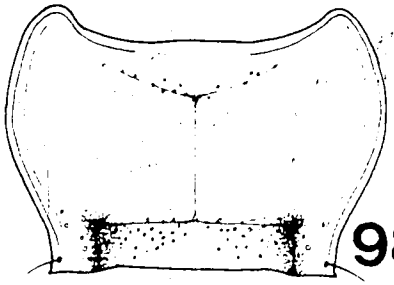

a
87
b
88
92
a
89
b
90
91
93

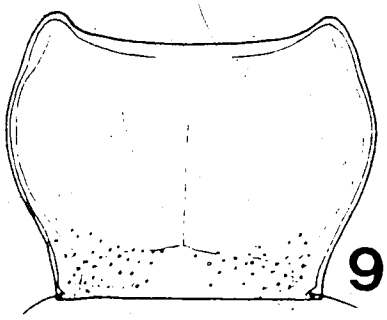
Figs. 93A-100. Pronotum, dorsal aspect. 93A. Nebria gyllenhali castanipes (Kirby) (Mount Washington, New Hampshire). 93B. Nebria gyllenhali lindrothi new subspecies (Wheeler Peak, New Mexico). 94. Nebria lyelli Van Dyke (Mount Lyell, California). 95. Nebria acuta acuta Lindroth (Mount Rainier, Washington). 96. Nebria acuta quileute new subspecies (Olympic Hot Springs, Washington). 97. Nebria sahlbergii modoc new subspecies (Warner Mountains, California). 98. Nebria sahlbergii triad new subspecies (Trinity Alps, California). 99. Nebria zioni zioni Van Dyke (Escalante Mountains, Utah). 100. Nebria suturalis LeConte ([a] Athabasca Glacier, Alberta; [b] Quandary Peak, Colorado). Scale line = 1.0 mm.

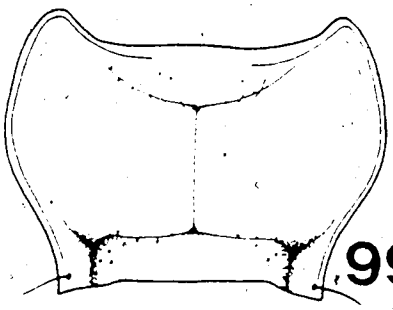

93A

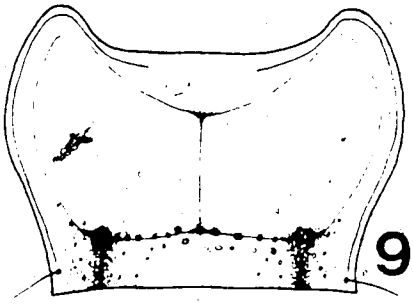

97

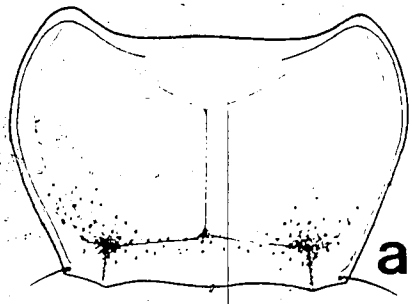

93B


98

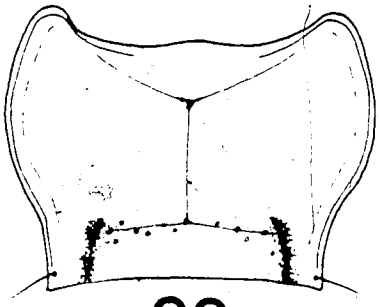

94

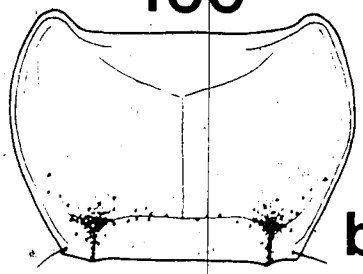

99


95

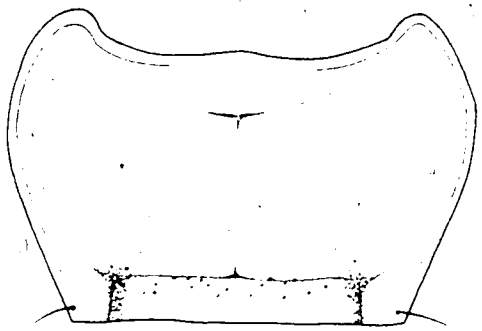

a

100

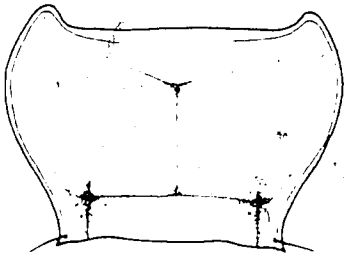

96


b

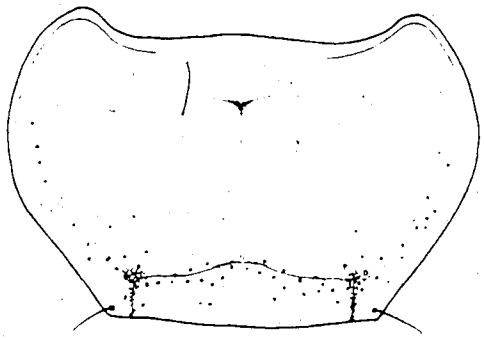
Figs. 101–107. Pronotum, dorsal aspect. 101. Nebria obliqua LeConte (Keystone, Wyoming). 102. Nebria appalachia Darlington (Soco Gap, North Carolina). 103. Nebria pallipes Say (Ste-Mélanie, Québec). 104. Nebria darlingtoni new species (Kyburz, California). 105. Nebria mannerheimii Fischer von Waldheim ([a] Cheekeye River, British Columbia; [b] Weiser, Idaho). 106. Nebria desolata Kavanaugh (11 miles southeast of Boulder, Utah). 107. Nebria gebleri gebleri Dejean (Cuprum, Idaho). Scale line = 1.0 mm.



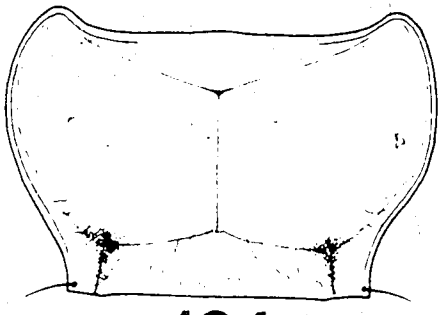
101



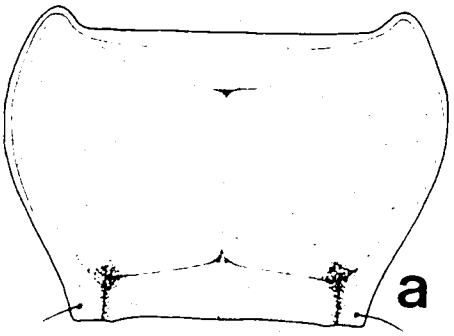
102



103

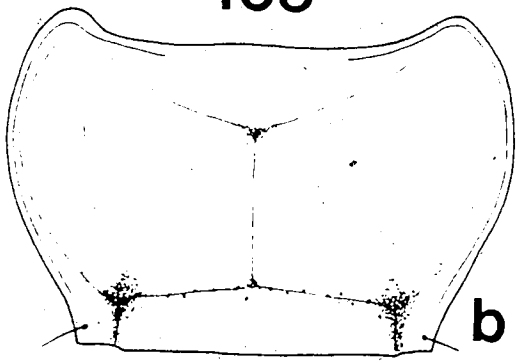


104

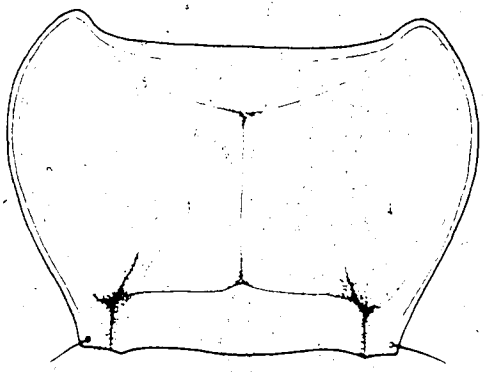


a

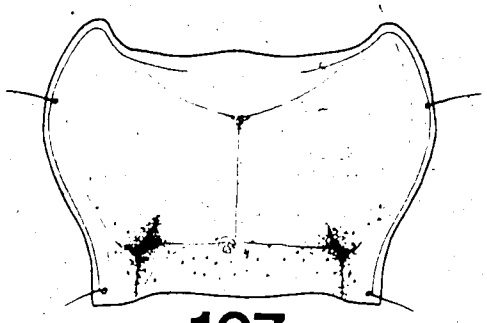
105



b

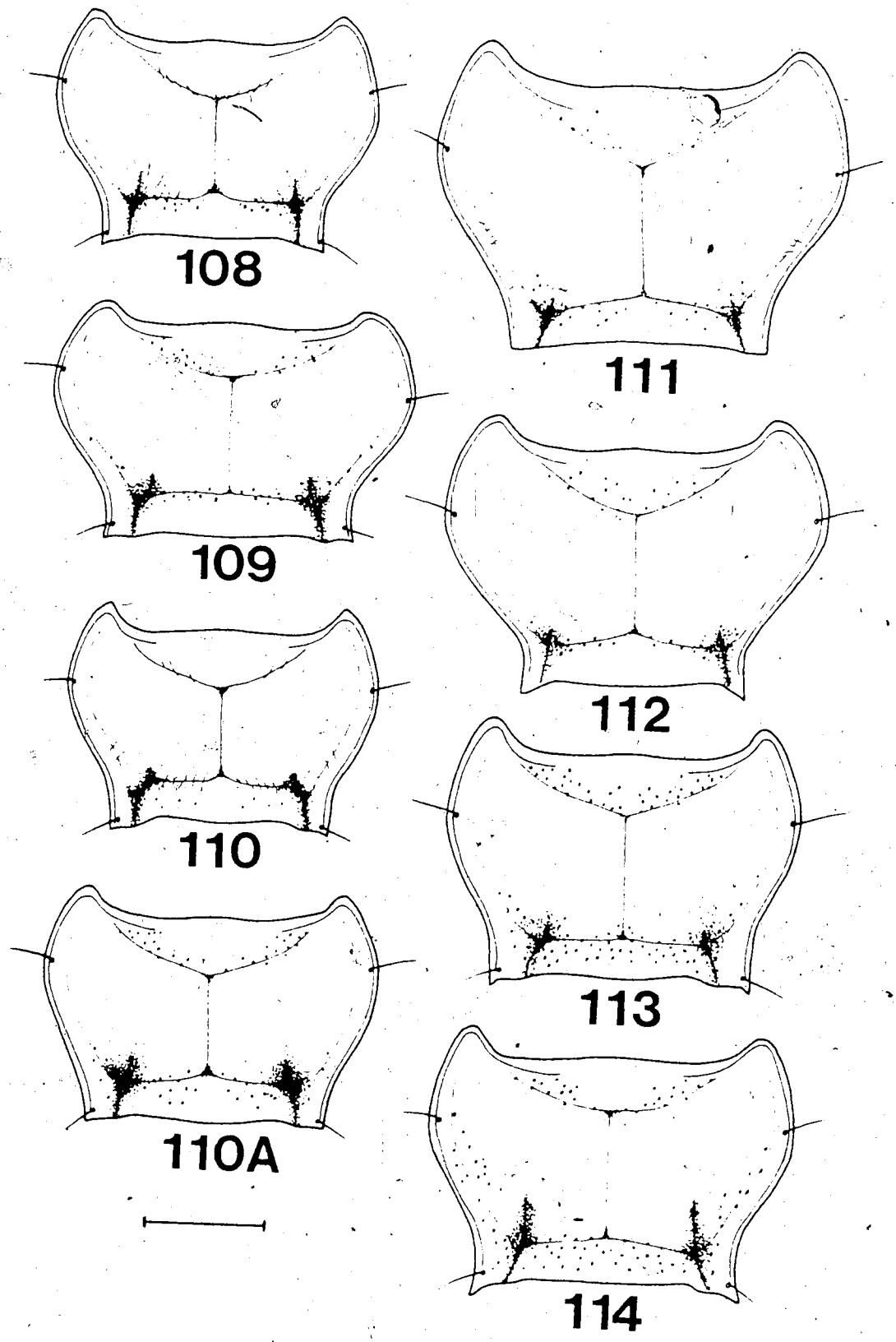


106

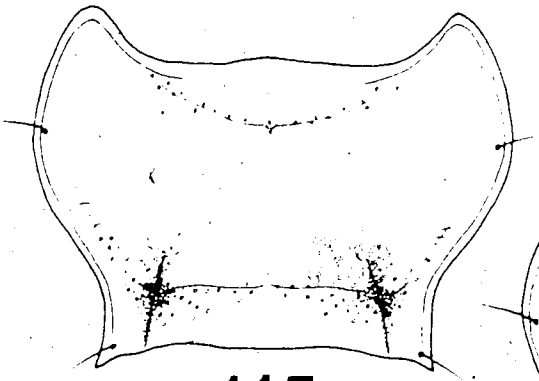


107

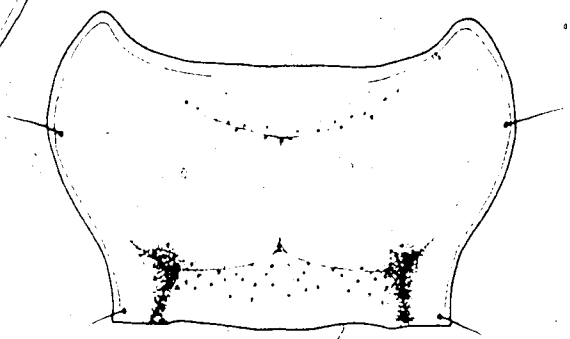
Figs. 108–114. Pronotum, dorsal aspect. 108. Nebria gebleri cascadensis new subspecies (Glacier, Washington). 109. Nebria gebleri rathvoni LeConte (Mount Lassen, California). 110. Nebria gebleri siskiyouensis new subspecies (Trinity Alps, California). 110A. Nebria gebleri strawberriensis new subspecies (Strawberry Mountains, Oregon). 111. Nebria carri new species (Dollarhide Summit, Idaho). 112. Nebria kincaidi kincaidi Schwarz (Olympic Hot Springs, Washington). 113. Nebria meanyi meanyi Van Dyke (Mount Rainier, Washington). 114. Nebria meanyi lamarckensis new subspecies (Upper Lamarck Lake, California). Scale line = 1.0 mm.


108
109
110
110A
111
112
113
114

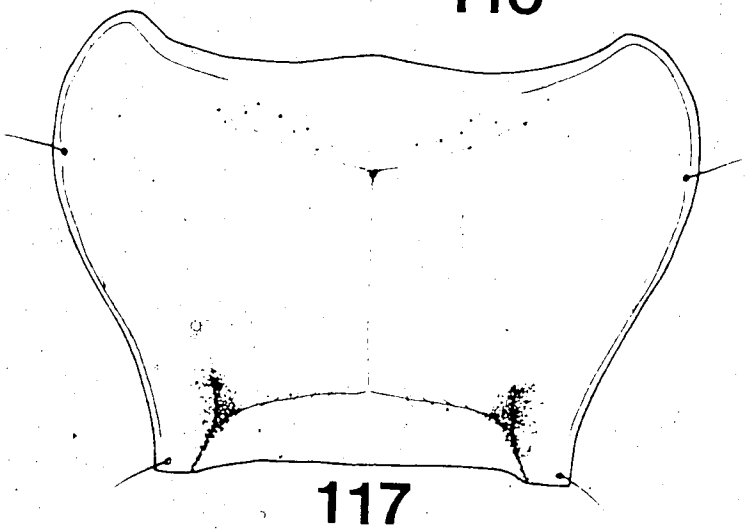
Figs. 115–118. Pronotum, dorsal aspect. 115. Nebria meanyi sylvatica new subspecies (Olympic Hot Springs, Washington). 116. Nebria metallica Fischer von Waldheim (Manning Provincial Park, British Columbia). 117. Nebria ingens ingens Horn (Mount Whitney, California). 118. Nebria piperi Van Dyke (Mount Rainier, Washington). Scale line = 1.0 mm.



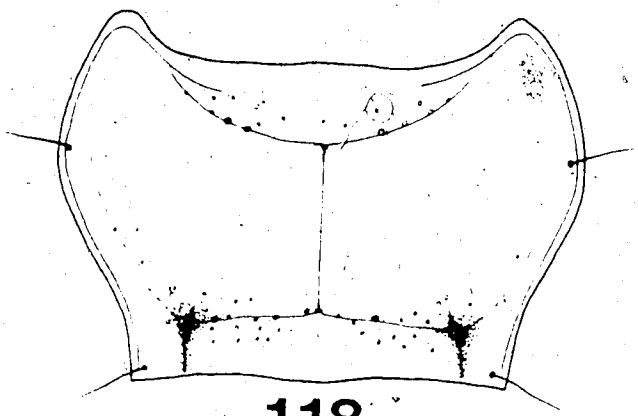
115



116

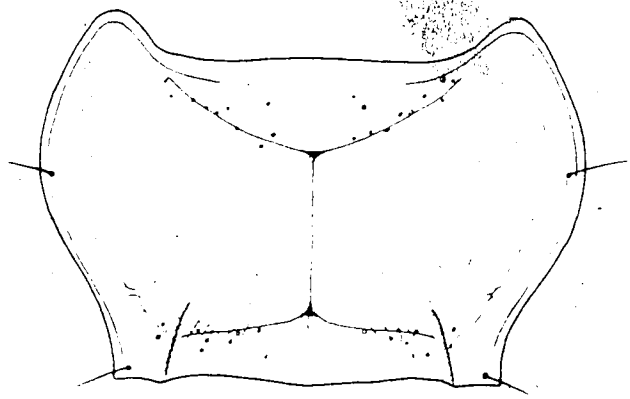


117

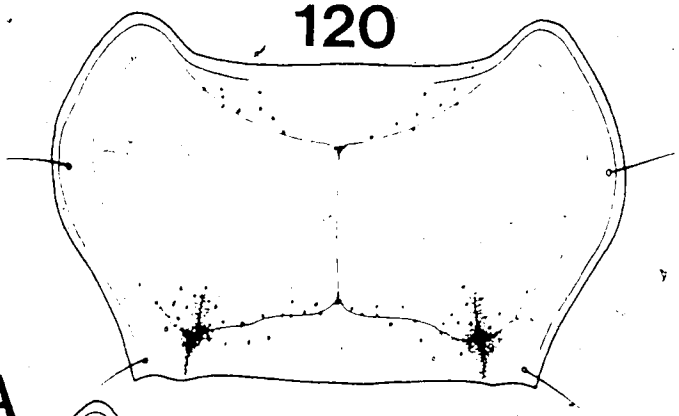


118

Figs. 119-121A. Pronotum, dorsal aspect. 119. Nebria schwarzi schwarzi Van Dyke (Kicking Horse River, British Columbia). 120. Nebria schwarzi beverlianna new subspecies (Hoback River, Wyoming). 120A. Nebria purpurata LeConte (Hoosier Pass, Colorado). 121. Nebria trifaria trifaria LeConte (Wasatch Mountains, Utah). 121A. Nebria trifaria utahensis new subspecies (Henry Mountains, Utah). Scale line = 1.0 mm.

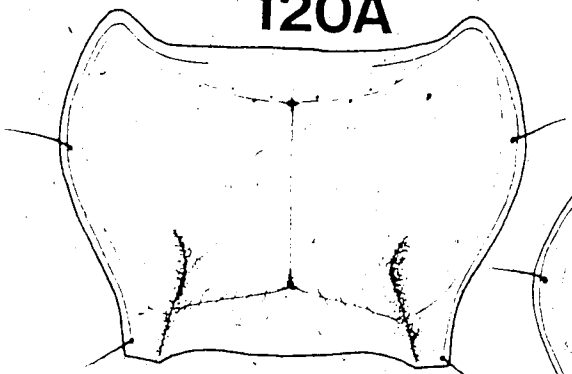


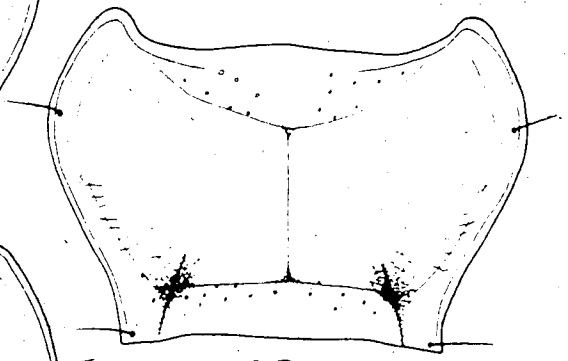
119



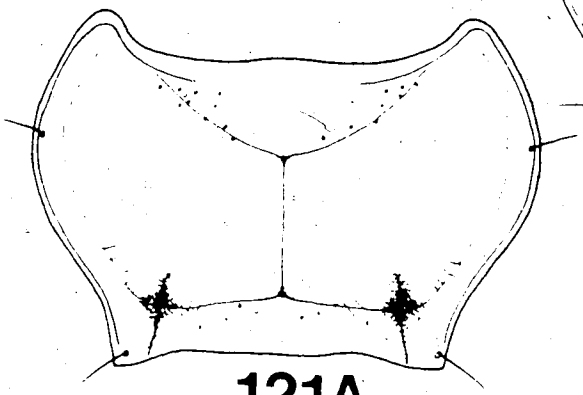
120

120A



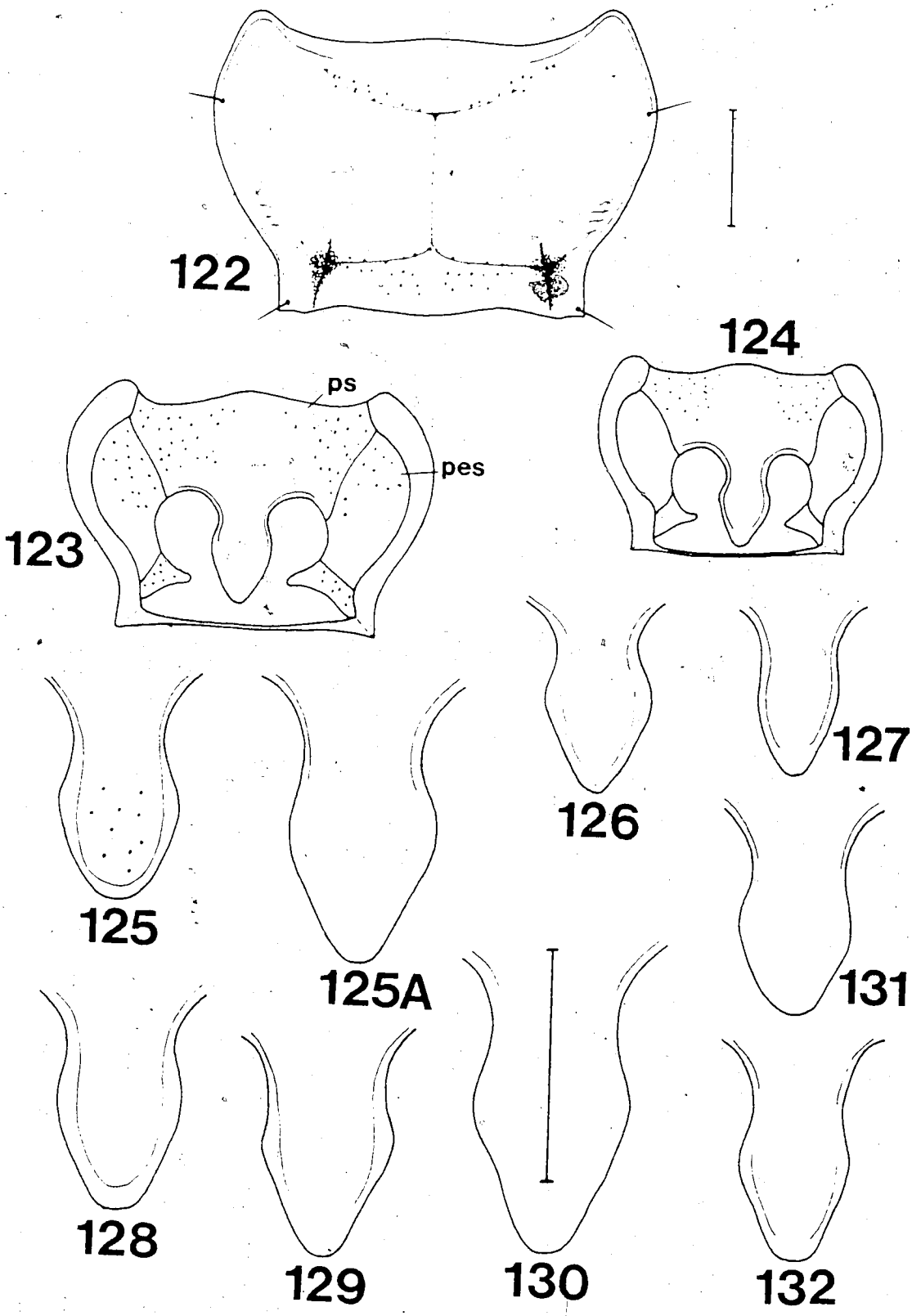


121

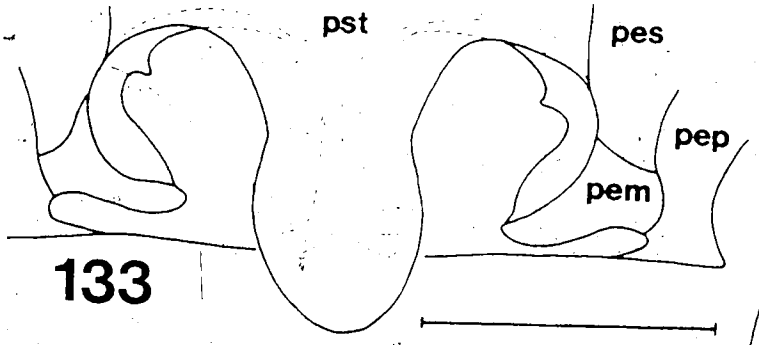


121A

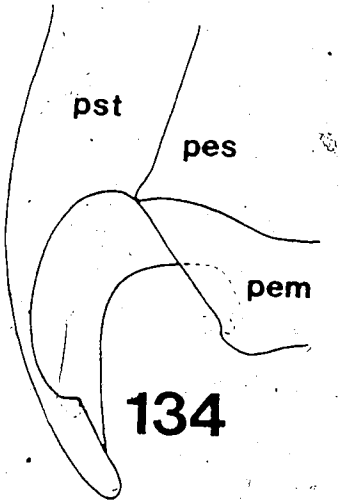
Fig. 122. Pronotum, dorsal aspect, Nebria coloradensis Van Dyke (Hoosier Pass, Colorado). Figs. 123-124. Prothoracic venter. 123. Nebria gouleti new species (Lewiston, Idaho). 124. Nebria sahlbergii modoc new subspecies (Warner Mountains, California). Figs. 125-132. Prosternal intercoxal process. 125. Nebria brevicollis (Fabricius) (Pitlochry, Scotland). 125A Nebria piperi Van Dyke (Mount Rainier, Washington). 126. Nebria fragilis fragilis Casey (North Fork Provo River, Utah). 127. Nebria appalachia Darlington (Soco Gap, North Carolina). 128. Nebria charlottae Lindroth (Massett, Queen Charlotte Islands). 129. Nebria gregaria Fischer von Waldheim (Unalaska Island, Aleutian Islands). 130. Nebria ingens riversi Van Dyke (Mount Lyell, California). 131. Nebria purpurata LeConte (Twin Lakes, Colorado). 132. Nebria arkansana uinta new subspecies (Logan River, Utah). All scale lines = 1.0 mm.


122
124
ps
pes
123
127
126
125
125A
131
128
129
130
132

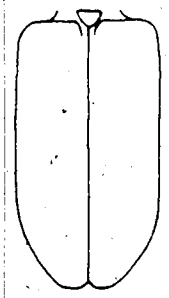
Figs. 133-134. Front coxal cavities, Nebria brevicollis (Fabricius). 133. Ventral aspect. 134. Left lateral aspect. Figs. 135-142. Elytral silhouette, dorsal aspect. 135. Generalized rectangular shape. 136. Generalized subrectangular shape. 137. Generalized subovoid shape. 138. Generalized subovoid-narrowed shape. 139. Generalized ovoid shape. 140. Generalized tear-shape. 141. Nebria gregaria Fischer von Waldheim (Unalaska Island, Aleutian Islands). 142. Nebria charlottae Lindroth (Massett. Queen Charlotte Islands). Figs. 143-145. Elytral silhouette, [a] dorsal aspect, [b] posterior aspect. 143. Nebria desolata Kavanaugh (11 miles southeast of Boulder, Utah). 144. Nebria piperi Van Dyke (Mount Rainier, Washington). 145. Nebria paradisi Darlington (Mount Rainier, Washington). Scale line = 1.0 mm.



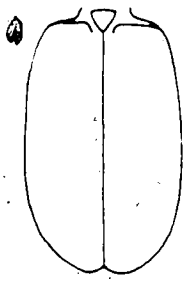
133



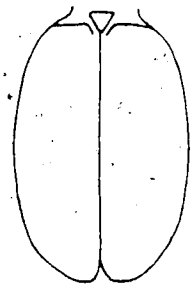
134



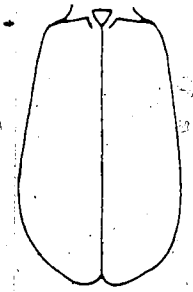
135



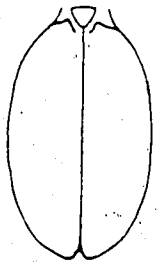
136



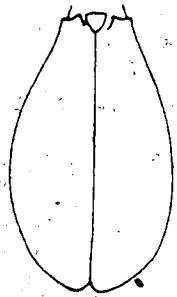
137



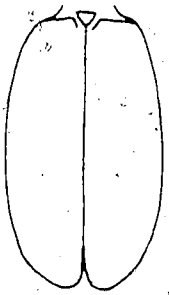
138



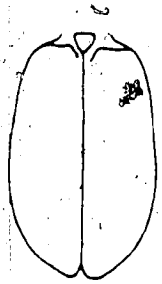
139



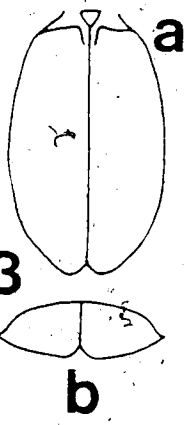
140



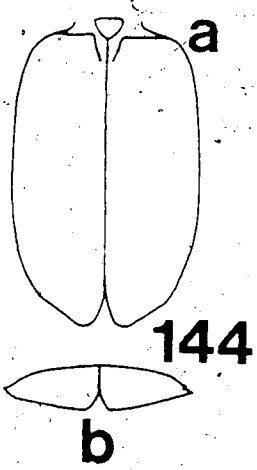
141



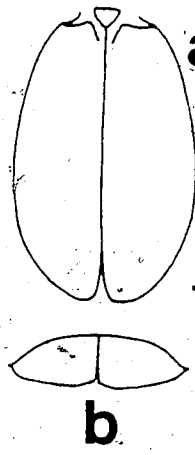
142



143

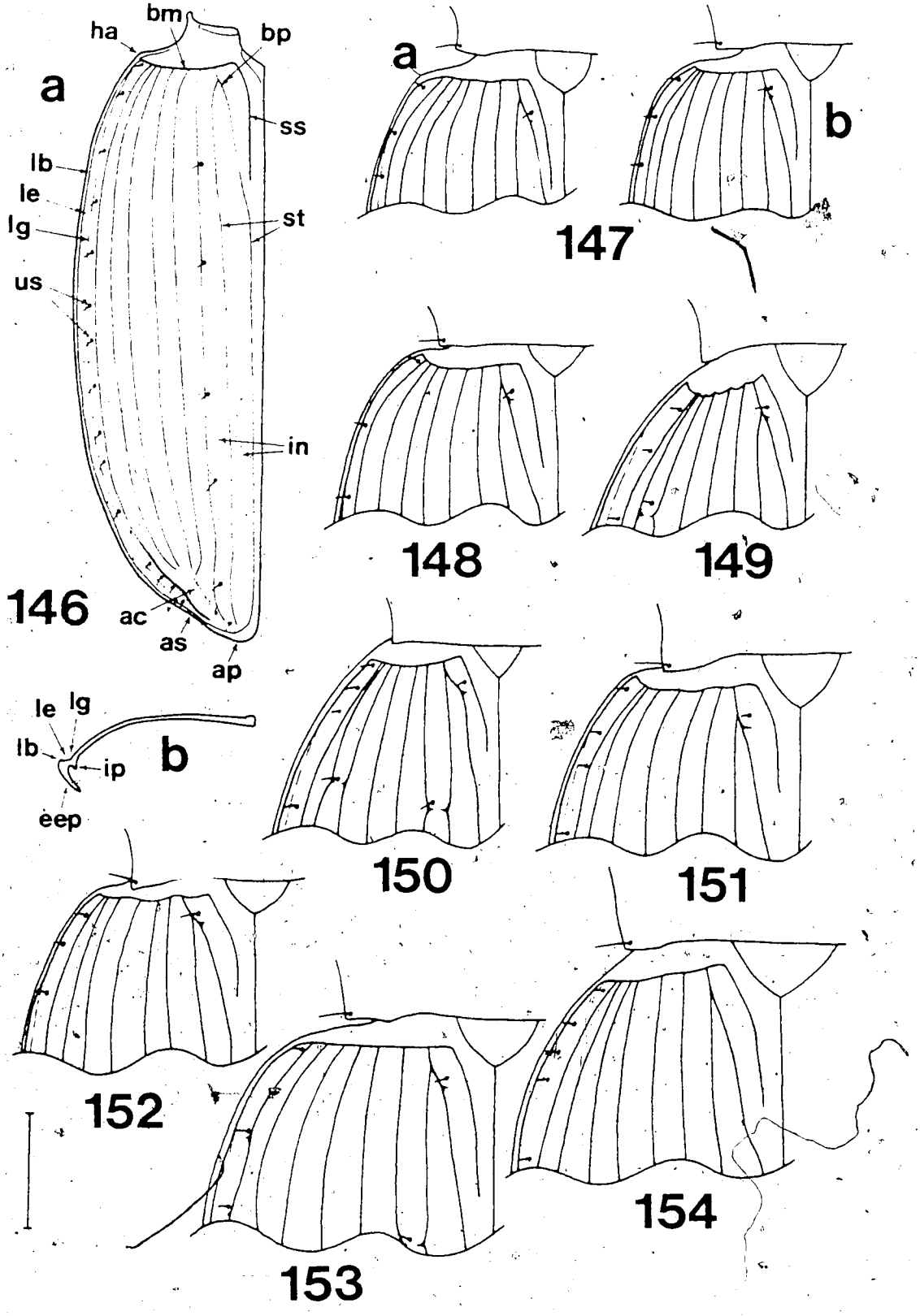


144

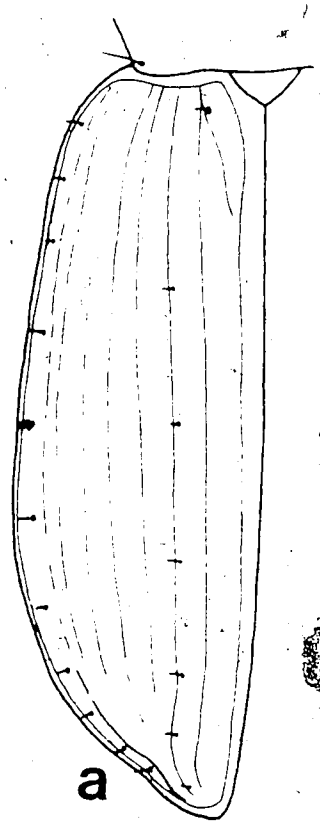


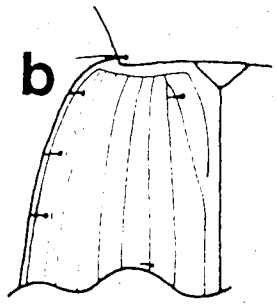
145

Fig. 146. Left elytron, generalized form and associated terms ([a] dorsal aspect; [b] cross-section at middle); ac = apical carina; ap = apex; as = subapical sinuation of lateral margin; bm = basal margination; bp = basal pore; eep = elytral epipleuron; ha = humeral angle; in = intervals; ip = internal plica; lb = lateral bead; le = lateral explanation; lg = lateral groove; ss = scutellar striole; st = stria; us = umbilicate series of setae. Figs. 147-154. Basal region of left elytron. 147. Nebria arkansana edwardsi new subspecies ([a] Rancheria, Yukon Territory; [b] Gorge Creek, Alberta). 148. Nebria altaica Gebler (Slyudanka, Irkutskaya Oblast, U.S.S.R.). 149. Nebria kincaidi kincaidi Schwarz (Prince Rupert, British Columbia). 150. Nebria kincaidi balli new subspecies (Mount Rainier, Washington). 151. Nebria meanyi meanyi Van Dyke (Mount Shasta, California). 152. Nebria meanyi lamarckensis new subspecies (Upper Lamarck Lake, California). 153. Nebria piperi Van Dyke (Mount Rainier, Washington). 154. Nebria ingens ingens Horn (Mount Whitney, California). Scale line = 1.0.

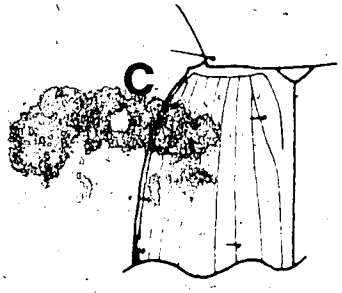

a
ha
bm
bp
ss
lb
le
lg
st
us
in
ac
as
ap
146
b
le
lg
lb
ip
eep
a
b
147
148
149
150
151
152
153
154

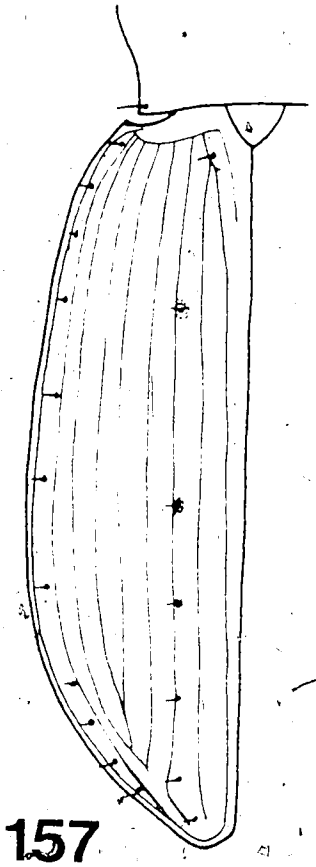
Figs. 155–158. Left elytron, dorsal aspect. 155. Nebria virescehs Horn ([a] Vancouver Island, British Columbia; [b] Kamiak Butte, Washington; [c] Bunker Hill Lookout, Washington). 156. Nebria frigida Sahlberg (Kolyma River, Siberia, U.S.S.R.). 157. Nebria acuta acuta Lindroth (Mount Rainier, Washington). 158. Nebria sahlbergii sahlbergii Fischer von Waldheim ([a] Mount Rainier, Washington; [b] Hope Trail, British Columbia). Scale line = 1.0 mm.



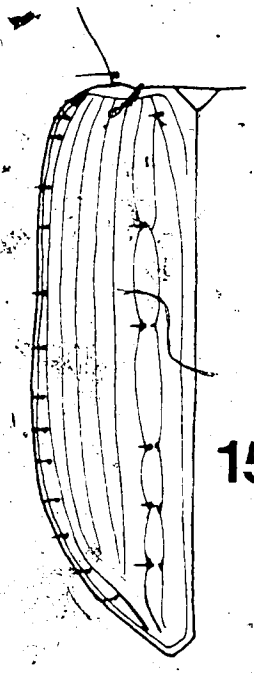


155

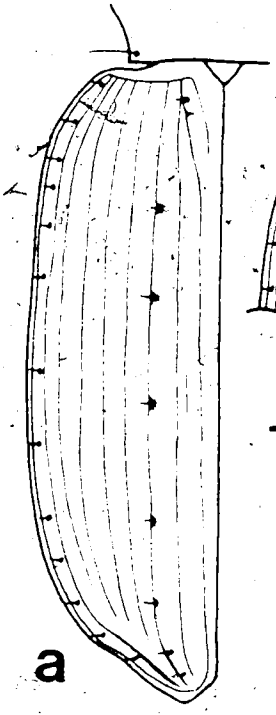


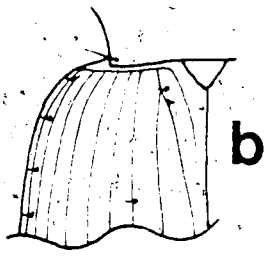


157



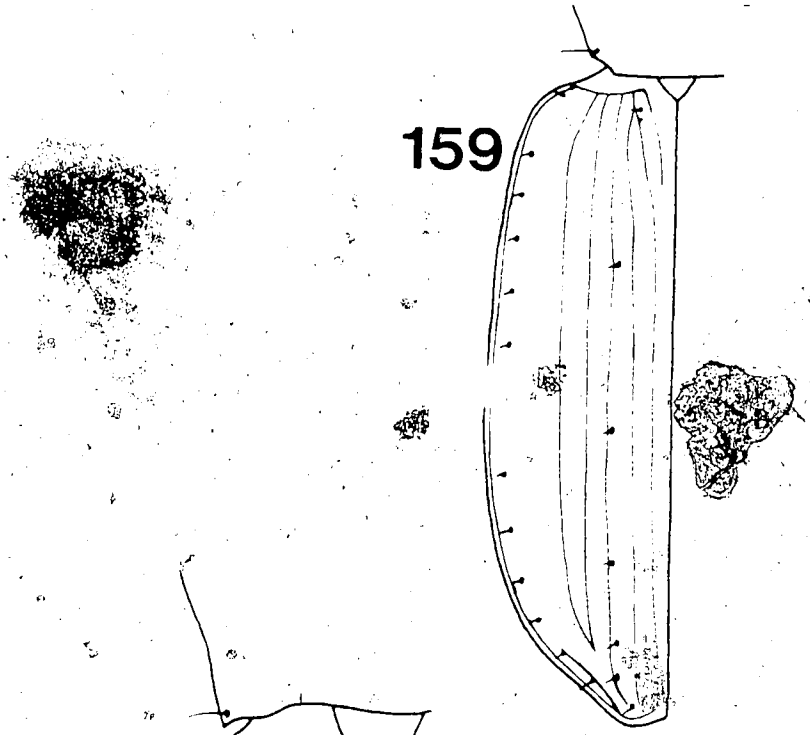
156



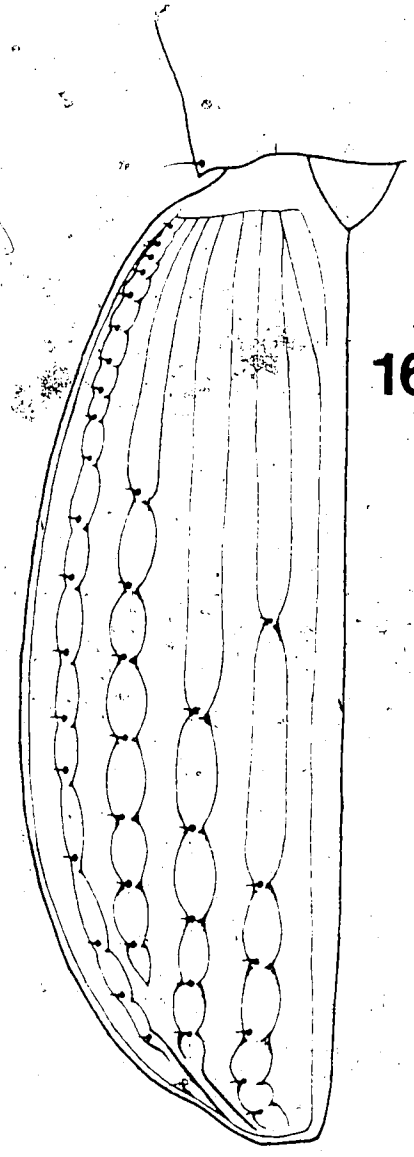


158

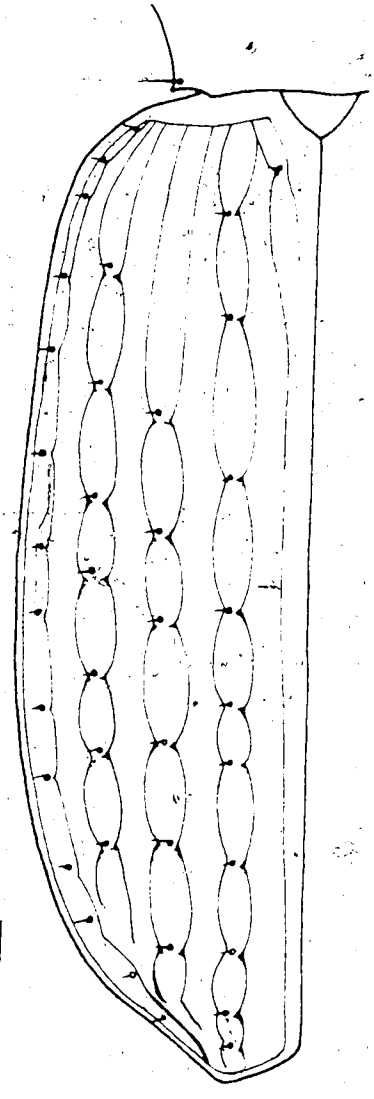
Figs. 159-161. Left elytron, dorsal aspect. 159. Nebria suturalis LeConte (Mount Mansfield, Vermont). 160. Nebria vandykei vandykei Bänninger (Mount Rainier, Washington). 161. Nebria schwarzi schwarzi Van Dyke (Wildhay River, Alberta). Scale line = 1.0 mm.



159

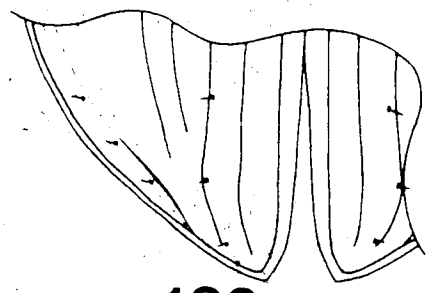


160

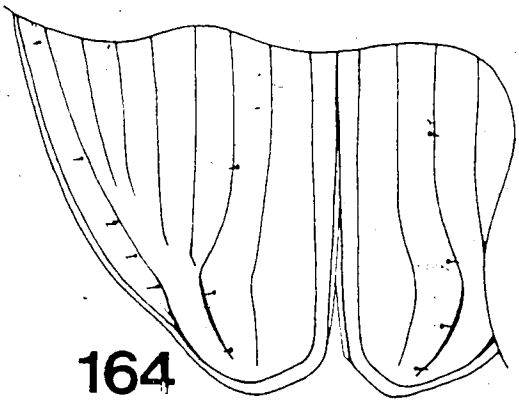


161

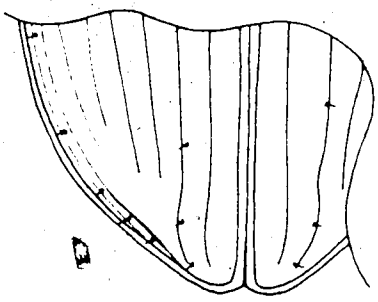
Figs. 162–168. Elytra, apical region, dorsal aspect. 162. Nebria virescens Horn (Kamiak Butte, Washington). 163. Nebria chalceola Bates (Mount Hiei, Kyoto, Japan). 164. Nebria paradisi Darlington (Mount St. Helens, Washington). 165. Nebria lacustris lacustris Casey (Mount Washington, New Hampshire). 166. Nebria pallipes Say (Gatlinburg, Tennessee). 167. Nebria meanyi meanyi Van Dyke (Mount Hood, Oregon). 168. Nebria schwarzi schwarzi Van Dyke (Kicking Horse River, British Columbia). Scale line = 1.0 mm.



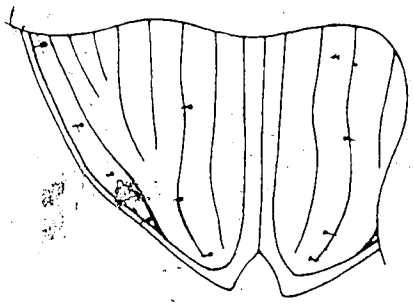
162



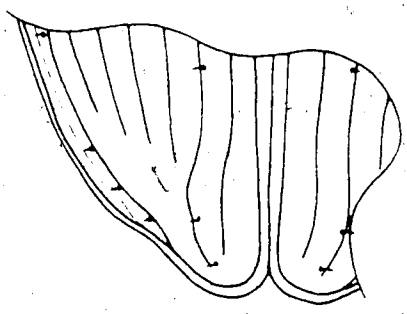
164



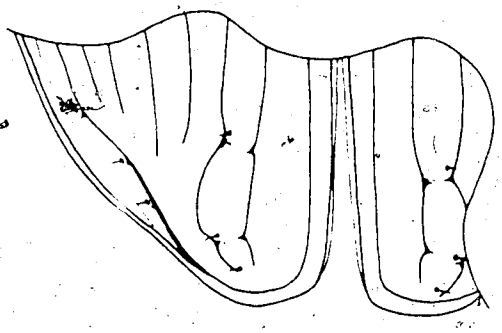
163



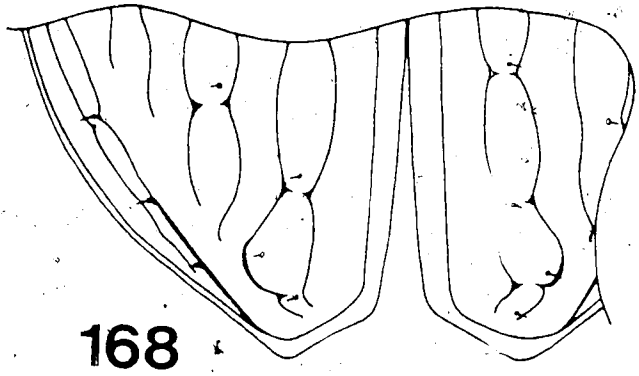
165



166

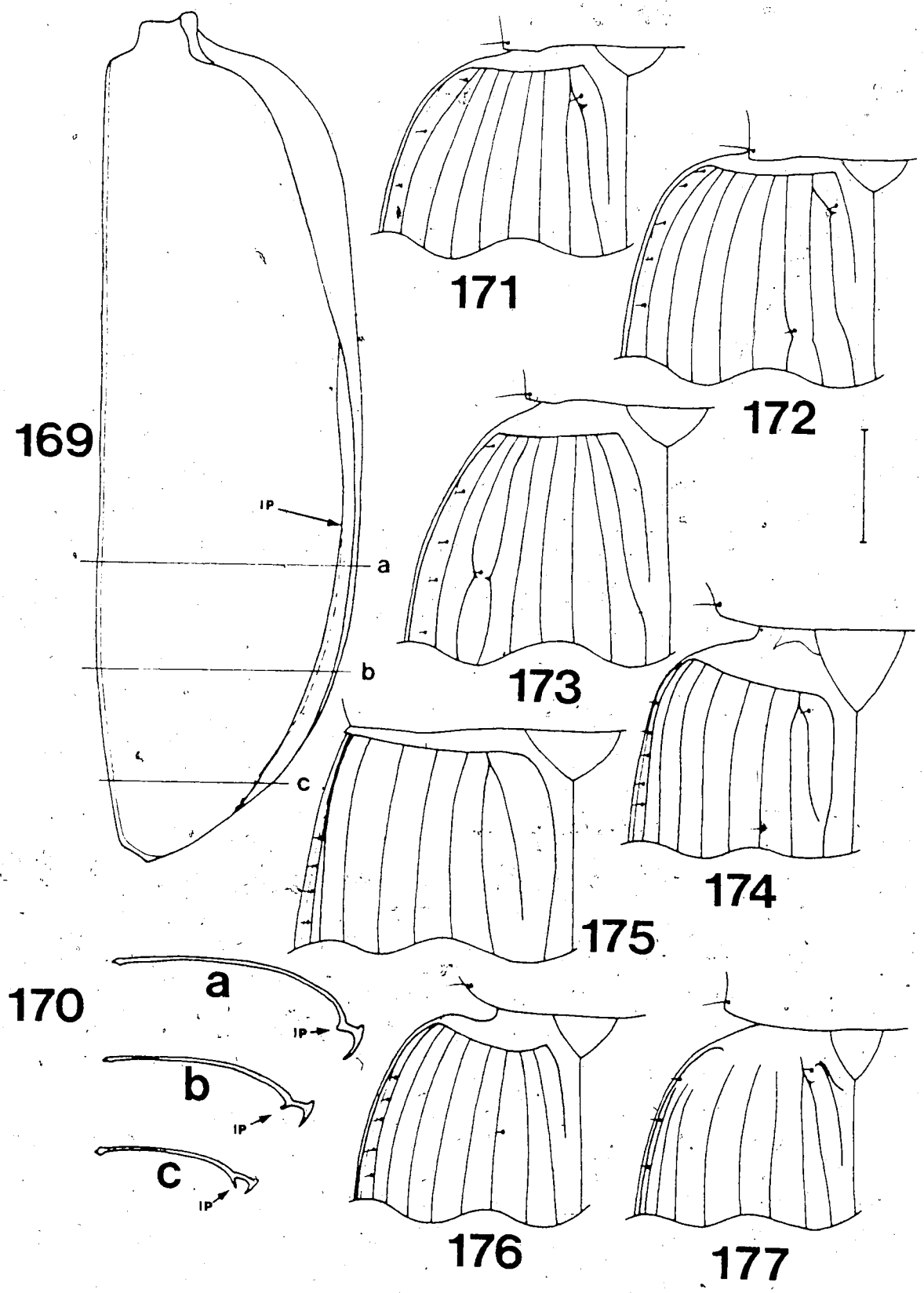


167



168

Fig. 169. Left elytron Nebria hudsonica LeConte, ventral aspect; ip = internal plica; a, b, and c refer to respective cross-sections in Fig. 170. Fig. 170. Left elytron Nebria hudsonica LeConte, cross-sections [a], [b], and [c] as in Fig. 169; ip = internal plica. Figs. 171-177. Left elytron, basal region. 171. Nebria gouleti new species (Clearwater River, Idaho). 172. Nebria metallica Fischer von Waldheim (Broad Bay, Unalaska Island, Aleutian Islands). 173. Nebria trifaria trifaria LeConte (Cedar Canyon, Utah). 174. Pterostichus adstrictus Eschscholtz (Edmonton, Alberta). 175. Amara insignis Dejean (Antelope, California). 176. Agonum maculicolle Dejean (Tehama County, California). 177. Patrobus longicornis Say (Edmonton, Alberta). Scale line = 1.0 mm.


169
IP
a
b
c
171
172
173
174
175
170
a
IP
b
IP
c
IP
176
177

Figs. 178-179. Fossil elytral fragments. 178. Nebria nivalis Paykull ([a] and [b] basal portions of right elytra; Scarborough Bluffs, Toronto, Ontario; ca. 70,000 years B.P. [A. Morgan, personal communication]). 179. Nebria pallipes Say and/or Nebria lacustris Casey ([a], [b], and [d] basal portions of left elytra, [c] same of right elytron; Don Valley Brickpit, Toronto, Ontario; ca. 100,000 years B.P. [personal communication, A. Morgan]). Scale line = 1.0 mm.

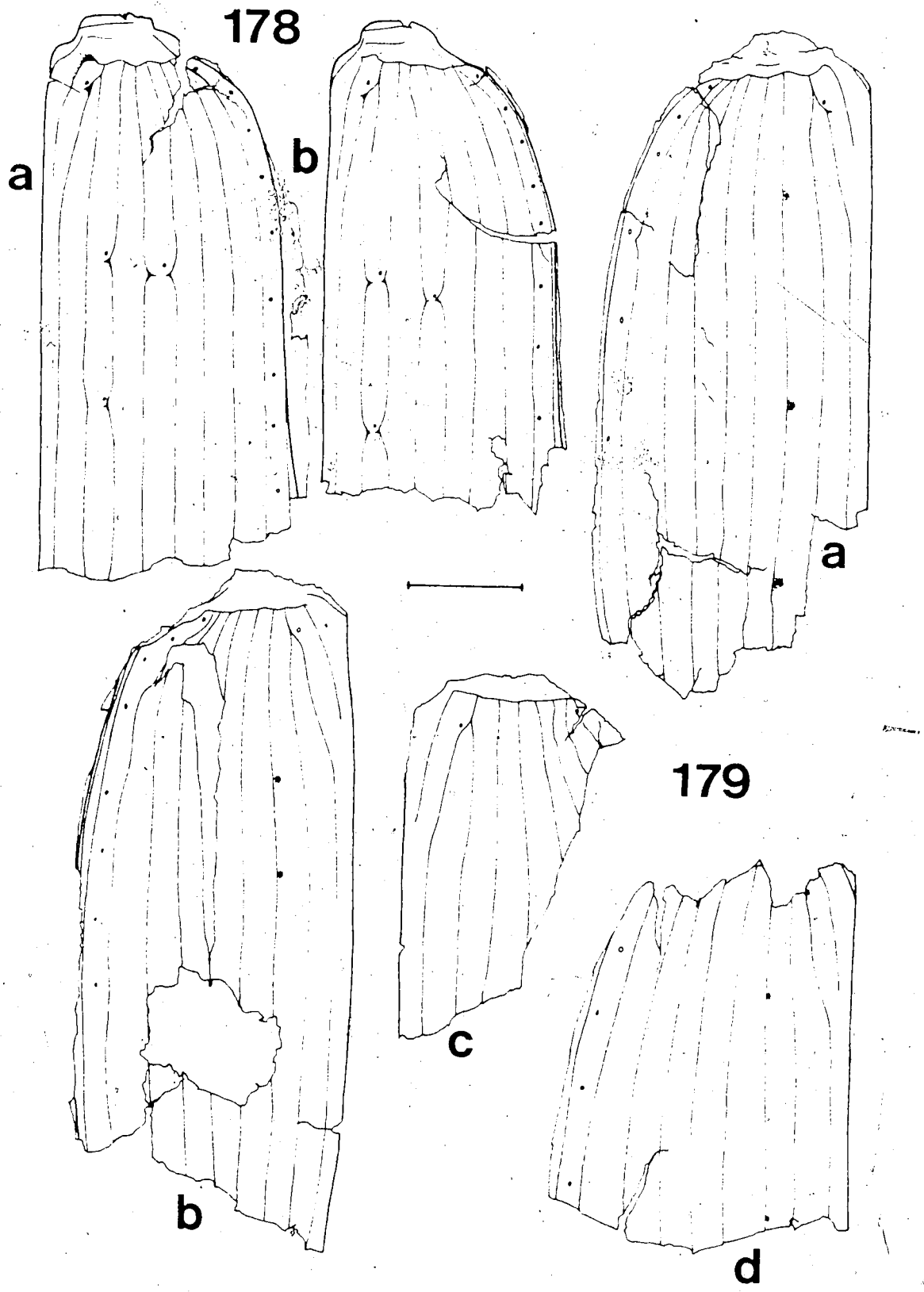

178
a
b
a
b
c
179
d

Fig. 180. Fossil elytral fragments, Nebria suturalis LeConte ([a] basal portion right elytron, [b] nearly entire left elytron, and [c] basal portion left elytron; Scarborough Bluffs, Toronto, Ontario; ca. 70,000 years B.P. [personal communication, A. Morgan]). Scale line = 1.0 mm.

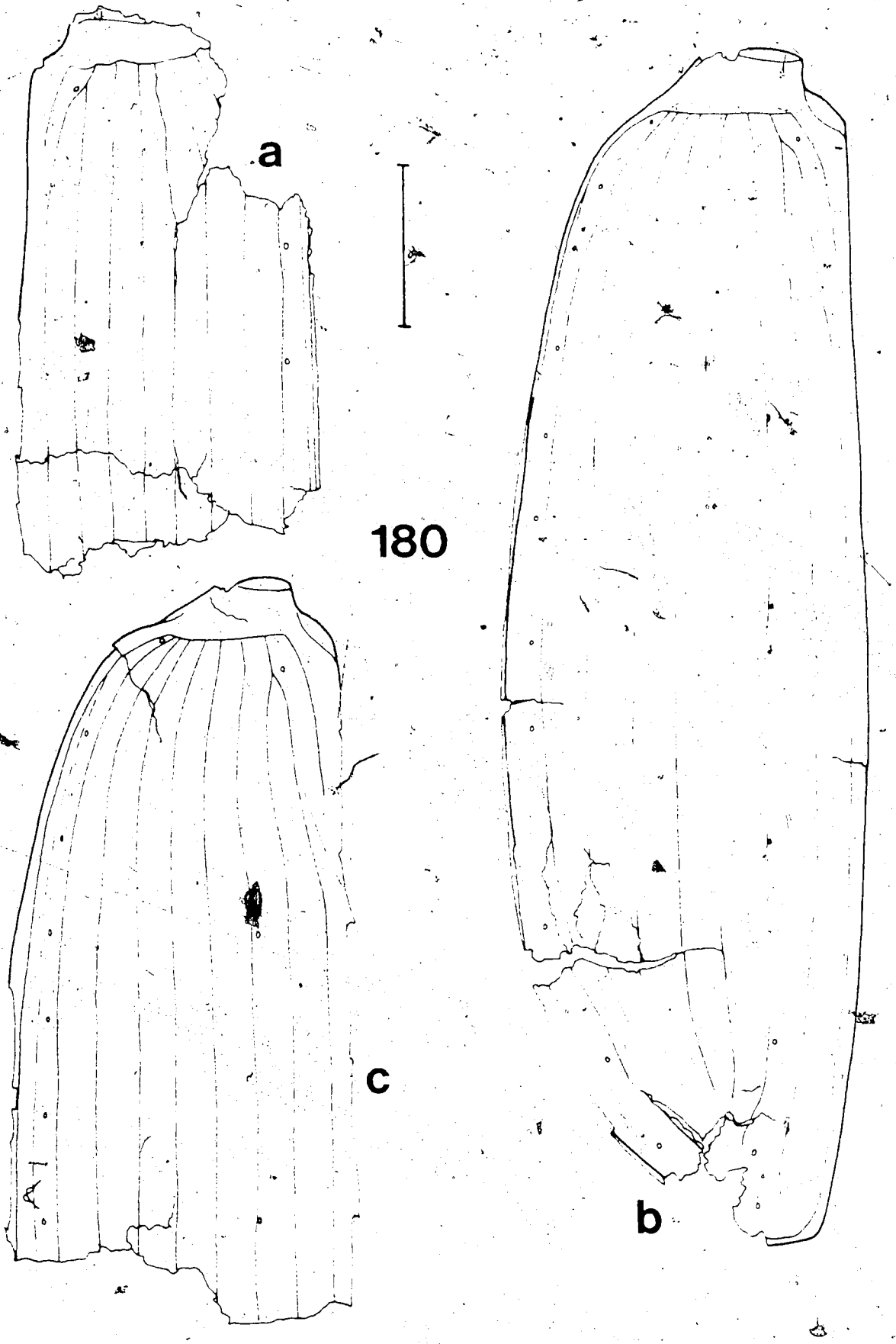
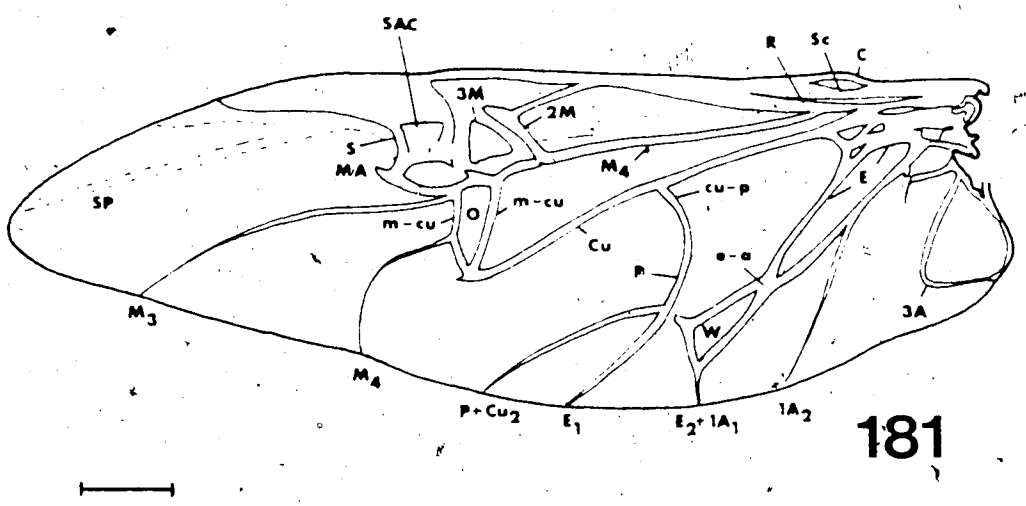
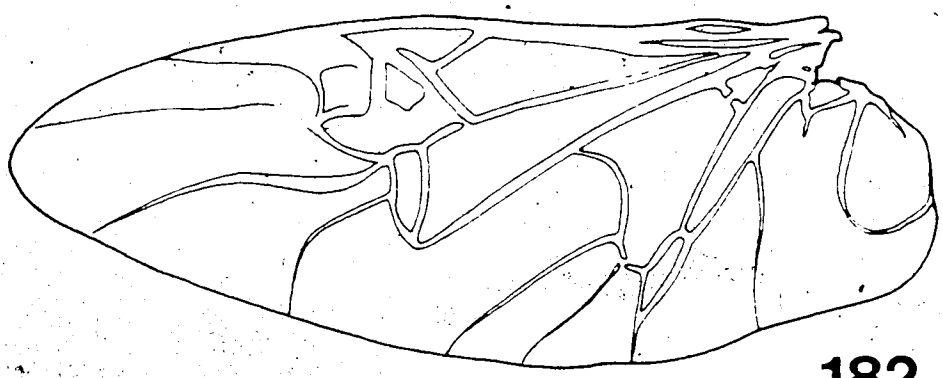

a
180
c
b

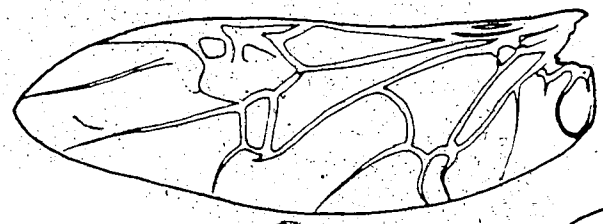
Fig. 181. Left hindwing, Nebria brevicollis (Fabricius) (Aydon Castle, Northumberland, England); A = Anal Vein; C = Costal Vein; Cu = Cubital Vein; cu-p = cubito-plical cross-vein; E = Empusal Vein; e-a = empusal-anal cross-vein; M = Median Vein; MA = Anterior Median Vein; m-cu = median-cubital cross-vein; O = Oblongum Cell; P = Plical Vein; R = Radial Vein; S = sector cross-vein; SAC = Anterior Sector Cell; Sc = Subcostal Vein; SP = Posterior Sector Vein; W = Wedge Cell. Figs. 182-185. Left hindwing, dorsal aspect. 182. Nebria virescens Horn (Vancouver Island, British Columbia). 183. Nebria appalachia Darlington (Soco Gap, North Carolina). 184. Nebria coloradensis Van Dyke (Mexican Cut Lake, Colorado). 185. Nebria charlottae Lindroth (Massett, Queen Charlotte Islands). Scale line = 1.0 mm.



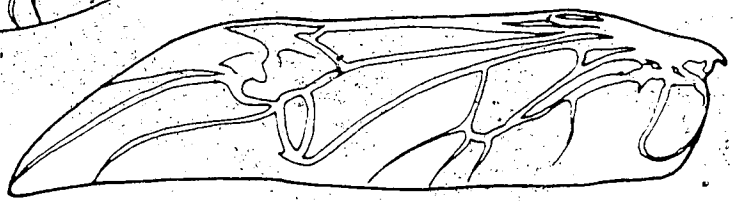
181



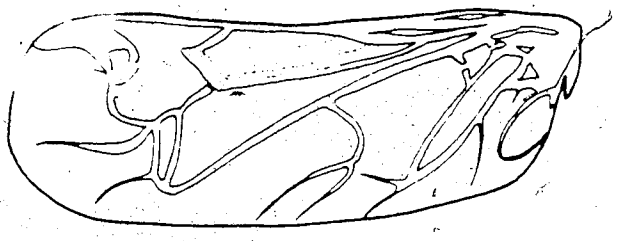
182



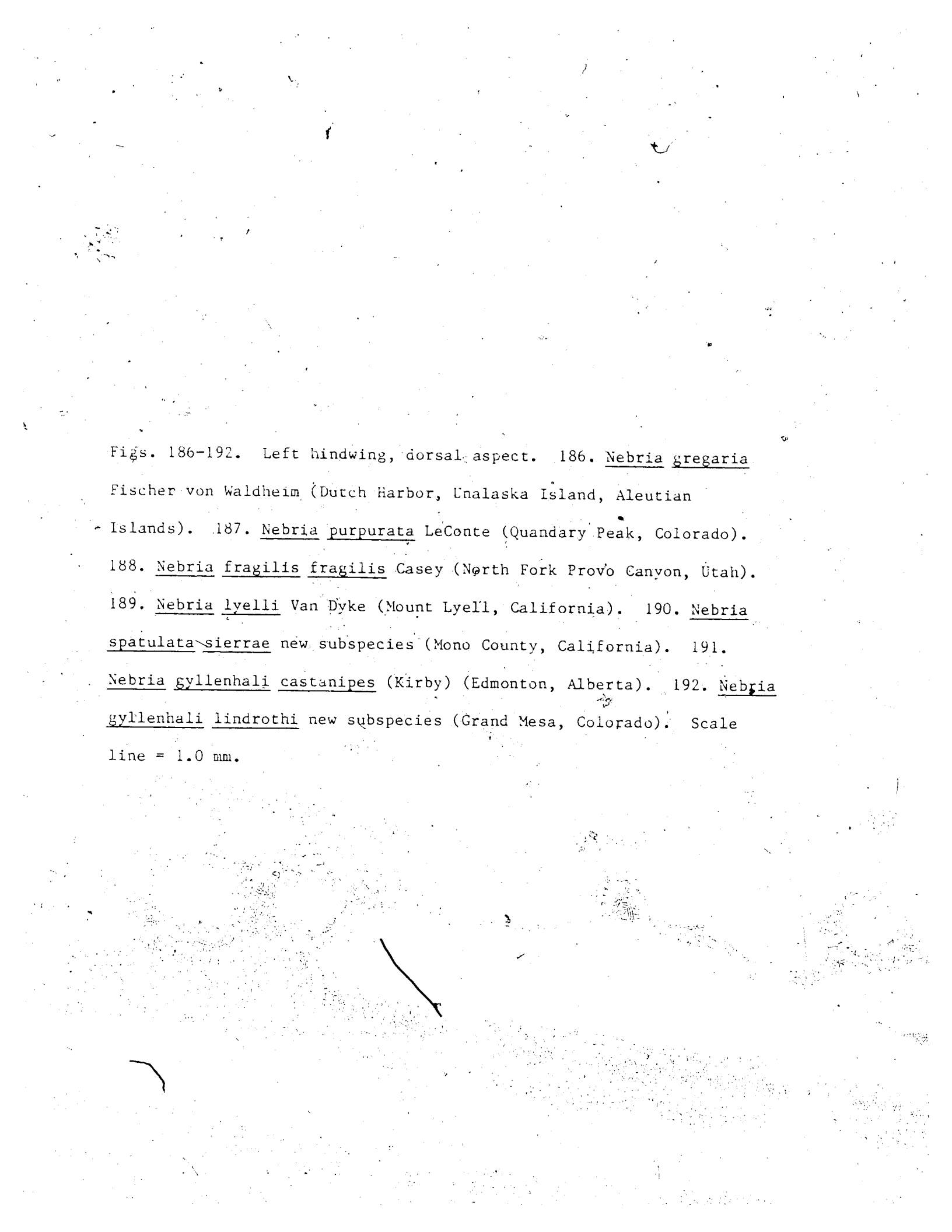
183



184

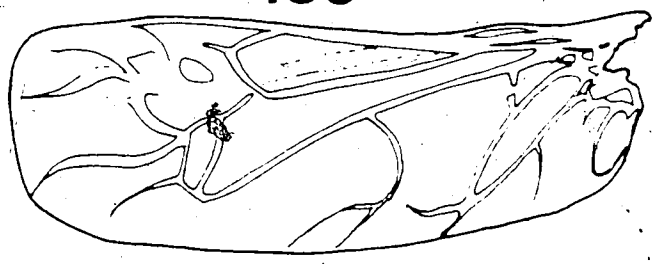


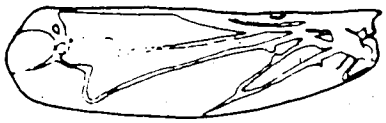
185



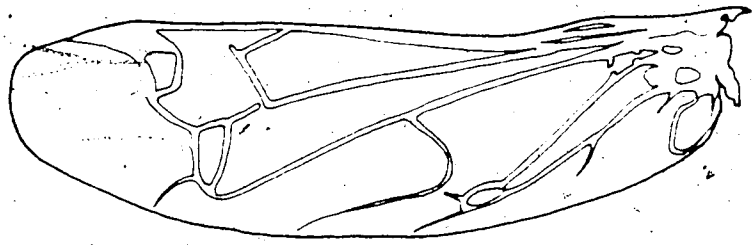
Figs. 186-192. Left hindwing, dorsal aspect. 186. Nebria gregaria Fischer von Waldheim (Dutch Harbor, Unalaska Island, Aleutian Islands). 187. Nebria purpurata LeConte (Quandary Peak, Colorado). 188. Nebria fragilis fragilis Casey (North Fork Provo Canyon, Utah). 189. Nebria lyelli Van Dyke (Mount Lyell, California). 190. Nebria spatulata sierrae new subspecies (Mono County, California). 191. Nebria gyllenhali castanipes (Kirby) (Edmonton, Alberta). 192. Nebria gyllenhali lindrothi new subspecies (Grand Mesa, Colorado). Scale line = 1.0 mm.

186





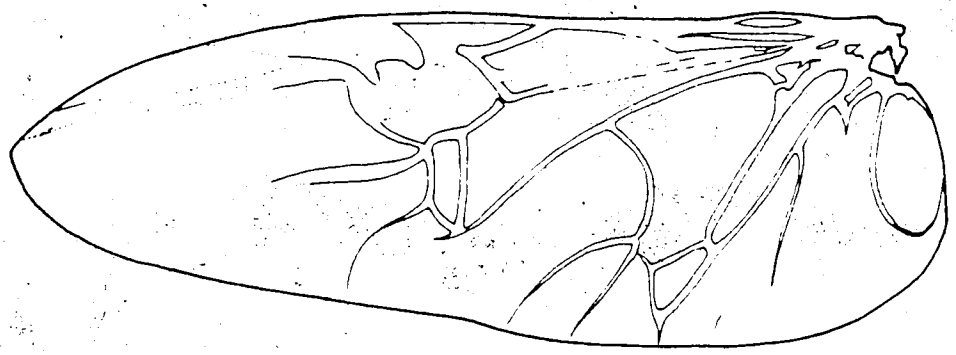
188



189

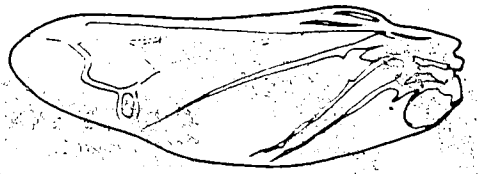
187

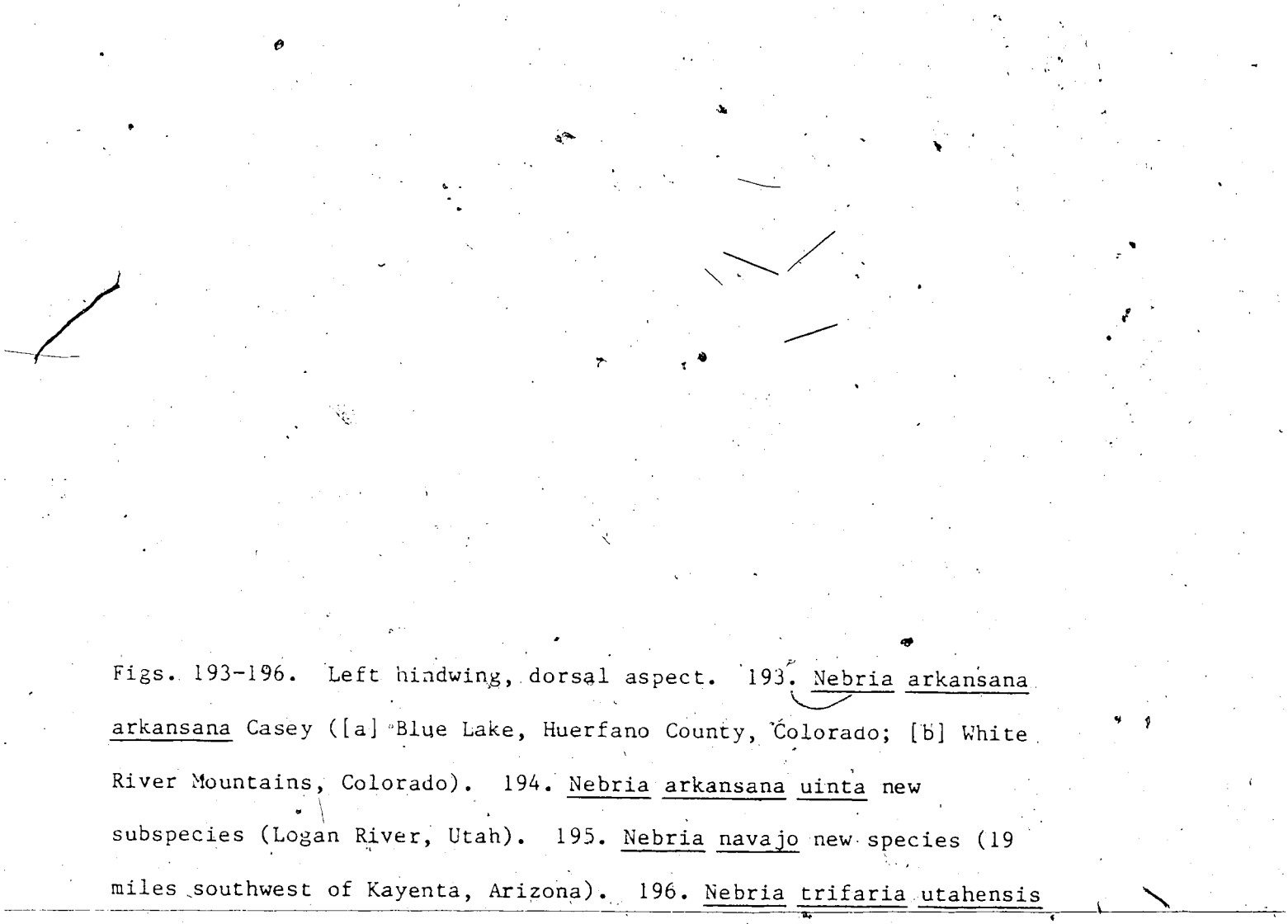
190



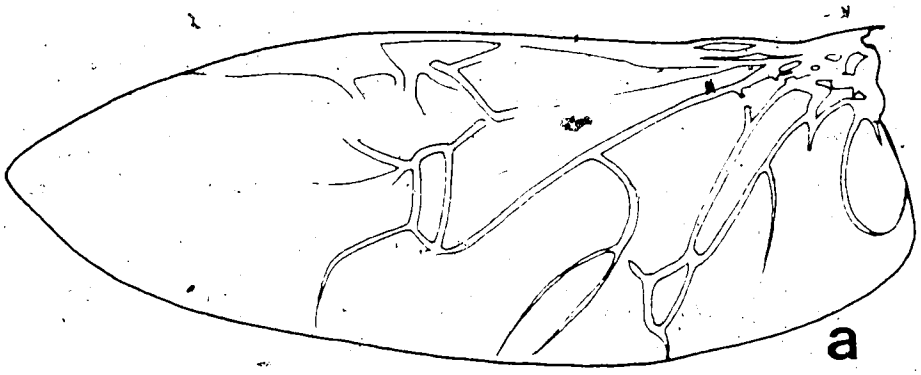
191

192

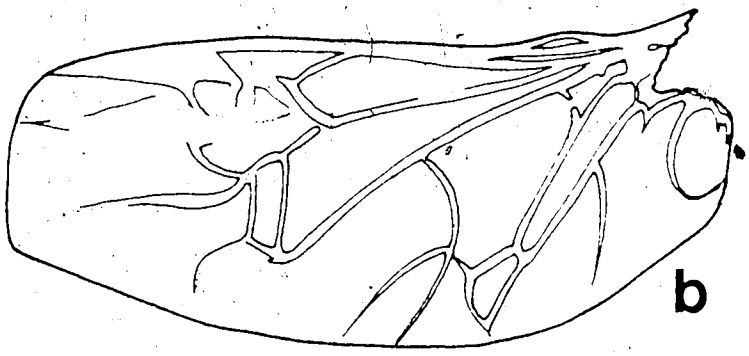


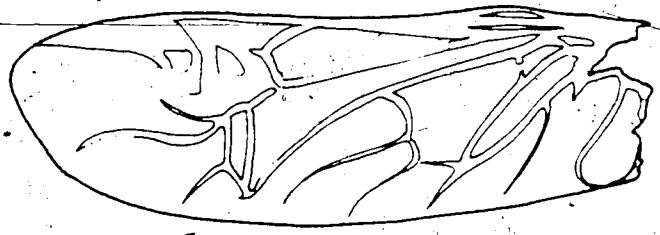


Figs. 193-196. Left hindwing, dorsal aspect. 193. Nebria arkansana arkansana Casey ([a] Blue Lake, Huerfano County, Colorado; [b] White River Mountains, Colorado). 194. Nebria arkansana uinta new subspecies (Logan River, Utah). 195. Nebria navajo new species (19 miles southwest of Kayenta, Arizona). 196. Nebria trifaria utahensis new subspecies (Henry Mountains, Utan). Scale line = 1.0 mm.

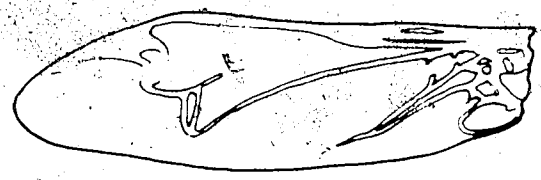


193

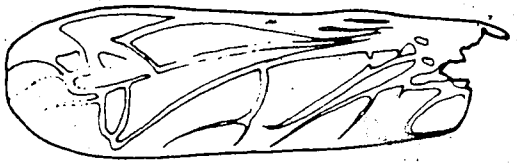




194



195



196

Figs. 197-200. Oblongum cell, left hindwing, dorsal aspect. 197. Nebria frigida Sahlberg (Eagle Summit, Alaska); Cu = Cubital Vein; M = Median Vein; m-cu = median-cubital cross-vein; O = Oblongum Cell. 198. Nebria trifaria catenata Casey (Wolf Creek Pass, Colorado). 199. Nebria hudsonica LeConte (Pinecliffe, Colorado). 200. Nebria obliqua LeConte (Golden, Colorado). Figs. 201-205. Wedge cell, left hindwing, dorsal aspect. 201. Nebria pallipes Say (Pauling, New York); A = Anal Vein; E = Empusal Vein; e-a = empusal-anal cross-vein; W = Wedge Cell. 202. Nebria darlingtoni new species (Riverton, California). 203. Nebria sahlbergii modoc new subspecies (Warner Mountains, California). 204. Nebria piperi Van Dyke (Mount Rainier, Washington). 205. Nebria schwarzi schwarzi Van Dyke (Kicking Horse River, British Columbia). Scale line = 1.0 mm.

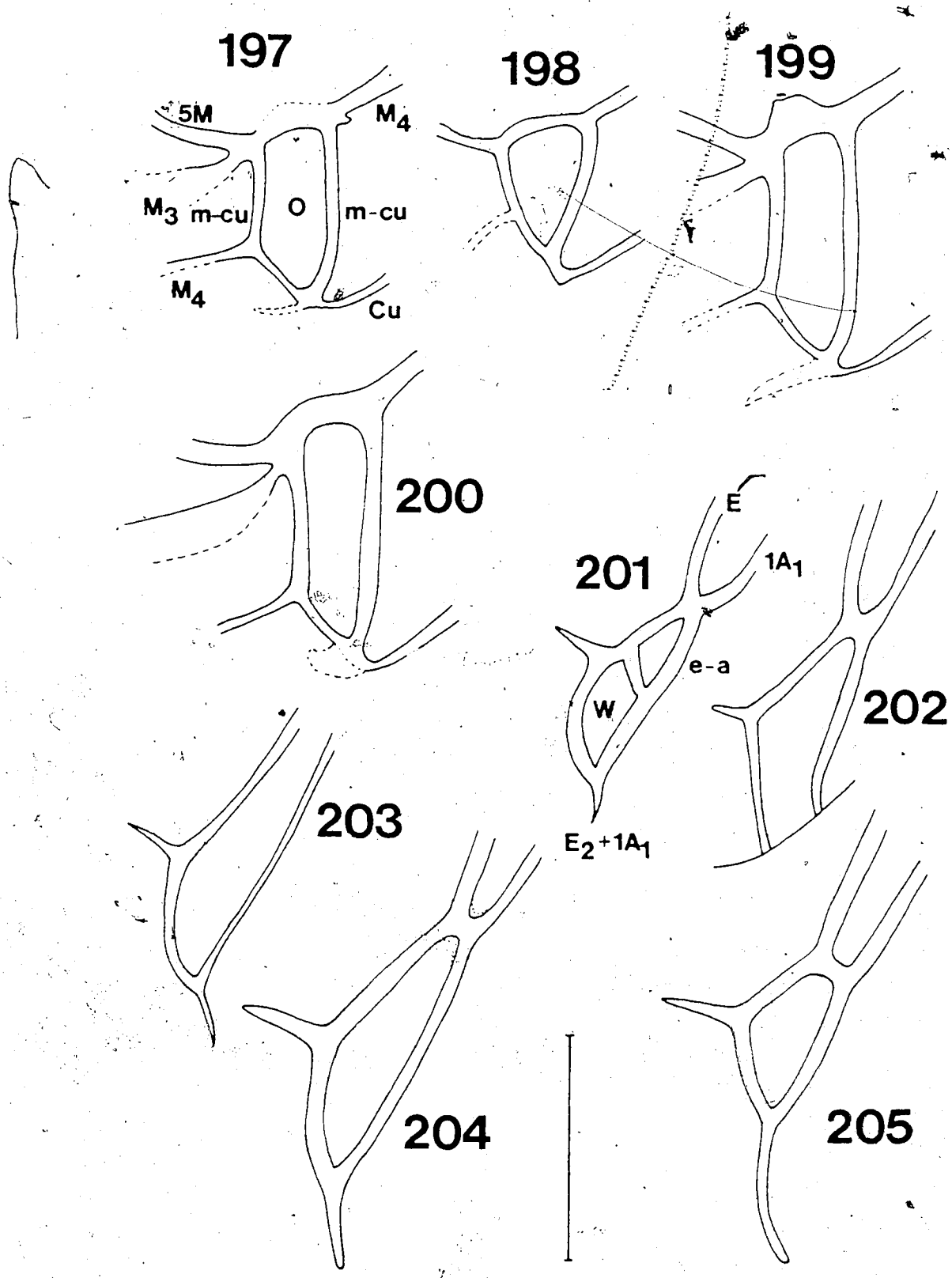
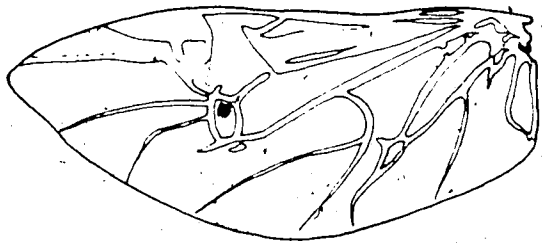
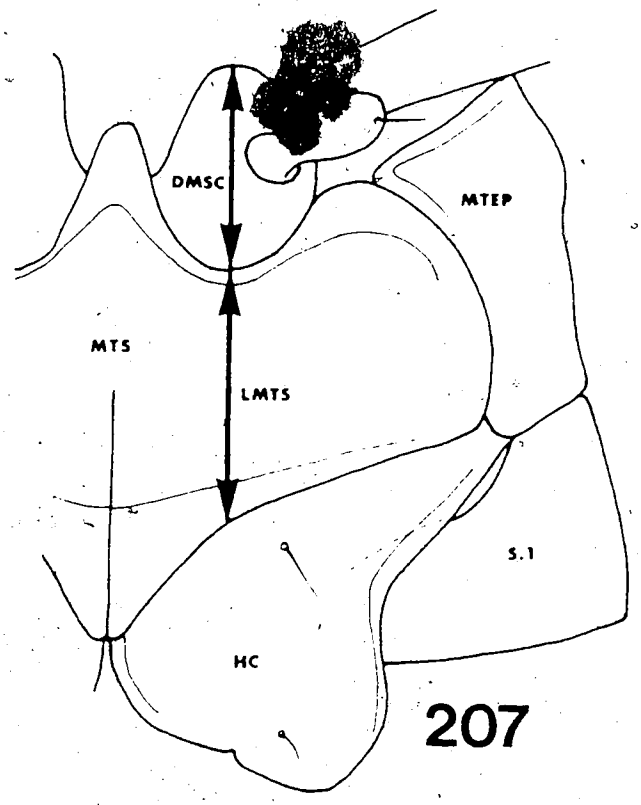

197
5M
M4
M3
m-cu
O
m-cu
M4
Cu
198
199
200
201
E
1A1
e-a
W
E2+1A1
202
203
204
205

Fig. 206. Left hindwing, dorsal aspect, Trachypachus gibbsi LeConte (Yosemite National Park, California). Fig. 207. Metathoracic venter illustrating measure of relative metasternum length; DMSC = diameter of mesocoxa; HC = hind coxa; LMTS = length of metasternum; MTEP = metepisternum; MTS = metasternum; S.1 = first visible abdominal sternum. Figs. 208-210. Metasternum. 208. Nebria piperi Van Dyke (Cheekeye River, British Columbia). 209. Nebria fragilis teewinot new subspecies (Togwotee Pass, Wyoming). 210. Nebria kincaidi balli new subspecies (Mount Rainier, Washington). Scale line = 1.0 mm.

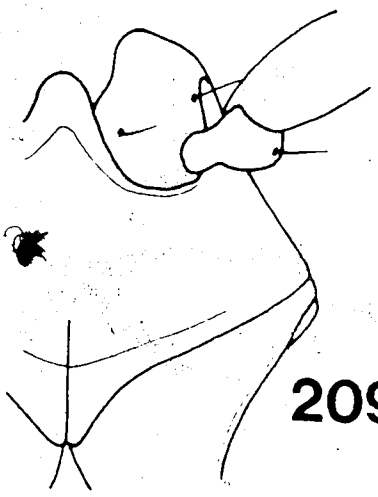


206

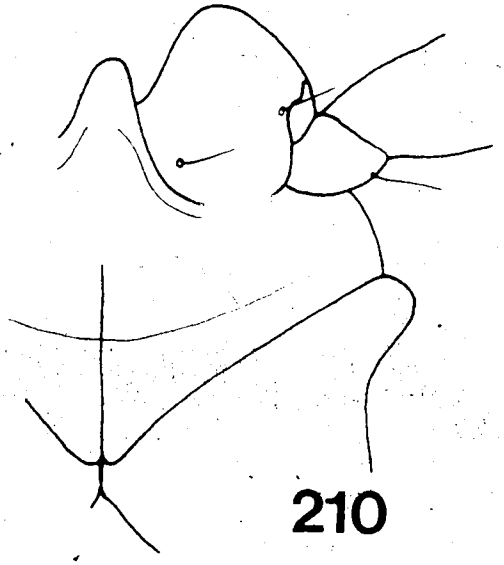


207

208

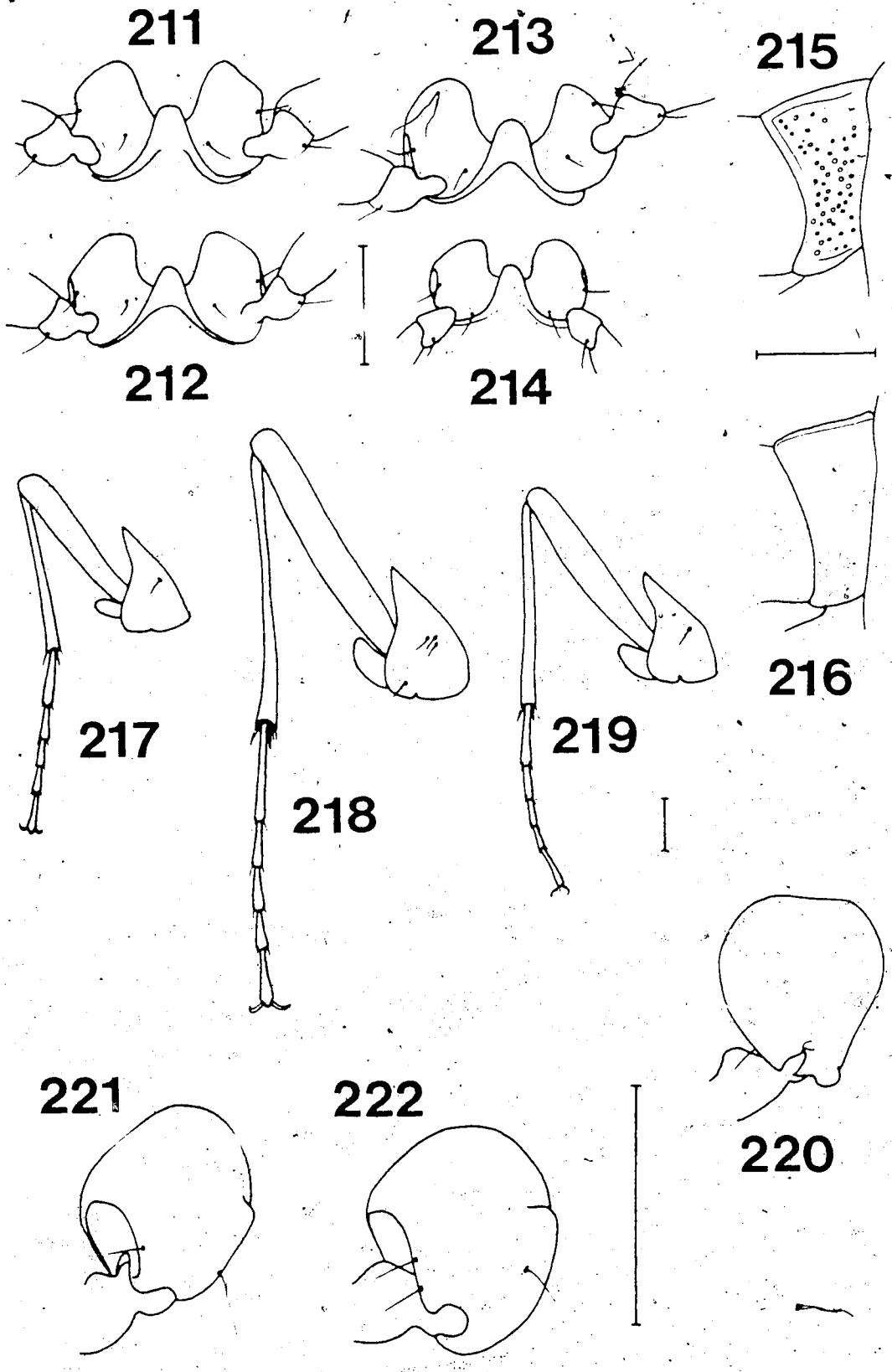


209

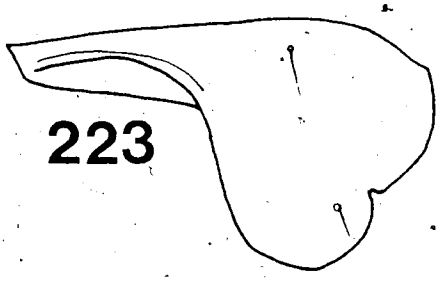


210

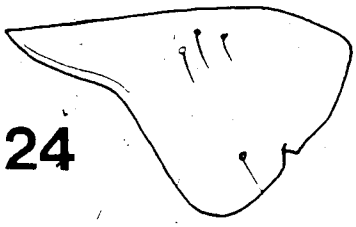
Figs. 211-214. Anterior intercoxal process of metasternum. 211. Nebria meanyi lamarckensis new subspecies (Upper Lamarck Lake, California). 212. Nebria zioni oasis new subspecies (Pine Valley Mountains, Utah). 213. Nebria brevicollis (Fabricius) (Chillingham, England). 214. Nebria virescens Horn (Alta Meadow, California). Figs. 215-216. Metepisternum. 215. Nebria brevicollis (Fabricius) (Chillingham, England). 216. Nebria obliqua LeConte (Wellville, Colorado). Figs. 217-219. Right hindleg, ventral aspect. 217. Nebria crassicornis crassicornis Van Dyke (Mount Rainier, Washington). 218. Nebria vandykei wyeast new subspecies (Mount Hood, Oregon). 219. Nebria gouleti new species (Clearwater River, Idaho). Fig. 220. Right front coxa, ventral aspect, Nebria obliqua LeConte (Panchuela Creek, New Mexico). Figs. 221-222. Right middle coxa, ventral aspect. 221. Nebria obliqua LeConte (Panchuela Creek, New Mexico). 222. Nebria metallica Fischer von Waldheim (Mount Rainier, Washington). All scale lines = 1.0 mm.


211
213
215
212
214
216
217
218
219
220
221
222

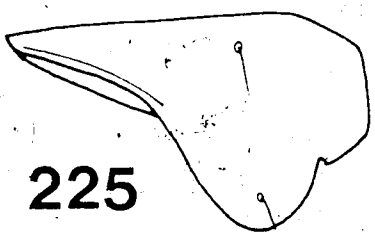
Figs. 223-229. Right hind coxa, ventral aspect. 223. Pelophila borealis (Paykull) (Calling Lake, Alberta). 224. Nebria fragilis fragilis Casey (American Fork Canyon, Utah). 225. Nebria virescens Horn (Corvallis, Oregon). 226. Nebria schwarzi schwarzi Van Dyke (Yoho River, British Columbia). 227. Nebria schwarzi beverlianna (Hoback River, Wyoming). 228. Nebria appalachia Darlington (Mount Mitchell, North Carolina). 229. Nebria desolata Kavanaugh (Escalante River, Utah). Fig. 230. Right front trochanter, ventral aspect, Nebria diversa LeConte (Tofino, British Columbia); FC = front coxa; FFe = front femur; FT = front trochanter. Fig. 231. Right middle trochanter, ventral aspect, Nebria diversa LeConte (Tofino, British Columbia); MC = middle coxa; MFe = middle femur; MT = middle trochanter. Fig. 232. Right hind trochanter, ventral aspect, Nebria diversa LeConte (Tofino, British Columbia); HC = hind coxa; HFe = hind femur; HT = hind trochanter. All scale lines = 1.0 mm.



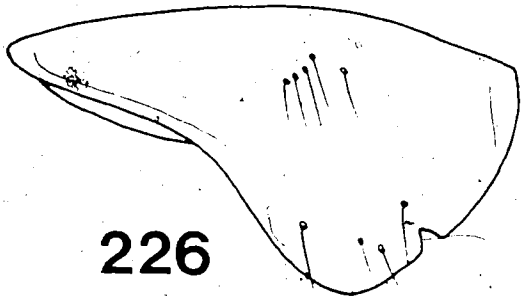
223



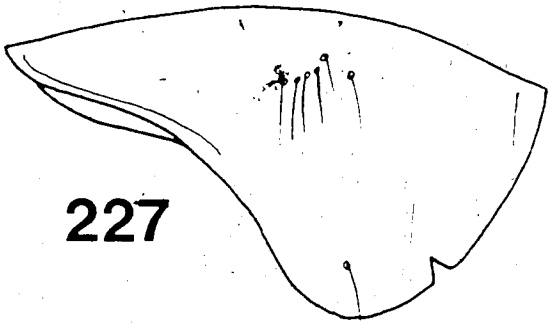
224



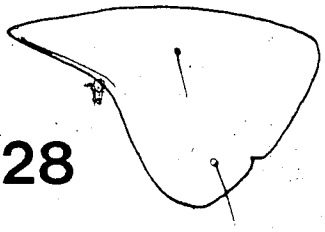
225



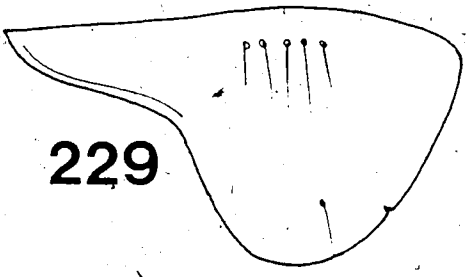
226



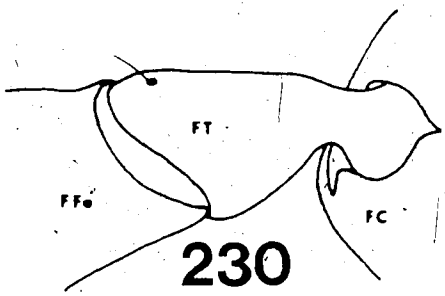
227



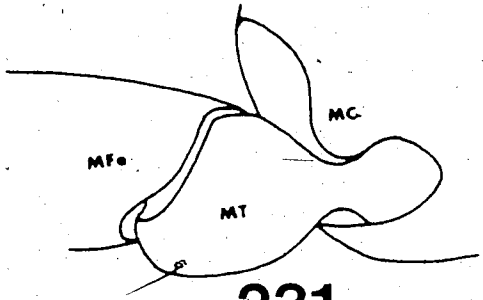
228



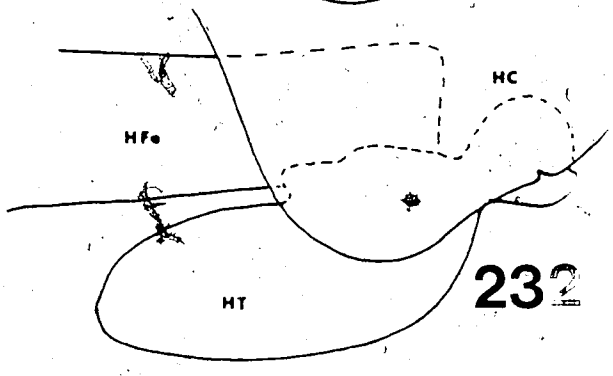
229



230



231



232

Fig. 233. Right front femur, Nebria brevicollis (Fabricius) (Newbiggen, England), ([a] anterior aspect, [b] posterior aspect).

Fig 34. Right middle femur, Nebria brevicollis (Fabricius) (Newbiggen, England), ([a] anterior apsect, [b] posterior aspect).

Fig. 2 ight hind femur, Nebria brevicollis (Fabricius) (Newbiggen, England), ([a] dorsal aspect, [b] ventral aspect). Scale line = 1.0 mm.

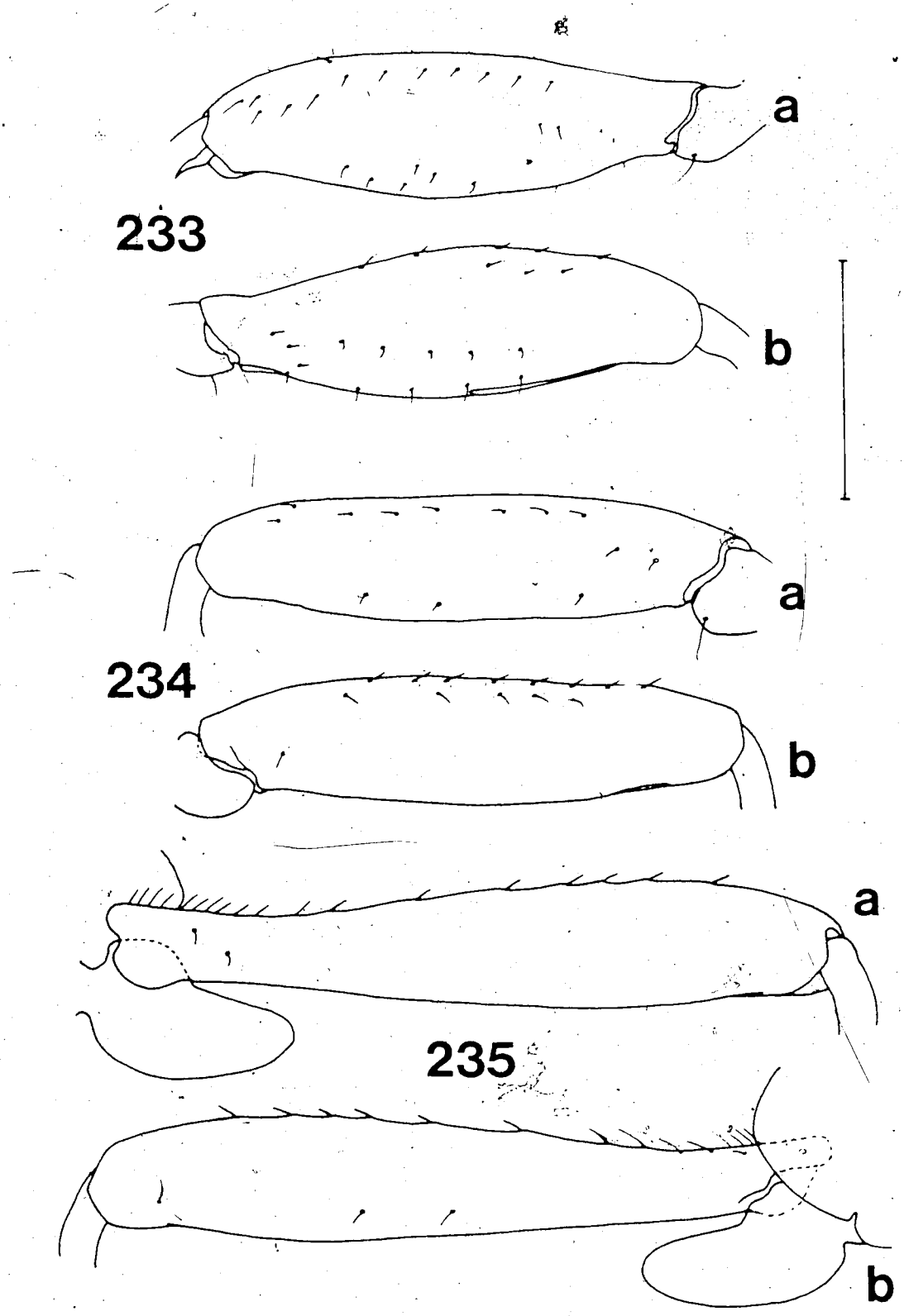
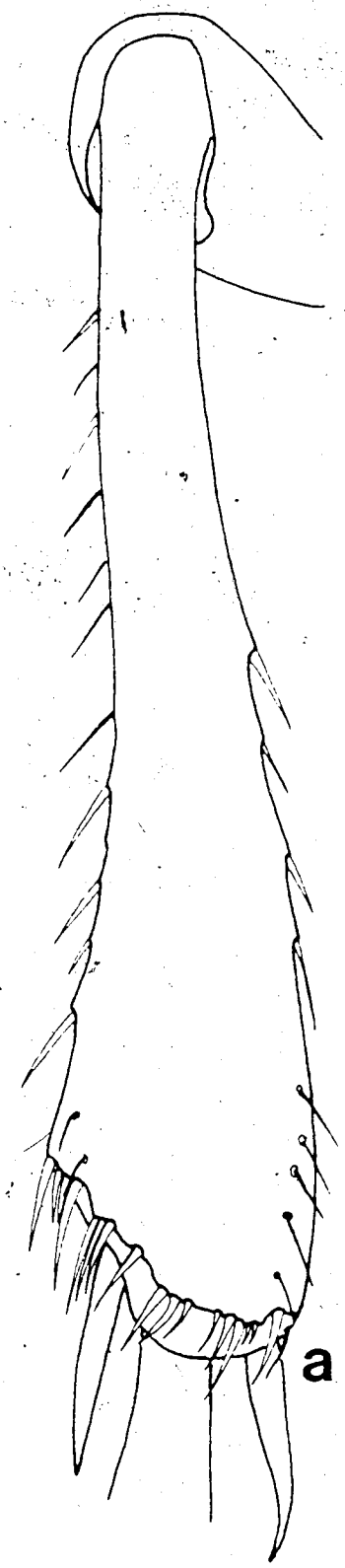
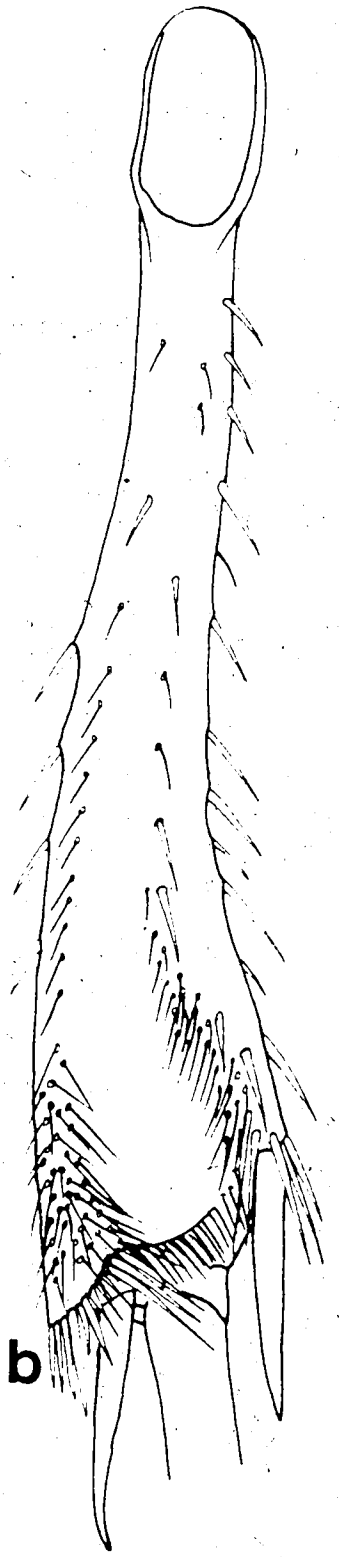

a
233
b
a
234
b
a
235
b

Fig. 236. Right front tibia, Nebria brevicollis (Fabricius) (Nocero, Umbra, Italy), ([a] anterior aspect, [b] posterior aspect). Scale line = 1.0 mm.

236

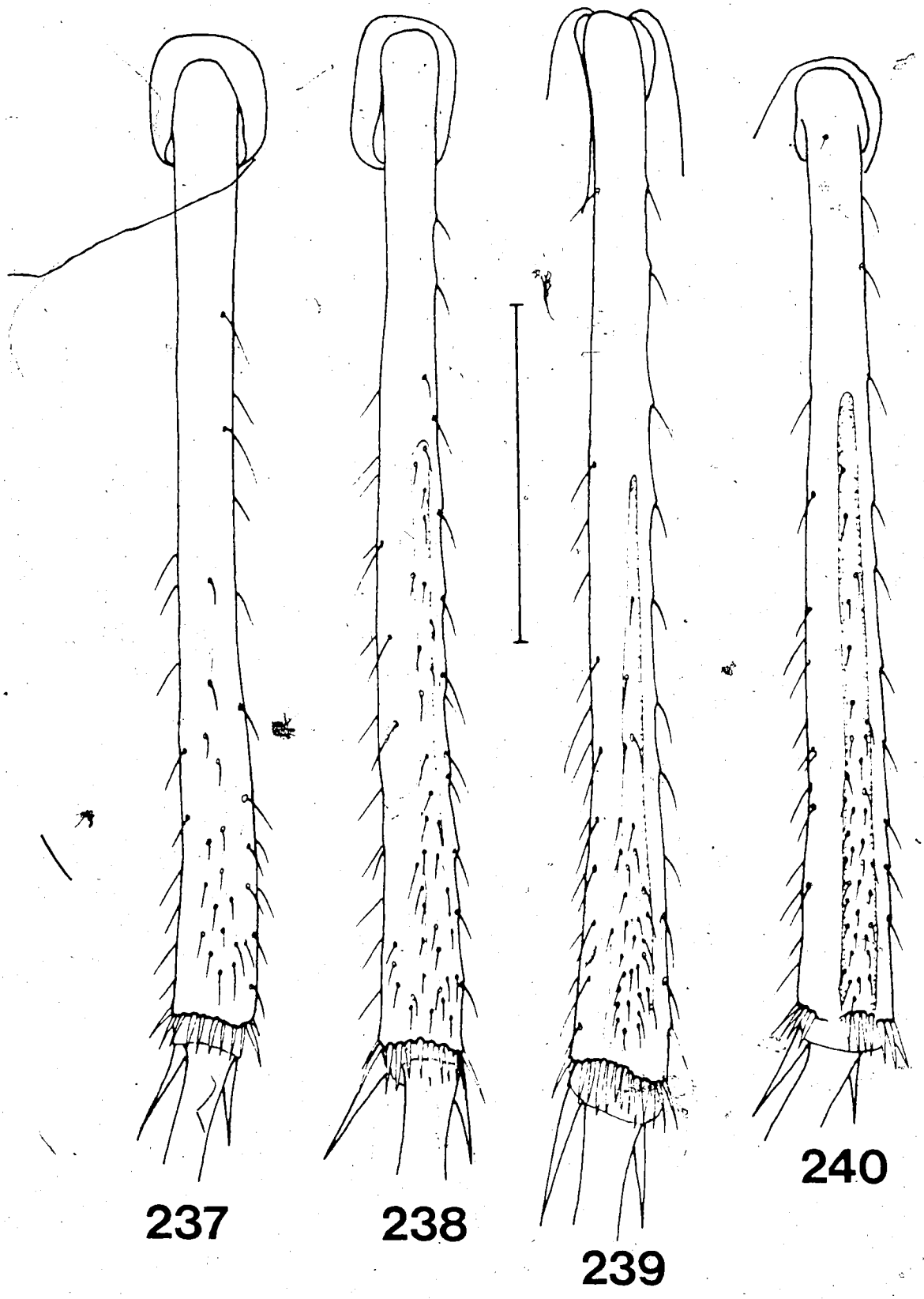


a



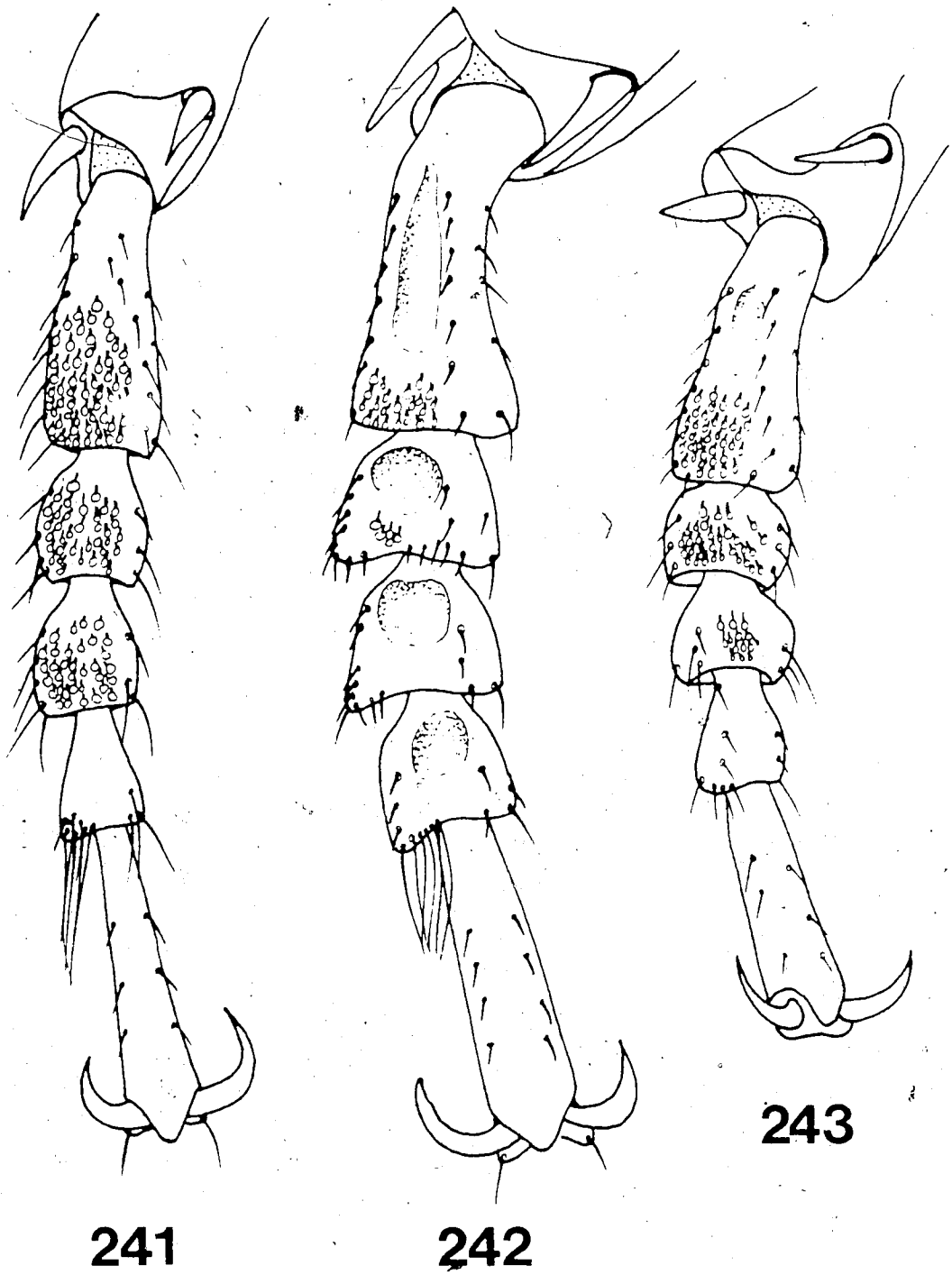
b

Figs. 237–240. Left middle tibia, lateral aspect. 237. Nebria pallipes Say) (Ste-Mélanie, Québec). 238. Nebria gouleti new species (Underwood, Washington). 239. Nebria carri new species (Towsley Spring, Idaho). 240. Nebria virescens Horn (Vancouver Island, British Columbia). Scale line = 1.0 mm.



237 238 239 240

Figs. 241–243. Right front tarsus, ventral aspect, male. 241. Nebria purpurata LeConte (Red River, New Mexico). 242. Nebria ingens ingens Horn (Mount Whitney, California). 243. Nebria ovipennis LeConte (Mount Rose, Nevada). Scale line = 1.0 mm.

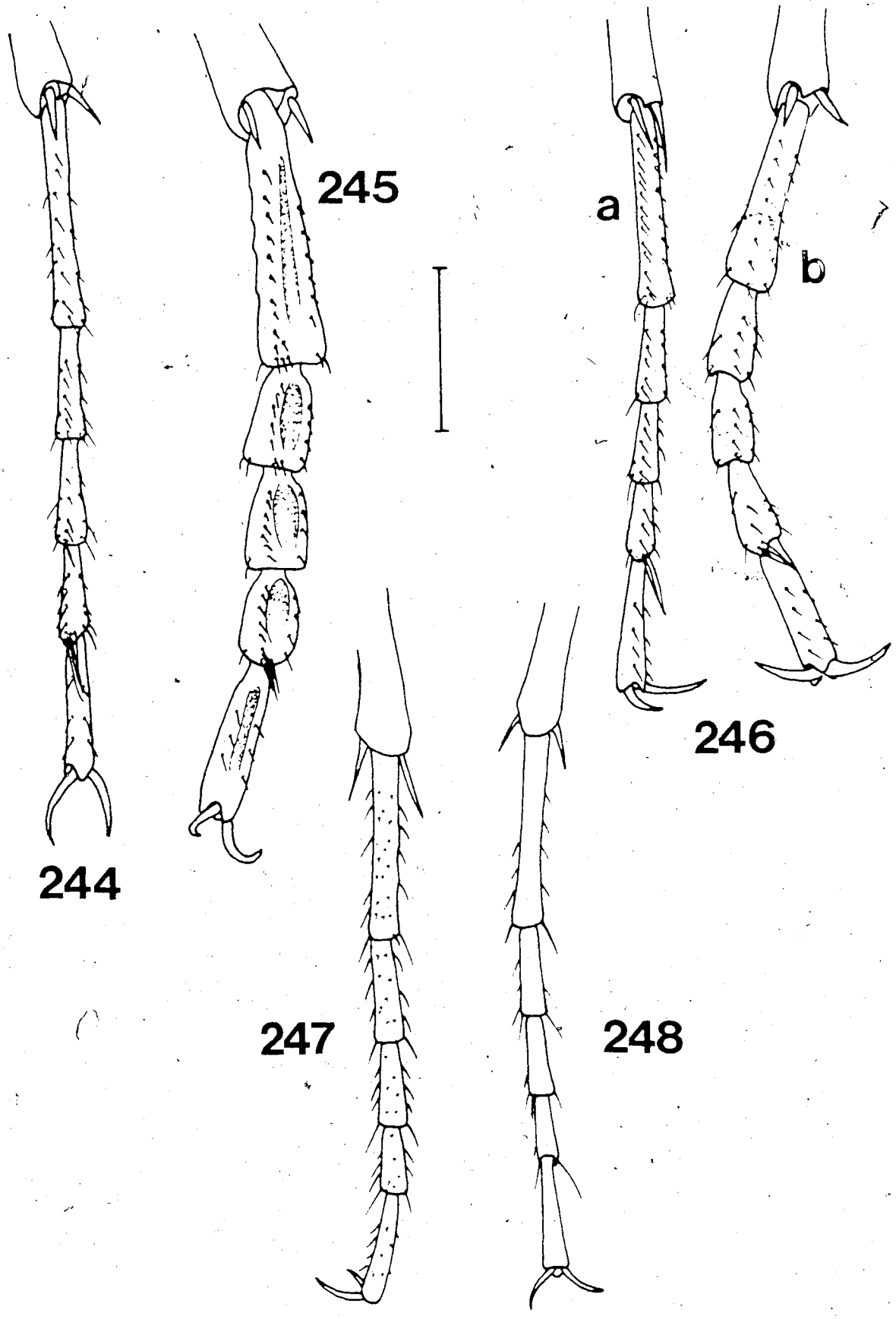


241

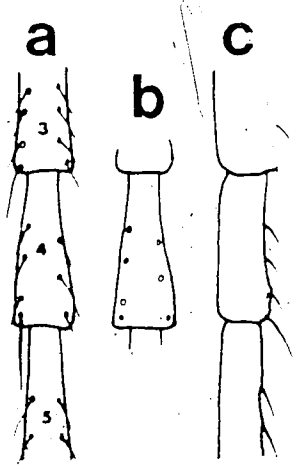
242

243

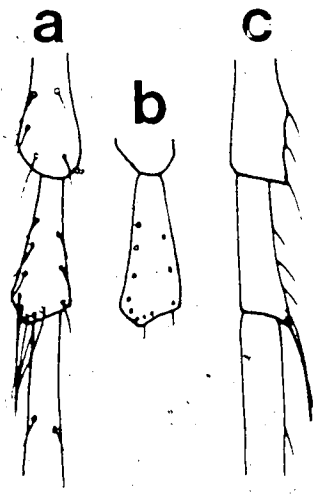
Figs. 244-248. Right hind tarsus, ventral aspect. 244. Nebria purpurata LeConte (Hoosier Pass, Colorado). 245. Nebria ingens ingens Horn (Mount Whitney, California). 246. Nebria ovipennis LeConte ([a] Franklin Lakes, California; [b] Mount Rose, Nevada). 247. Nebria brevicollis (Fabricius) (Chillingham, England). 248. Nebria eschscholtzii Ménétriés (San Bernardino Mountains, California). Scale line = 1.0 mm.


244
245
246
a
b
247
248

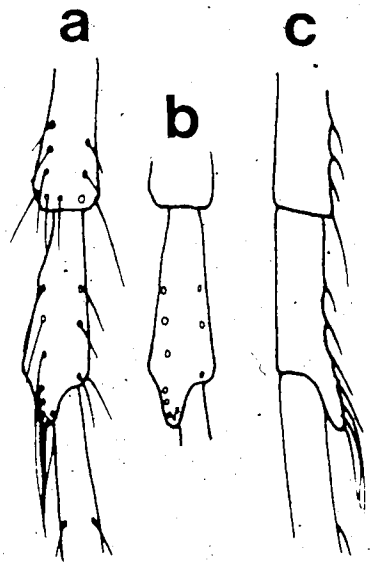
Figs. 249-252. Fourth tarsomere, right hind tarsus ([a] ventral aspect, setae illustrated; [b] ventral aspect, setae not illutrated; [c] lateral aspect). 249. Nebria virescens Horn (Corvallis, Oregon); 3 = third tarsomere; 4 = fourth tarsomere; 5 = fifth tarsomere. 250. Nebria arkansana edwardsi new subspecies (Sheep River, Alberta). 251. Nebria nivalis gaspesiana new subspecies (Mont Albert, Québec). 252. Nebria paradisi Darlington (Mount Hood, Oregon). Scale line = 1.0 mm.



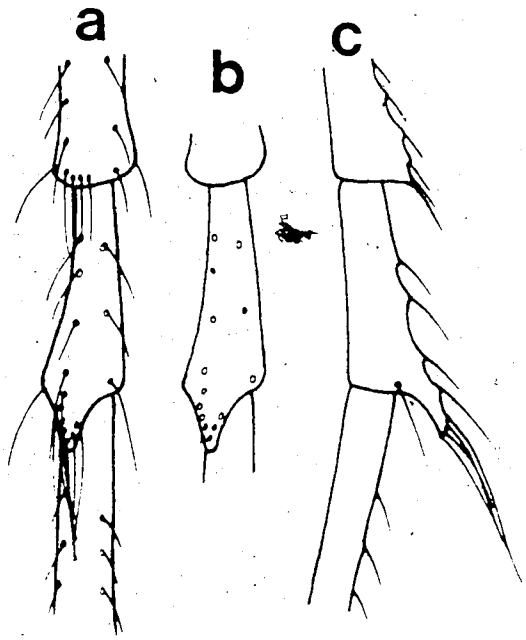
249



250

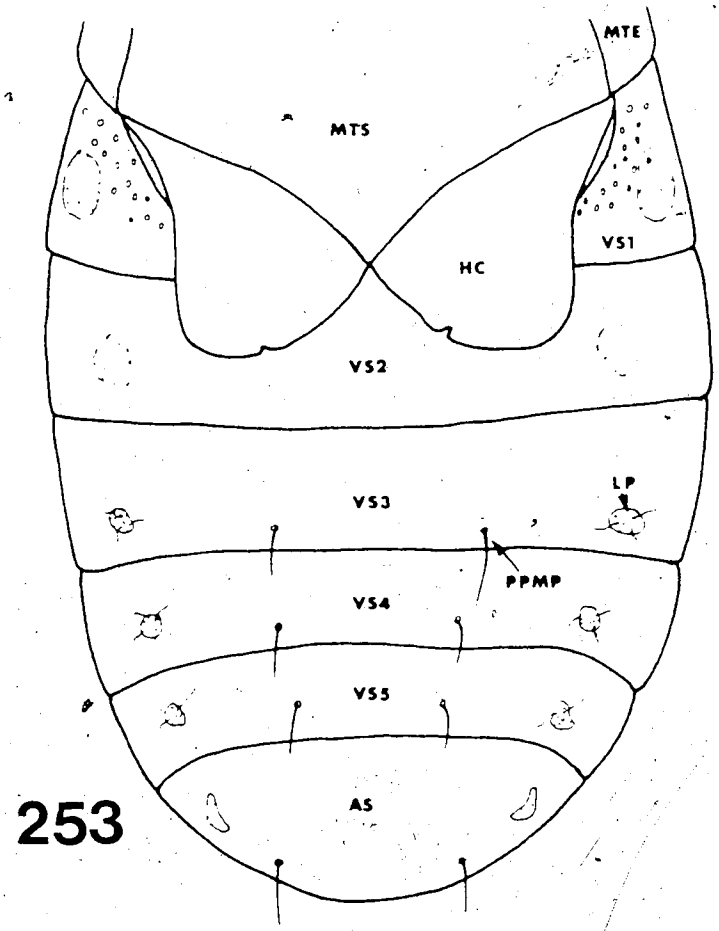


251

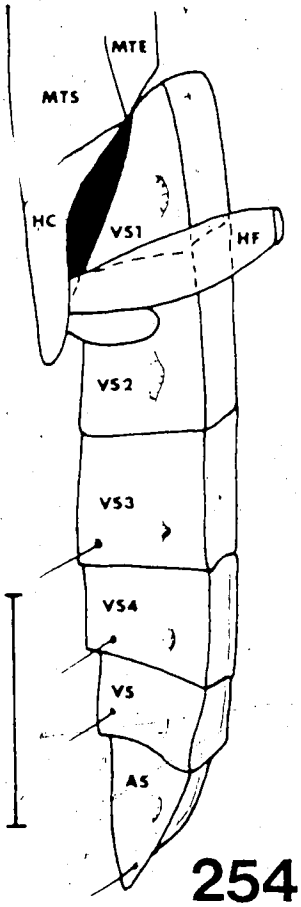


252

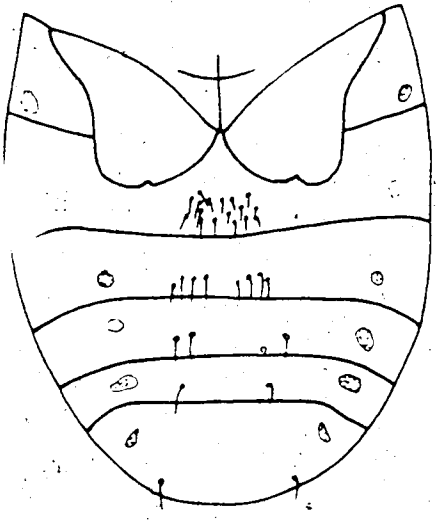
Figs. 253–254. Abdominal venter, Nebria frigida Sahlberg (Nome, Alaska); AS = anal sternum; HC = hind coxa; HF = hind femur; LP = lateral pit; MTE = metepisternum; MTS = metasternum; PPMP = posterior paramedial puncture; VS1 to VS5 = first to fifth visible sterna. 253. Ventral aspect. 254. Left lateral aspect. Fig. 255. Abdominal venter, ventral aspect, Nebria hudsonica LeConte, male (Clearwater River, Idaho). Fig. 256. Anal sternum, ventral aspect, Nebria hudsonica LeConte, female (Underwood, Washington). Fig. 257. Abdominal venter, ventral aspect, Nebria appalachia Darlington (Mount Mitchell, North Carolina). All scale lines = 1.0 mm.



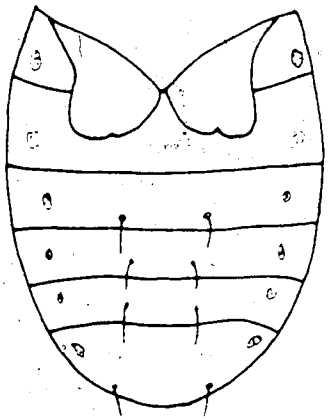
253



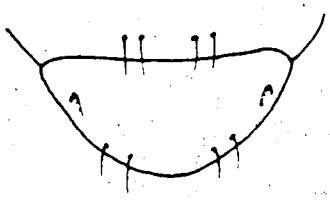
254



255



257



256

Fig. 258. Abdominal venter, ventral aspect, Nebria vandykei wyeast new subspecies, male (Middle Sister Peak, Oregon); APLP = anterior paralateral puncture. Fig. 259. Anal sternum, ventral aspect, Nebria vandykei wyeast new subspecies, female (Middle Sister Peak, Oregon). Fig. 260. Male genitalia, general form and associated terms ([a] left lateral aspect; [b] dorsal aspect); A = apex of median lobe; AA = angle of bend in axis of median lobe; AO = apical orifice of median lobe; BB = basal bulb of median lobe; BO = basal orifice of median lobe; DBS = dorsobasal sclerite; IS = internal sac; LP = left paramere; MS = mid-shaft of median lobe; PAS pre-apical shaft of median lobe; RP = right paramere. All scale lines = 1.0 mm.

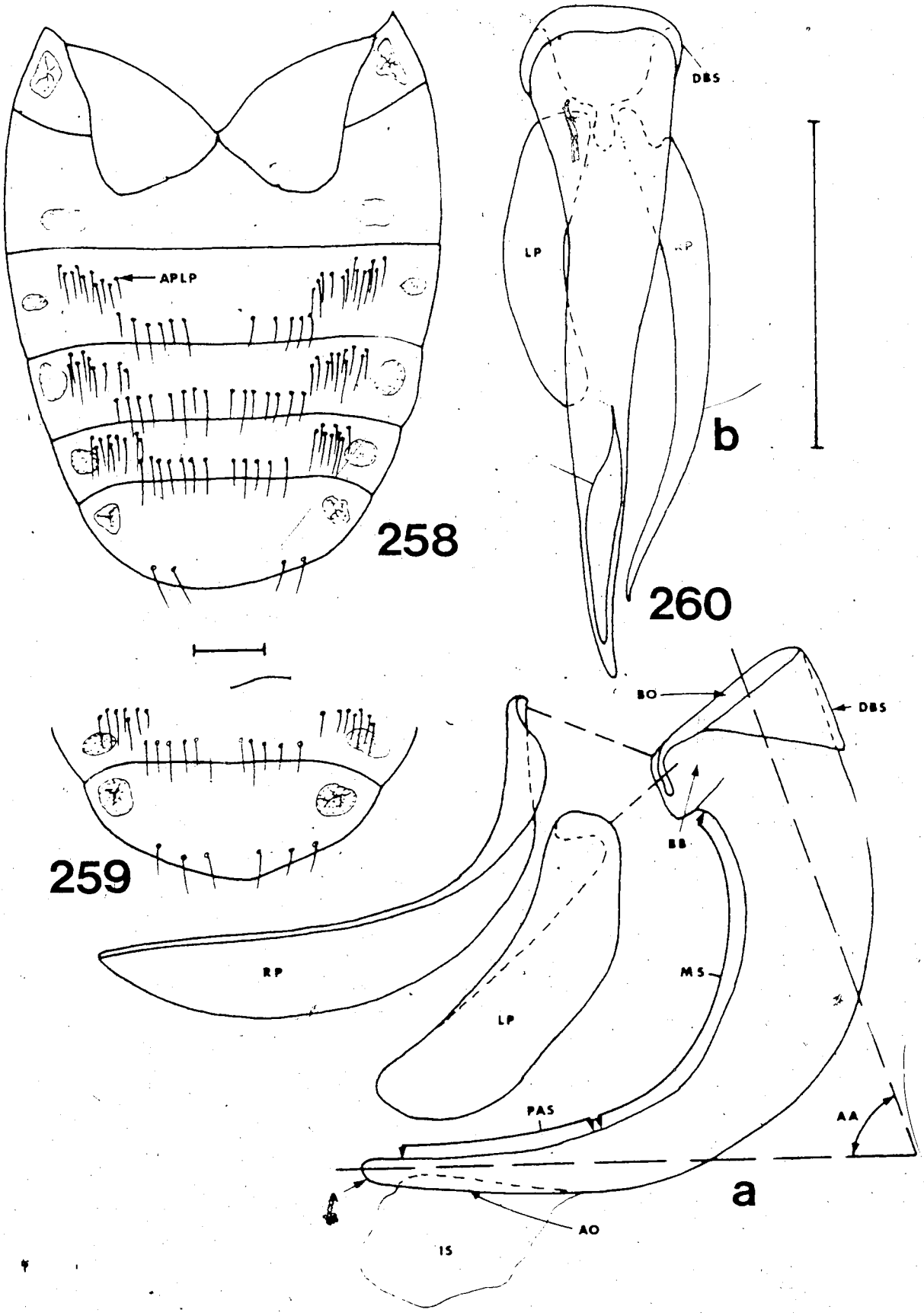
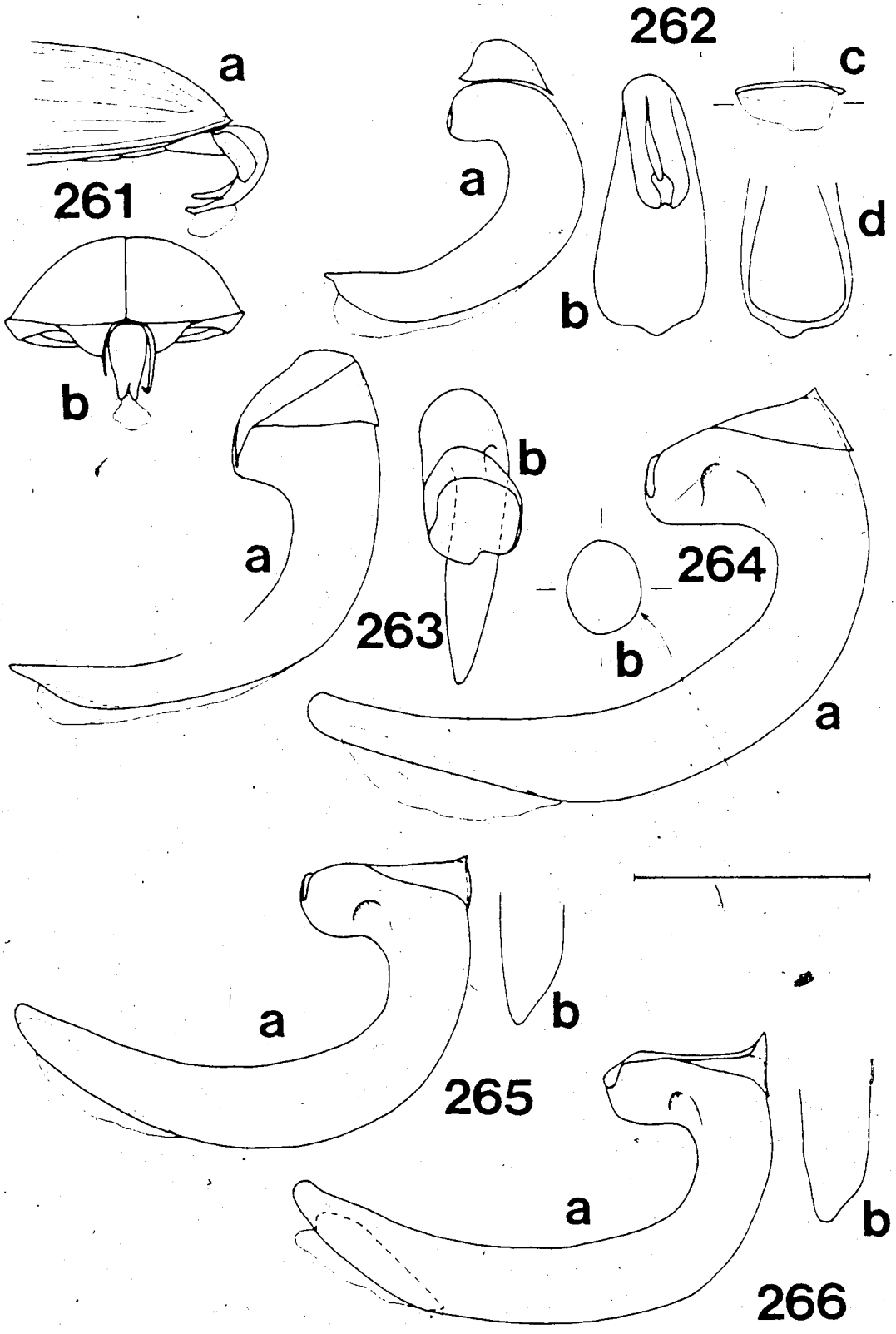
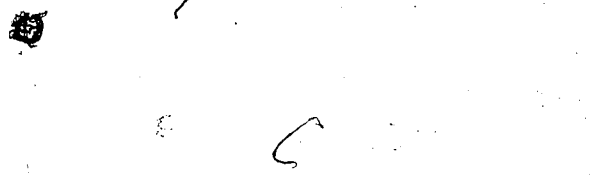
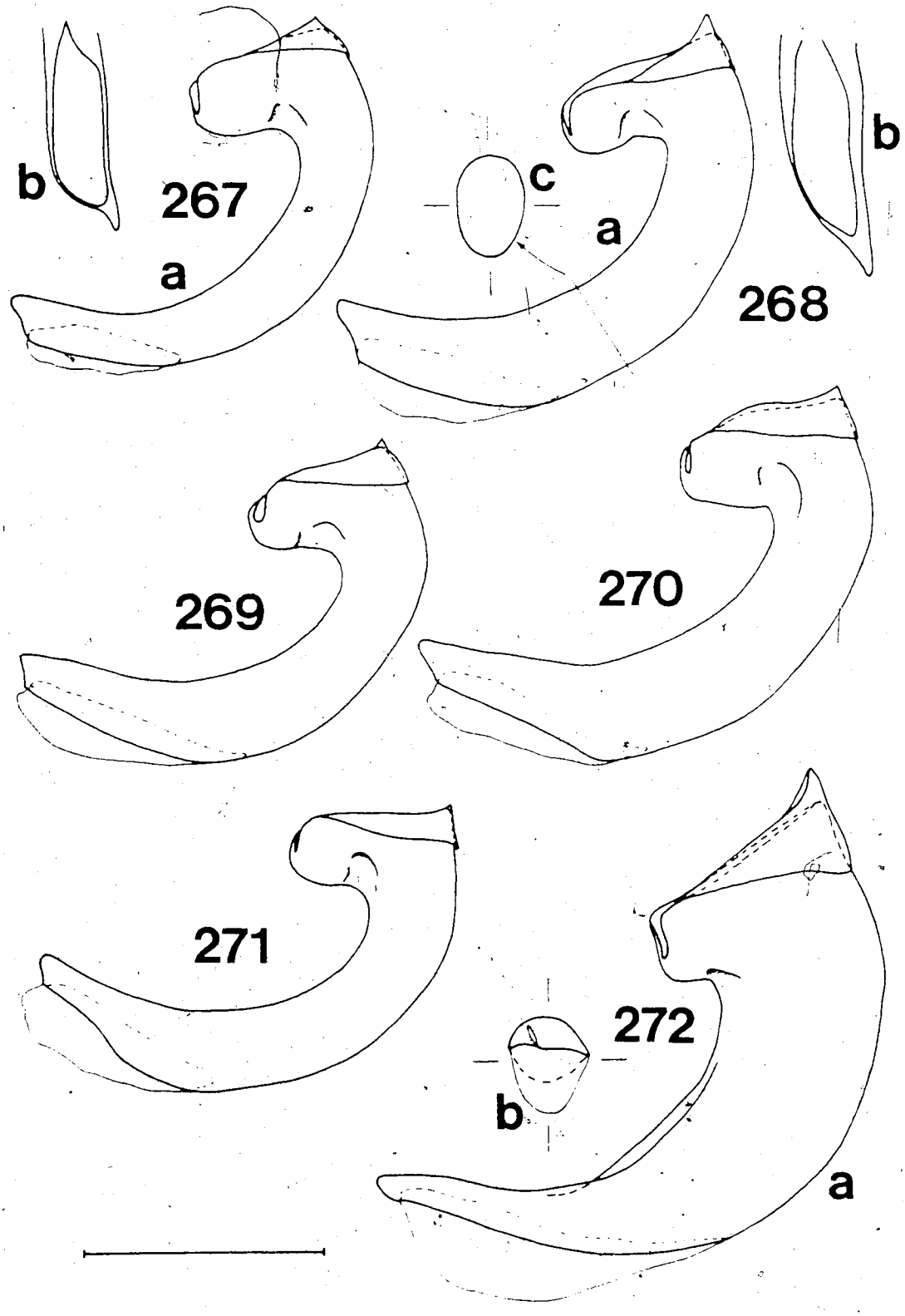

APLP
258
DBS
LP
RP
b
260
259
BO
DBS
BB
RP
MS
LP
PAS
AA
a
AO
IS

Fig. 261. Orientation of male genitalic structures in copulatory position ([a] left lateral aspect; [b] posterior aspect). Figs. 262-266. Median lobe of male genitalia. 262. Nebria virescens Horn (Vancouver Island, British Columbia), ([a] left lateral aspect; [b] ventral aspect; [c] apical aspect; [d] dorsal aspect, apical region only). 263. Nebria brevicollis (Fabricius) (Pitlochry, Scotland), ([a] left lateral aspect; [b] ventral aspect). 264. Nebria paradisi arlington (Mount Rainier, Washington), ([a] left lateral aspect; [b] mid-shaft cross-section). 265. Nebria acuta acuta Lindroth (Mount Rainier, Washington), ([a] left lateral aspect; [b] ventral aspect, apical region only). 266. Nebria acuta quileute new subspecies (Olympic Hot Springs, Washington), ([a] left lateral aspect; [b] ventral aspect, apical region only). Scale line = 1.0 mm.

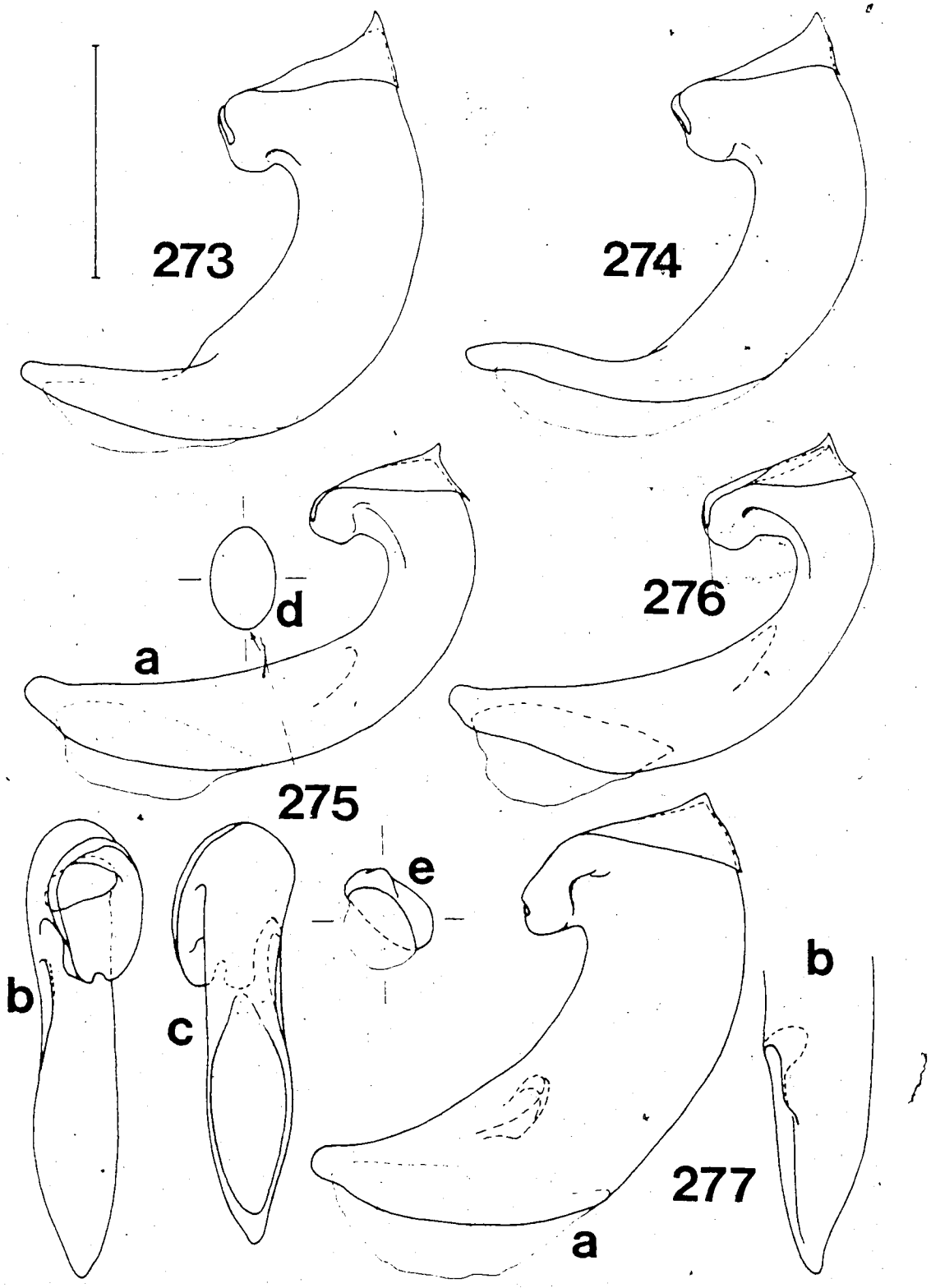

a
261
b
262
a
b
c
d
a
b
263
264
b
a
a
b
265
a
b
266



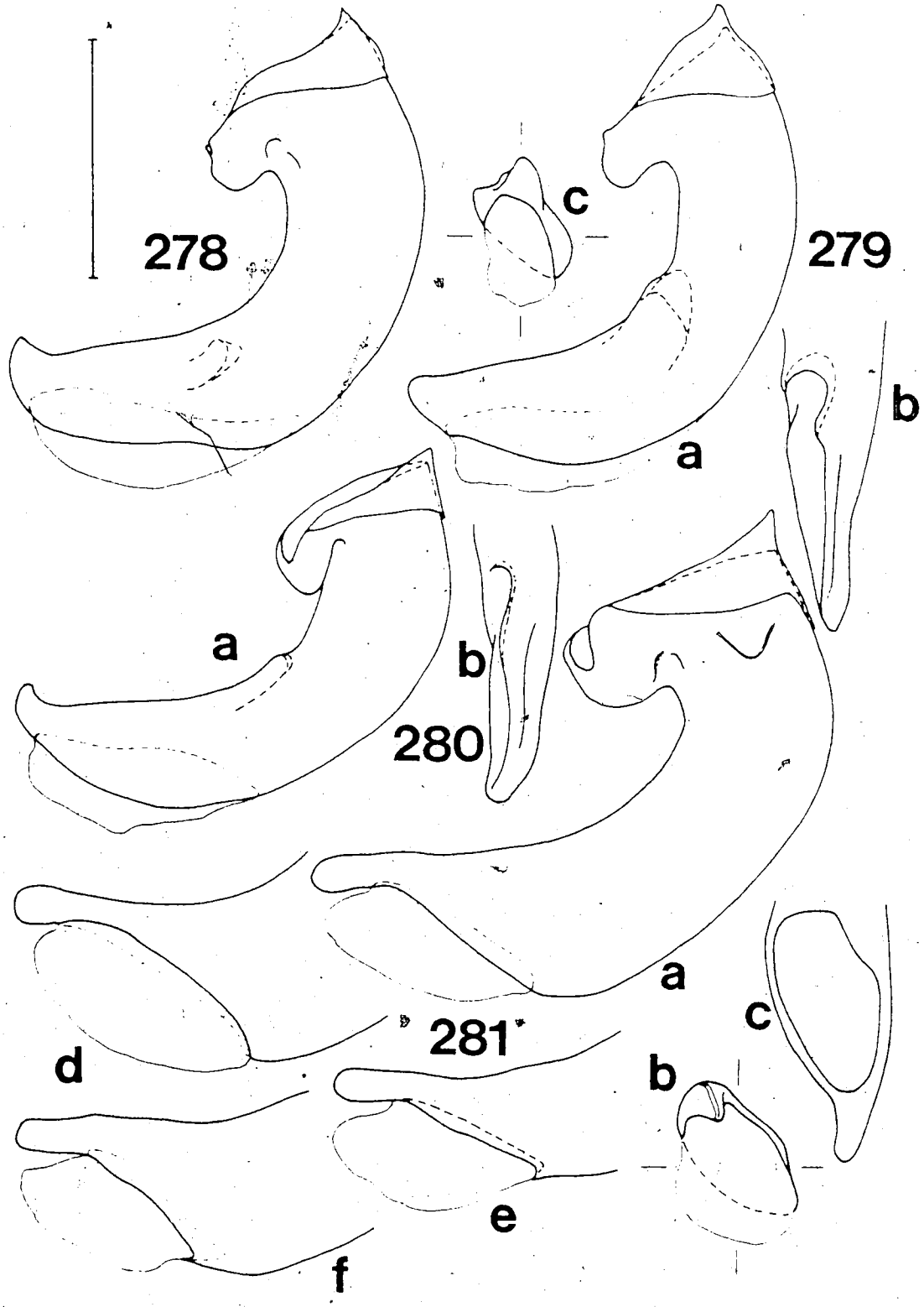
Figs. 267- 272. Median lobe of male genitalia. 262. Nebria sahlbergii sahlbergii Fischer von Waldheim (Cannon Beach, Oregon), ([a] left lateral aspect; [b] dorsal aspect, apical region only). 268. Nebria arkansana edwardsi new subspecies (Lake Oesa, Yoho National Park, British Columbia), ([a] left lateral aspect; [b] dorsal aspect, apical region only; [c] mid-shaft cross-section). 269. Nebria arkansana oowah new subspecies (La Sal Mountains, Utah), left lateral aspect. 270. Nebria arkansana uinta new subspecies (Logan River, Utah), left lateral aspect. 271. Nebria fragilis fragilis Casey (North Fork Provo River, Utah), left lateral aspect. 272. Nebria desolata Kavanaugh (11 miles southeast of Boulder, Utah), ([a] left lateral aspect; [b] apical aspect). Scale line = 1.0 mm.


b
267
a
c
a
268
b
269
270
271
272
b
a

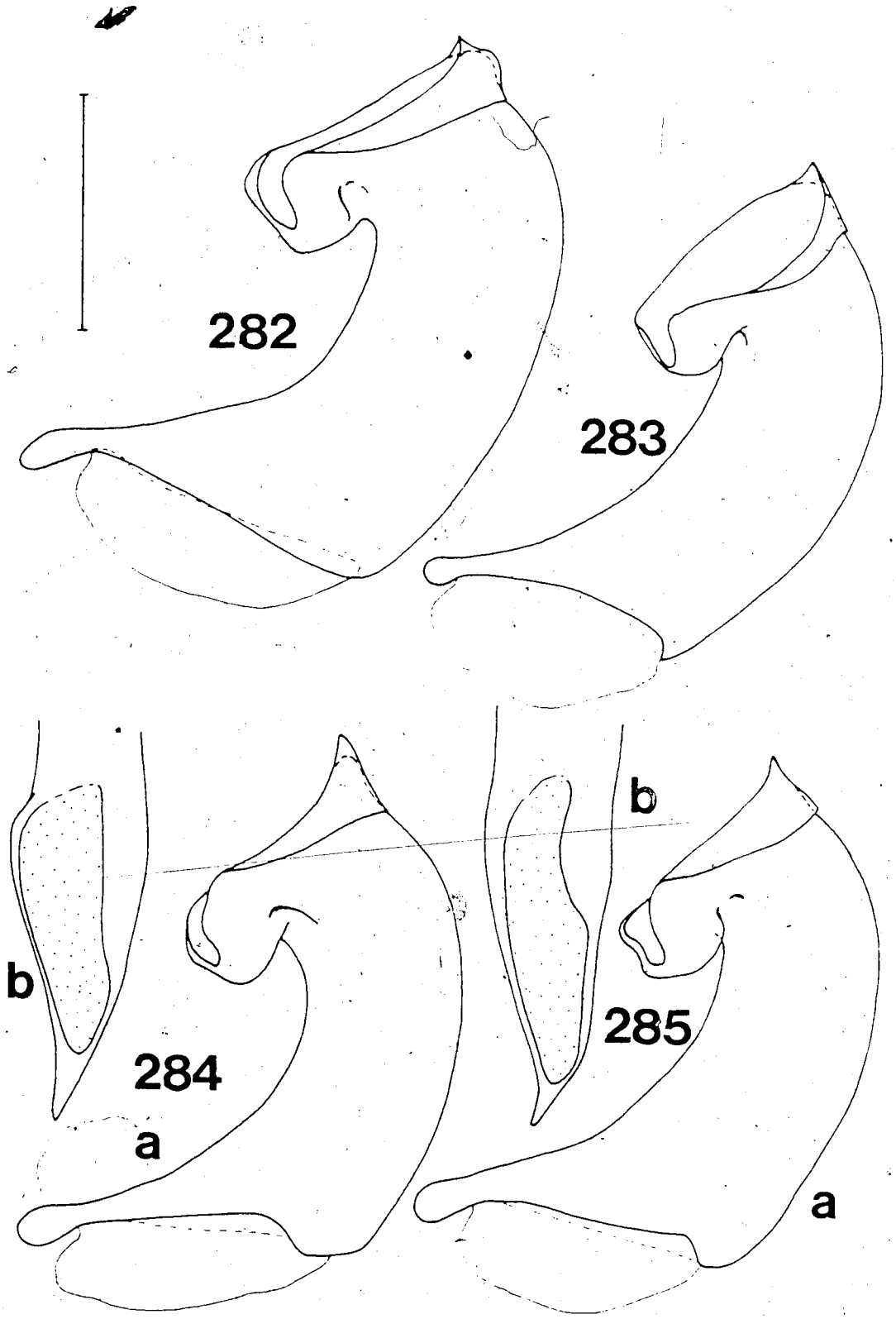
Figs. 273- 277. Median lobe of male genitalia. 273. Nebria navajo new species (19 miles southwest of Kayenta, Arizona), left lateral aspect. 274. Nebria eschscholtzii Ménétriés (10 miles southwest of Bickelton, Washington), left lateral aspect. 275. Nebria gebleri gebleri Dejean (Waterton Park, Alberta), ([a] left lateral aspect; [b] ventral aspect; [c] dorsal aspect; [d] mid-shaft cross-section; [e] apical aspect). 276. Nebria gebleri strawberriensis new subspecies (Strawberry Mountains, Oregon), left lateral aspect. 277. Nebria carri new species (Dollarhide Summit, Idaho), ([a] left lateral aspect; [b] ventral aspect, apical region only). Scale line = 1.0 mm.


273
274
d
a
276
275
e
b
c
b
277
a

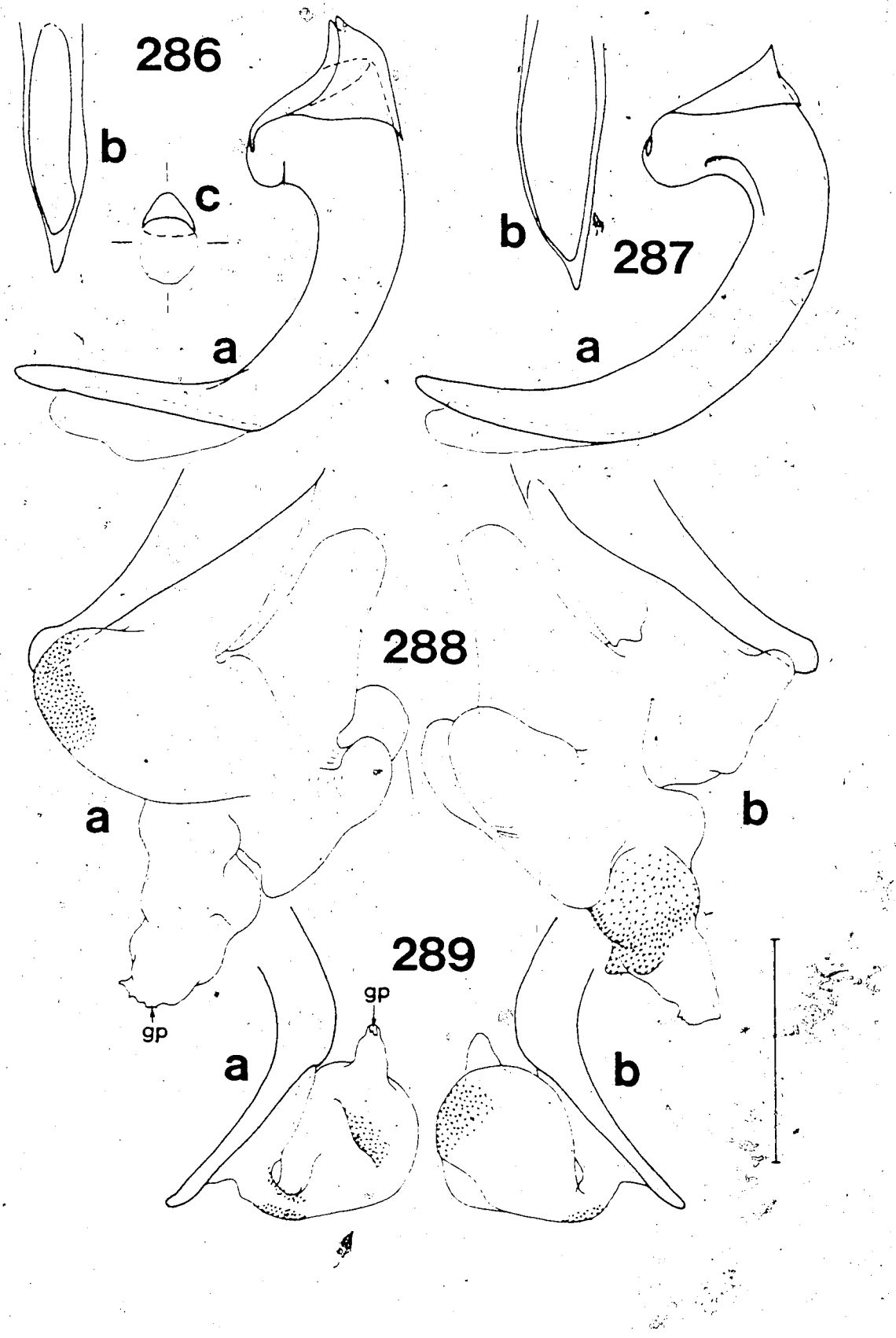
Figs. 278- 281. Median lobe of male genitalia. 273. Nebria kincaidi kincaidi Schwarz (Olympic Hot Springs, Washington), left lateral aspect. 279. Nebria spatulata sierrae new subspecies (Mono County, California), [a] left lateral aspect; [b] ventral aspect, apical region only; [c] apical aspect). 280. Nebria ovipennis LeConte (Franklin Lakes, California), ([a] left lateral aspect; [b] ventral aspect, apical region only). 281. Nebria trifaria trifaria LeConte, ([a] American Fork Canyon, Utah, left lateral aspect; [b] same locality, apical aspect; [c] same locality, dorsal aspect, apical region only; [d] Cedar Breaks National Monument, Utah, left lateral aspect; [e] Grand Teton National Park, Wyoming, left lateral aspect; [f] Ward, Colorado, left lateral aspect). Scale line = 1.0 mm.


278
c
279
a
b
a
b
280
a
c
281
d
b
e
f

Figs. 282-285. Median lobe of male genitalia. 282. Nebria trifaria catenata Casey (Wolf Creek Pass, Colorado), left lateral aspect. 283. Nebria trifaria utahensis new subspecies (Henry Mountains, Utah), left lateral aspect. 284. Nebria coloradensis Van Dyke (Quandary Peak, Colorado), ([a] left lateral aspect; [b] dorsal aspect, apical region only). 285. Nebria piute Erwin and Ball (Circleville Mountain, Utah), ([a] left lateral aspect; [b] dorsal aspect, apical region only). Scale line = 1.0 mm.


282
283
b
284
a
b
285
a

Figs. 286-287. Median lobe of male genitalia. 286. Nebria gouleti new species (Bayhorse Creek, Idaho), ([a] left lateral aspect; [b] dorsal aspect, apical region only; [c] apical aspect). 287. Nebria zioni oasis new subspecies (Pine Valley Mountains, Utah), ([a] left lateral aspect; [b] dorsal aspect, apical region only). Figs. 288-289. Internal sac of median lobe, ([a] left lateral aspect; [b] right lateral aspect). 288. Nebria vandykei vandykei Bänninger (Mount Rainier, Washington). 289. Nebria gyllenhali castanipes (Kirby) Edmonton, Alberta). Scale line = 1.0 mm.


286
b
c
a
b
287
a
288
a
b
289
gp
gp
a
b

Figs. 290-291. Parameres, Nebria virescens Horn (Vancouver Island, British Columbia). 290. Right paramere, lateral aspect. 291. Left paramere, lateral aspect. Fig. 291A. Left paramere, lateral aspect, Nebria paradisi Darlington (Mount Rainier, Washington). Figs. 292-293. Parameres, Nebria gouleti new species (Bayhorse Creek, Idaho). 292. Right paramere, lateral aspect. 293. Left paramere, lateral aspect. Fig. 294. Parameres, Nebria brevicollis (Fabricius) (Pitlochry, Scotland), ([a] right paramere, lateral aspect; [b] left paramere, lateral aspect). Fig. 295. Left paramere, lateral aspect, Nebria ovipennis LeConte (Franklin Lakes, California). Fig. 296. Right paramere, medial aspect, Nebria schwarzi beverlianna new subspecies (Hoback River, Wyoming); mps = medial parameric sclerite. Fig. 297. Ring sclerite in relation to median lobe; ([a] dorsal aspect; [b] ventral aspect). Fig. 298. Ring sclerite, Nebria, generalized, ([a] dorsal aspect; [b] posterior aspect); n = notch through which passes duct of pygidial defense gland; ps = pouch sclerite; t9 = ninth tergum. Fig. 299. Ring sclerite, dorsal aspect, Amphizoa lecontei Matthew. All scale lines = 1.0 mm.

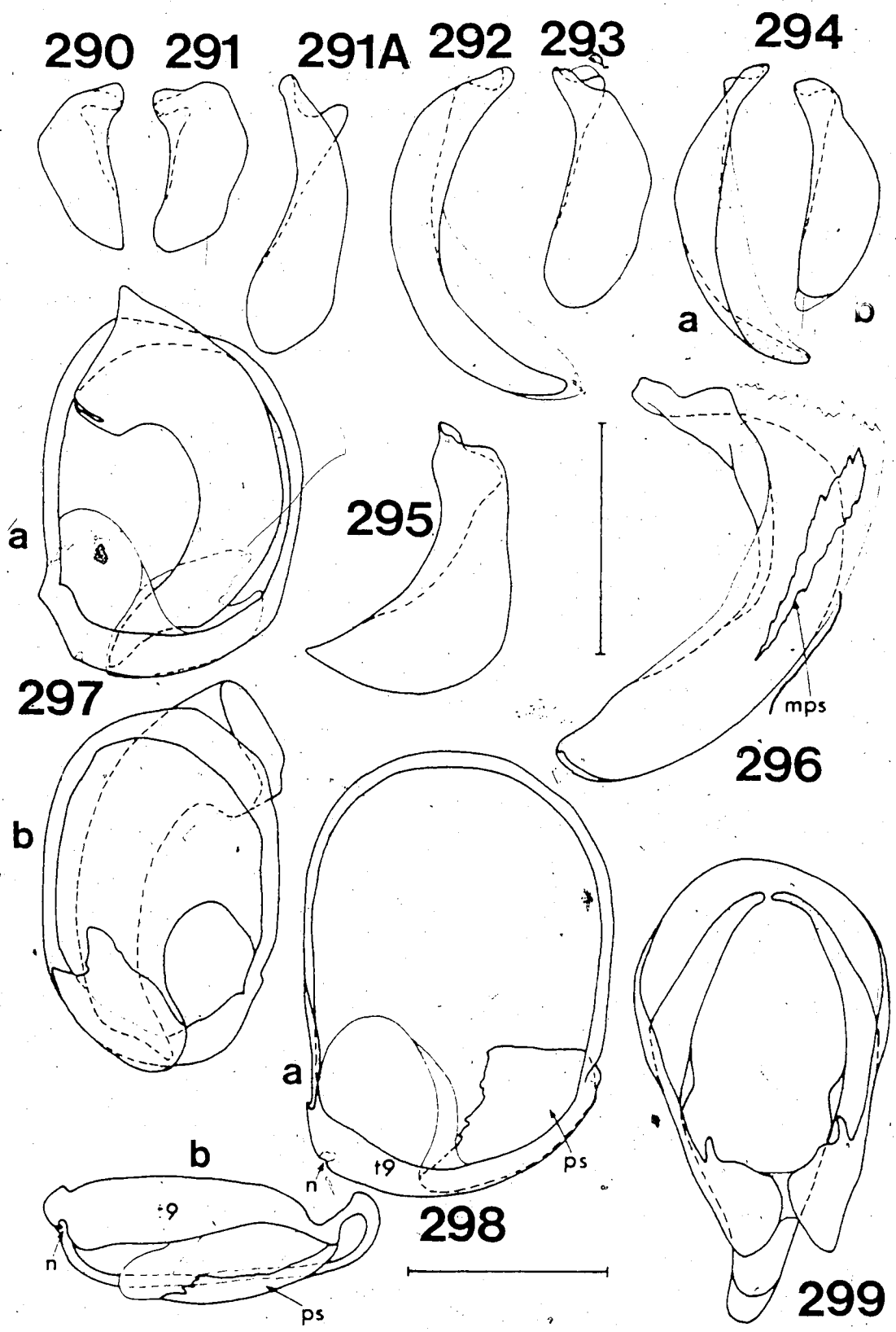
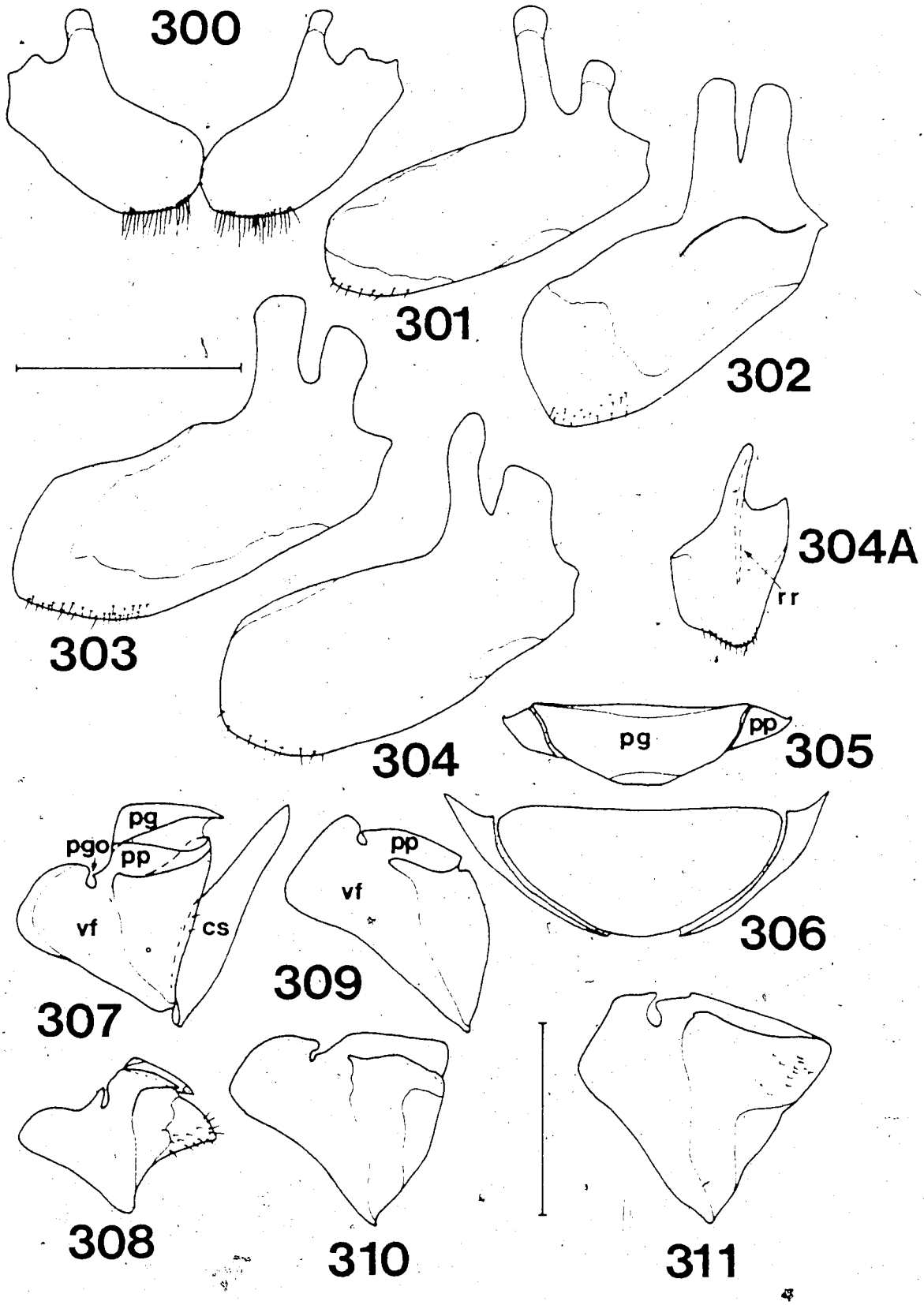
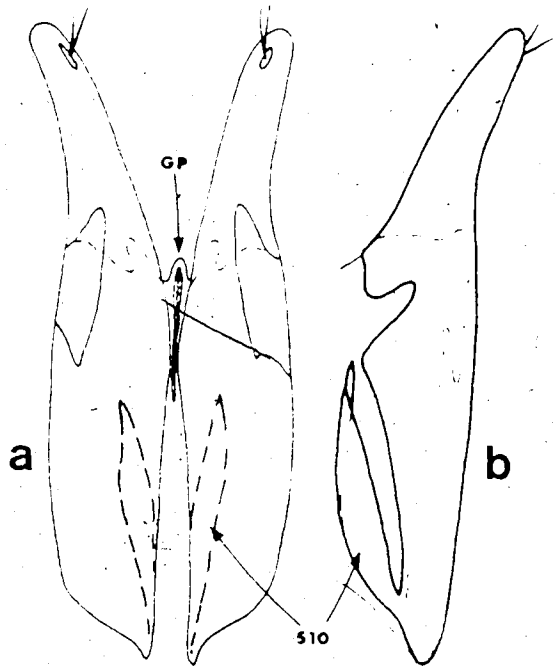

290
291
291A
292
293
294
a
b
295
a
297
mps
296
b
a
b
t9
n
ps
298
t9
n
ps
299

Fig. 300. Eighth sternum (both hemisternites), ventral aspect, Nebria virescens Horn (Vancouver Island, British Columbia). Figs. 301-304A. Eighth sternum (left hemisternite only), ventral aspect. 301. Nebria metallica Fischer von Waldheim (White River, Washington). 302. Nebria gouleti new species (Clearwater River, Idaho). 303. Nebria paradisi Darlington (Mount Rainier, Washington). 304. Nebria carri new species (Dollarhide Summit, Idaho). 304A. Trachypachus gibbsi LeConte (Eugene, Oregon). Figs. 305-306. Proctiger and paraprocts, ventral aspect. 305. Nebria virescens Horn (Vancouver Island, British Columbia). 306. Nebria diversa LeConte (Waldport, Oregon). Figs. 307-311. Valvifer and paraproct, left lateral aspect; cs = coxostylus; pg = proctiger; pgo = notch which bears orifice of duct of pygidial defense gland; pp = paraproct; vf = valvifer. 307. Nebria arkansana edwardsi new subspecies (Glacier National Park, Montana). 308. Nebria virescens Horn (Vancouver Island, British Columbia). 309. Nebria lacustris bellorum new subspecies (West Prong Little Pigeon River, Tennessee). 310. Nebria lyelli Van Dyke (Mount Lyell, California). 311. Nebria gregaria Fischer von Waldheim (Unalaska Island, Aleutian Islands). All scale lines = 1.0 mm.

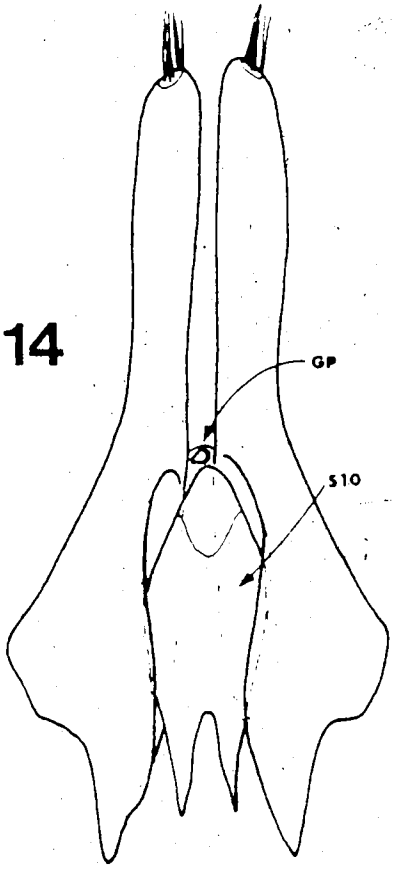

300
301
302
303
304
304A
rr
305
pg
pp
306
307
pg
pgo
pp
vf
cs
309
pp
vf
308
310
311

Figs. 312-314. Coxostyli and tenth sternum; GP = gonopore; S10 = tenth sternum (single or as paired hemisternites). 312. Nebria paradisi Darlington (Mount Rainier, Washington), ([a] ventral aspect; [b] right coxostylus and right tenth hemisternite, medial aspect). 313. Nebria boreal is LeConte (Columbia Icefields, Alberta), right coxostylus and right tenth hemisternite, medial aspect. 314. Amphizoa lecontei Matthew (Hoback River, Wyoming), ventral aspect. Scale line = 1.0 mm.

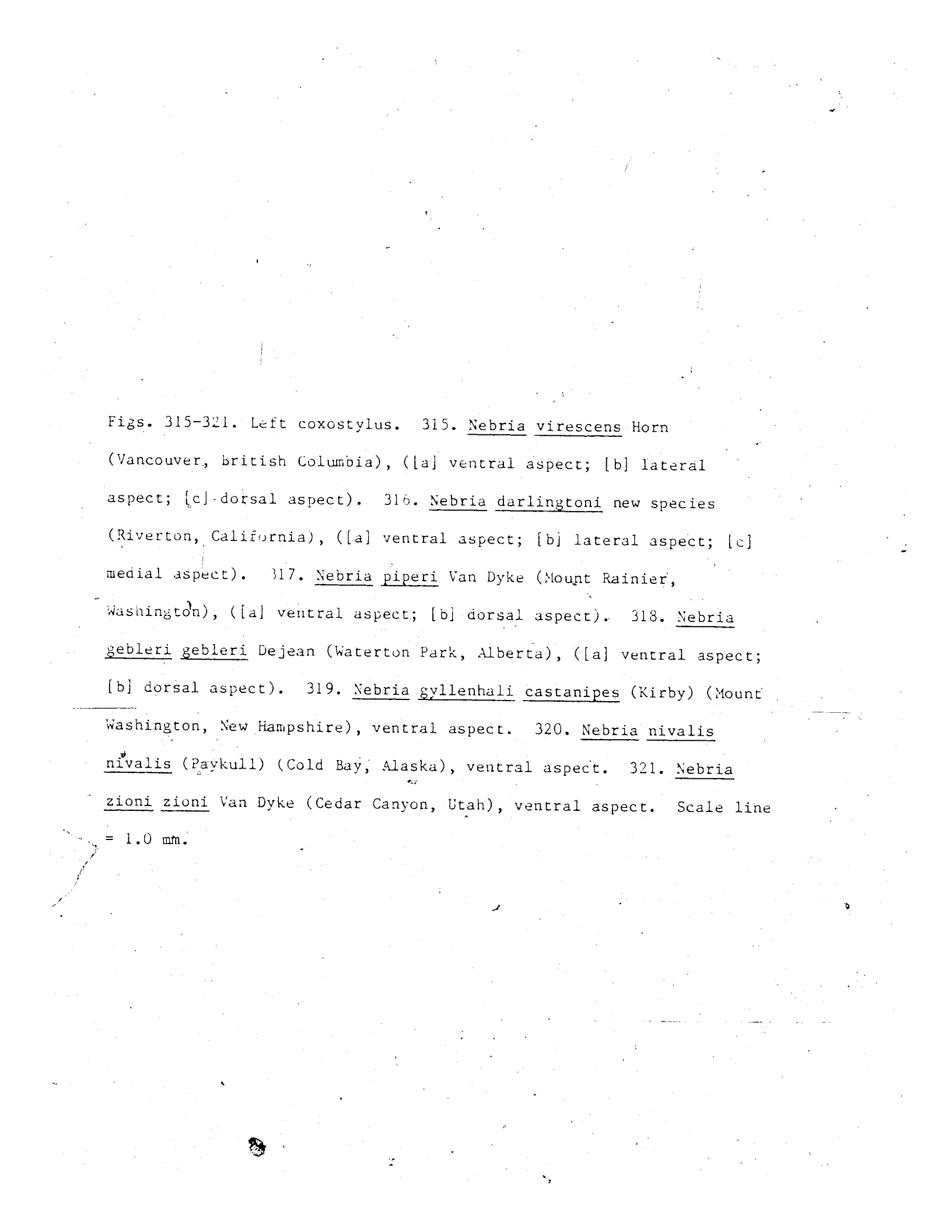


312

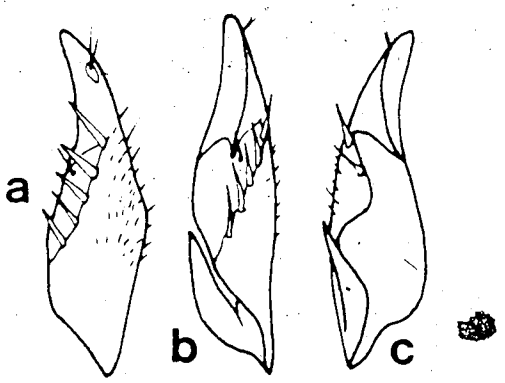
313



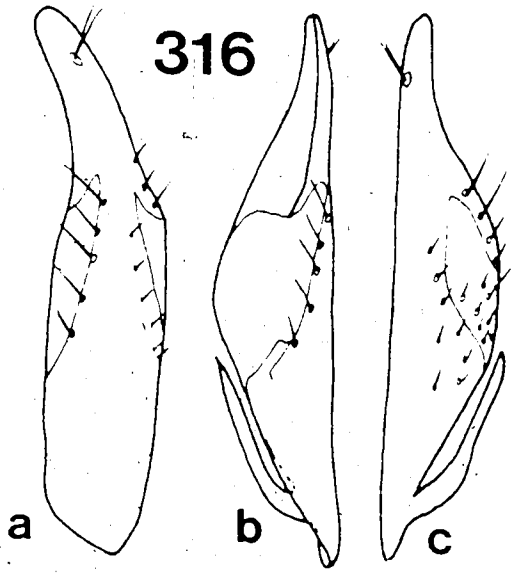
314

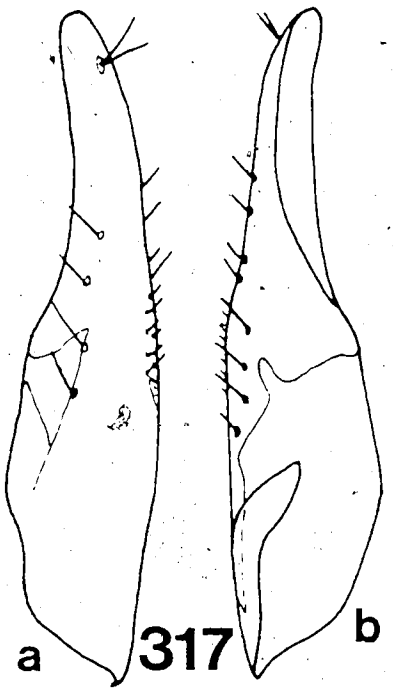


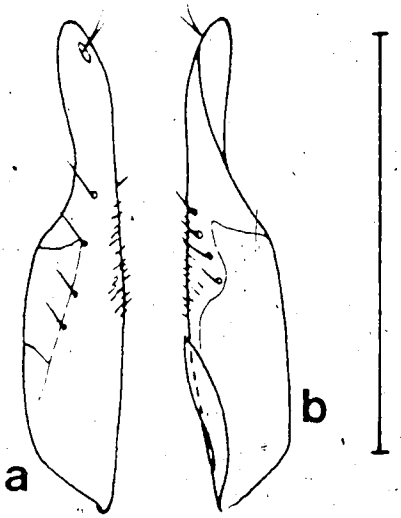
Figs. 315-321. Left coxostylus. 315. Nebria virescens Horn (Vancouver, british Columbia), ([a] ventral aspect; [b] lateral aspect; [c] dorsal aspect). 316. Nebria darlingtoni new species (Riverton, California), ([a] ventral aspect; [b] lateral aspect; [c] medial aspect). 317. Nebria piperi Van Dyke (Mount Rainier, Washington), ([a] ventral aspect; [b] dorsal aspect). 318. Nebria gebleri gebleri Dejean (Waterton Park, Alberta), ([a] ventral aspect; [b] dorsal aspect). 319. Nebria gyllenhali castanipes (Kirby) (Mount Washington, New Hampshire), ventral aspect. 320. Nebria nivalis nivalis (Paykull) (Cold Bay, Alaska), ventral aspect. 321. Nebria zioni zioni Van Dyke (Cedar Canyon, Utah), ventral aspect. Scale line = 1.0 mm.



315



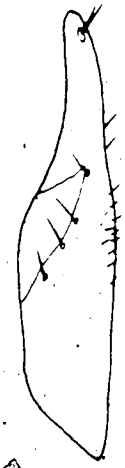




318

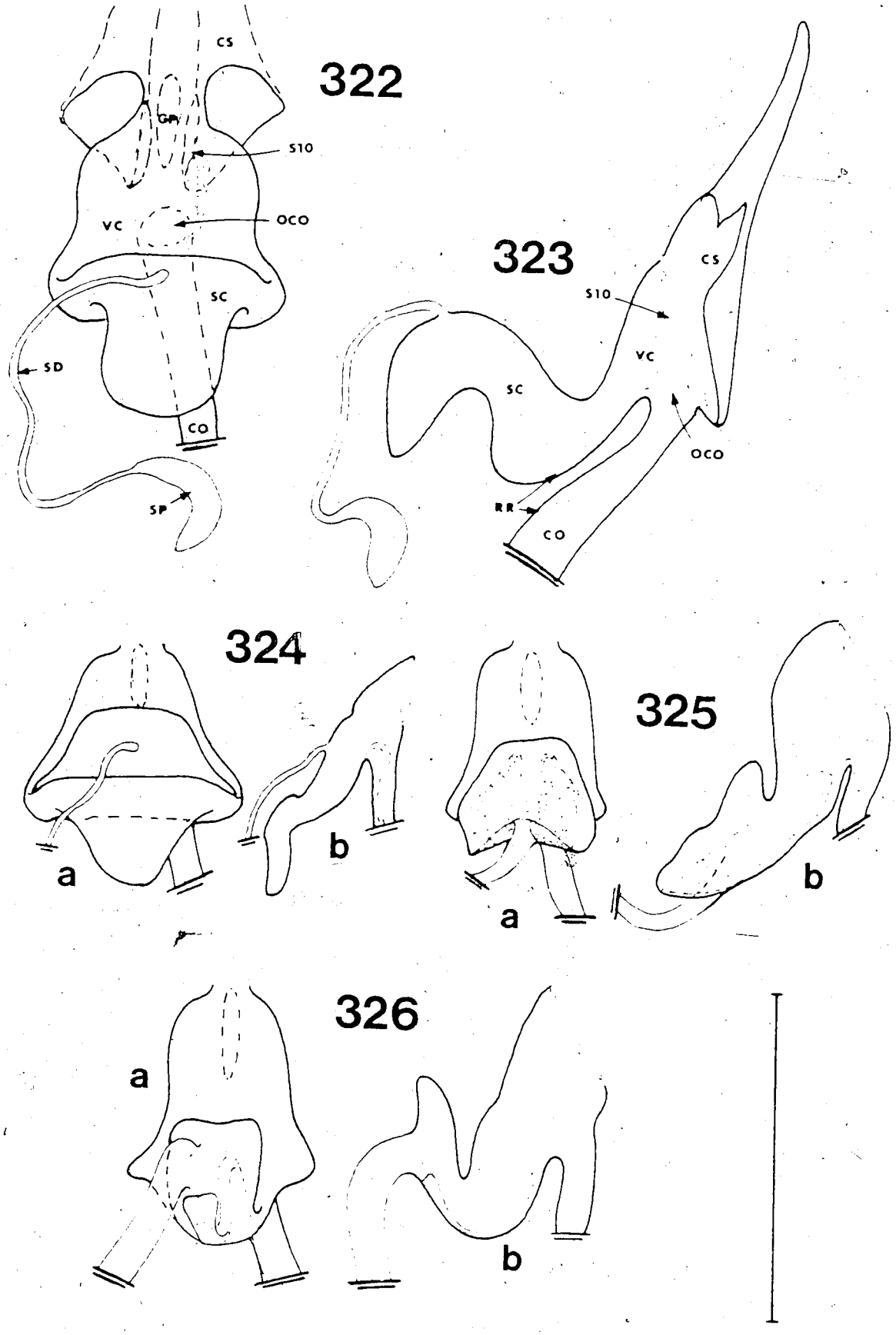
319

320

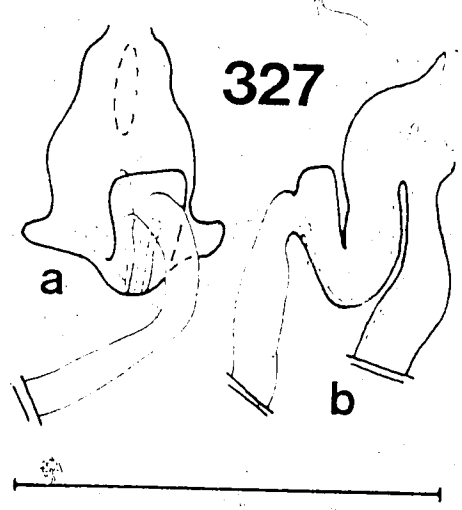


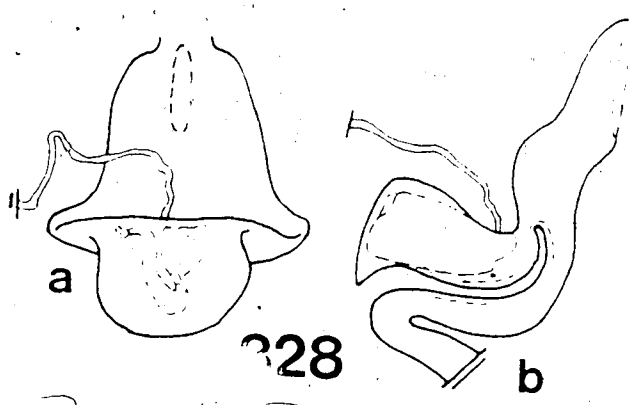
321

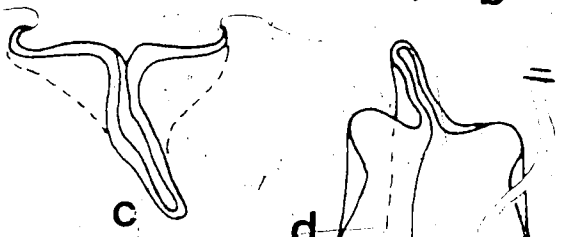
Figs. 322-323. Bursa copulatrix and associated structures, general form and associated terms; CO = common oviduct; CS = coxostylus; GP = gonopore; OCO = orifice of common oviduct on bursa copulatrix; RR = reinforcement rod; SC = spermathecal chamber of bursa; SD = spermathecal duct; SP = spermatheca; S10 = tenth sternum; VC = vestibular chamber of bursa. 322. Ventral aspect. 323 Left lateral aspect. Figs. 324-326. Bursa copulatrix, ([a] ventral aspect; [b] left lateral aspect); stippled areas denote shape and location of distinct sclerites or moderately to markedly sclerotized, but less clearly defined, areas. 324. Nebria virescens Horn (Vancouver, British Columbia). 325. Nebria hudsonica LeConte (Hoback Junction, Wyoming). 326. Nebria crassicornis crassicornis Van Dyke (Mount Rainier, Washington). Scale line = 1.0 mm.

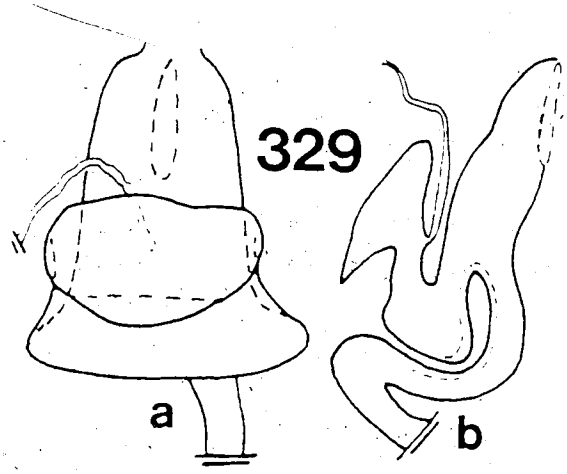

322
CS
GP
S10
VC
OCO
SC
SD
CO
SP
323
CS
S10
VC
SC
OCO
RR
CO
324
a
b
325
a
b
326
a
b

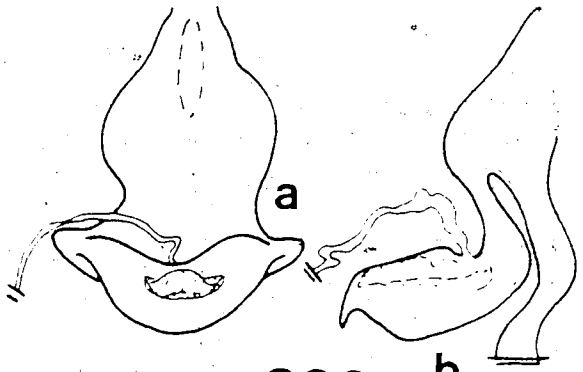
Figs. 327-330. Bursa copulatrix; ([a] ventral aspect; [b] left lateral aspect; [c] and [d] bursal sclerite enlarged, varied in aspect); stippled areas denote shape and location of distinct sclerites or moderately to markedly sclerotized, but less clearly defined, areas. 327. Nebria frigida Sahlberg (Eagle Summit, Alaska). 328. Nebria acuta acuta Lindroth (Mount Rainier, Washington), ([c] sclerite enlarged, dorsal aspect; [d] sclerite enlarged, posterior aspect). 329. Nebria acuta quileute new subspecies (Olympic Hot Springs, Washington). 329A. Nebria sahlbergii sahlbergii Fischer von Waldheim (Medicine Lake, Alberta), ([c] sclerite enlarged, dorsal aspect; [d] sclerite enlarged, left lateral aspect). 330. Nebria sahlbergii modoc new subspecies (Warner Mountains, California), ([a] sclerite enlarged, dorsal aspect; [b] sclerite enlarged, left lateral aspect). Scale line for [a]'s and [b]'s = 1.0 mm; scale line for [c]'s and [d]'s = 0.10 mm.

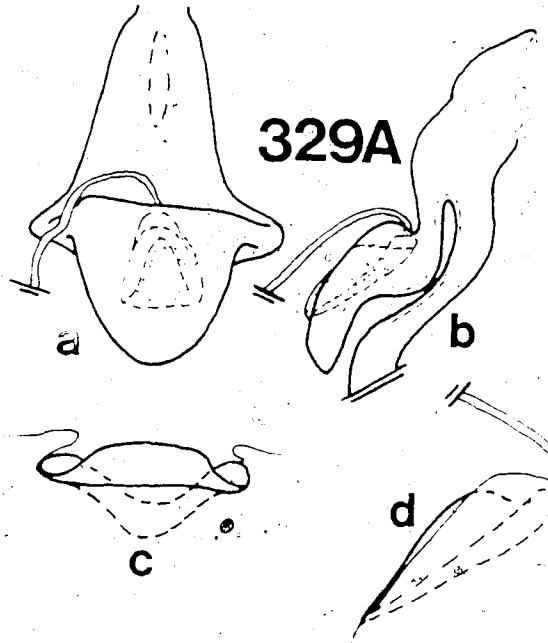

327
a
b

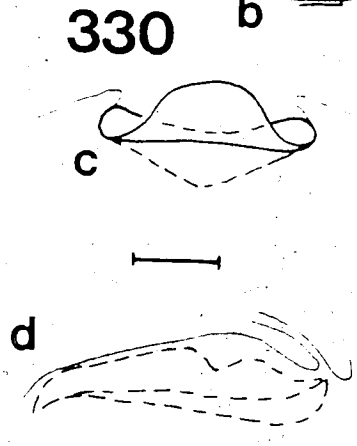

a
328
b


c
d

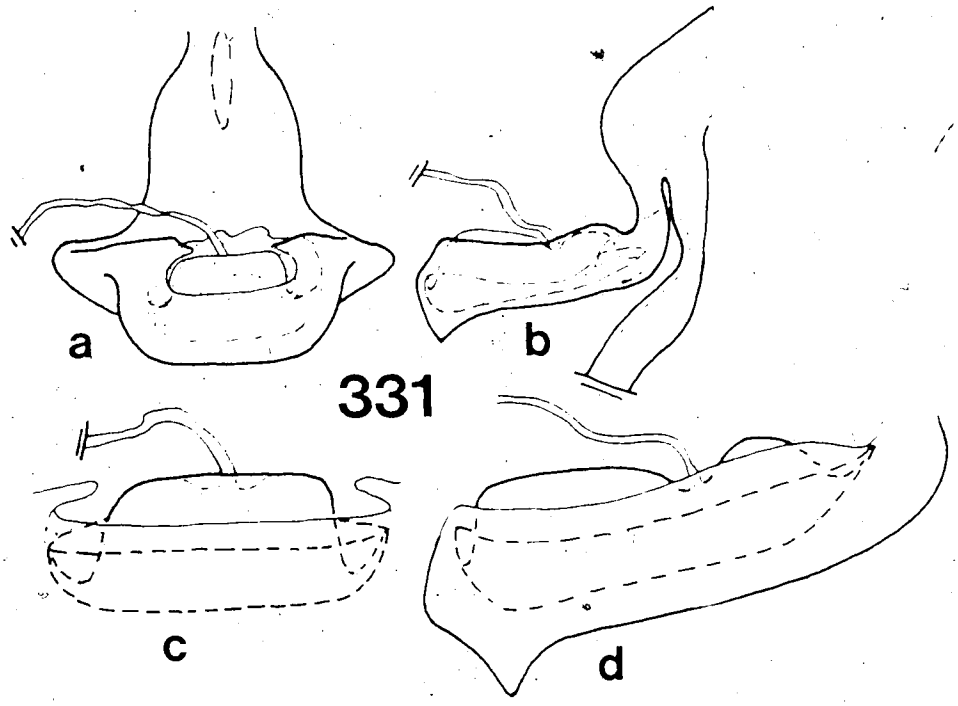

329
a
b

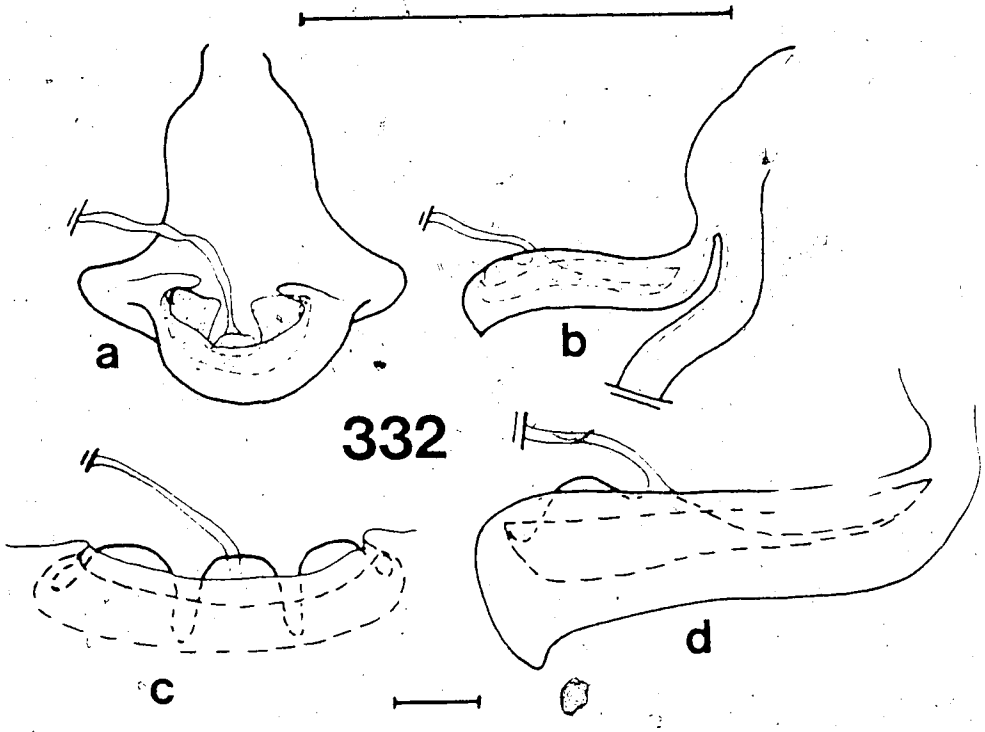

a
b


329A
a
b
c
d

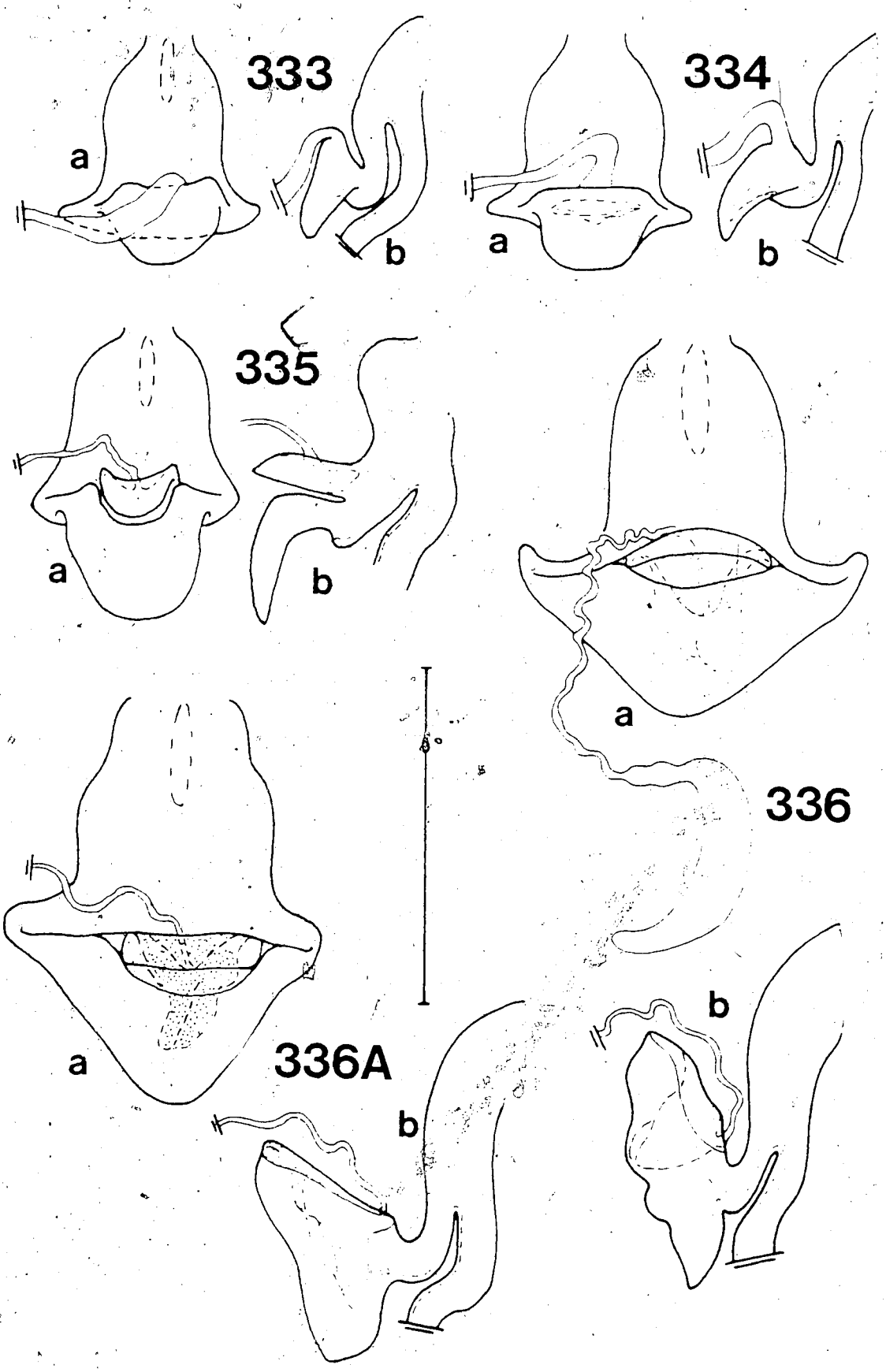

330
c
d

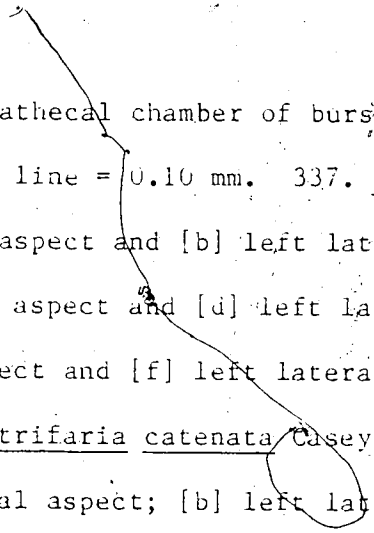
Figs. 331-332. Bursa copulatrix; ([a] ventral aspect; [b] left lateral aspect; [c] and [d] bursal sclerite enlarged, varied in aspect); stippled areas denote shape and location of distinct sclerites or moderately to markedly sclerotized, but less clearly defined, areas. 331. Nebria arkansana edwardsi new subspecies (Amiskwi Falls, British Columbia), ([c] sclerite enlarged, dorsal aspect; [d] sclerite enlarged, left lateral aspect). 332. Nebria arkansana owah new subspecies (La Sal Mountains, Utah), ([c] sclerite enlarged, dorsal aspect; [d] sclerite enlarged, left lateral aspect). Scale line for [a]'s and [b]'s = 1.0 mm; scale line for [c]'s and [d]'s = 0.10 mm


a
b
331
c
d

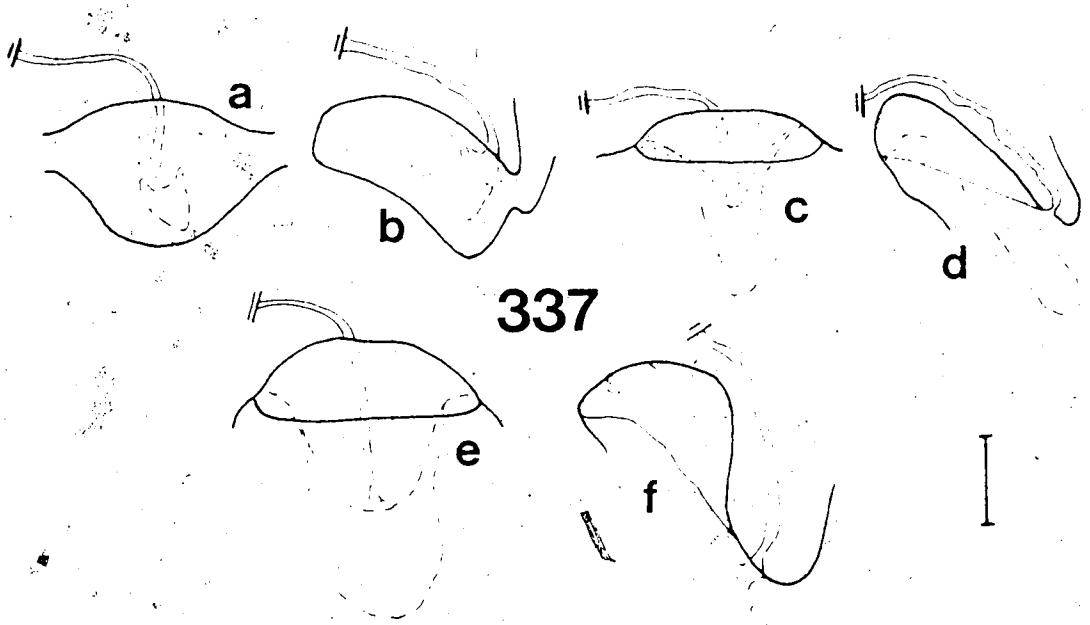

a
b
332
c
d

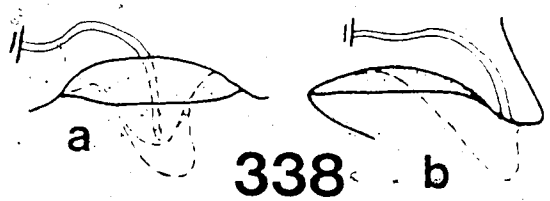
Figs. 333-336A. Bursa copulatrix; ([a] ventral aspect; [b] left lateral aspect); stippled areas denote shape and location of distinct sclerites or moderately to markedly sclerotized, but less clearly defined, areas. 333. Nebria gebleri gebleri Dejean (Waterton Park, Alberta). 334. Nebria gebleri strawberriensis new subspecies (Strawberry Mountains, Oregon). 335. Nebria kincaidi kincaidi Schwarz (Olympic Hot Springs, Washington). 336. Nebria coloradensis Van Dyke (Tarryall Creek, Colorado). 336A. Nebria piute Ball and Erwin (Circleville Mountain, Utah). Scale line for [a]'s and [b]'s = 1.0 mm; scale line for [c]'s and [d]'s = 0.10 mm.


333
a
b
334
a
b
335
a
b
a
336
336A
a
b
b

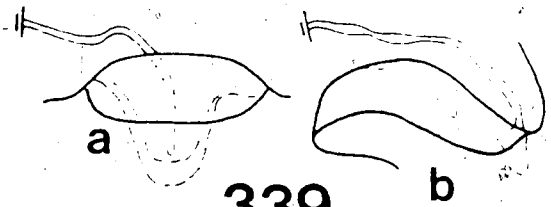


Figs. 337-339. Spermathecal chamber of bursa copulatrix, enlarged, aspect varied; scale line = 0.10 mm. 337. Nebria trifaria trifaria LeConte ([a] dorsal aspect and [b] left lateral aspect, Ward, Colorado; [c] dorsal aspect and [d] left lateral aspect, Logan River, Utah; [e] dorsal aspect and [f] left lateral aspect, Bluebell Knoll, Utah). 338. Nebria trifaria catenata Casey (Wolf Creek Pass, Colorado), ([a] dorsal aspect; [b] left lateral aspect). 339. Nebria trifaria utahensis new subspecies (Henry Mountains, Utah) ([a] dorsal aspect; [b] left lateral aspect). Figs. 340-341. Bursa copulatrix. 340. Nebria paradisi Darlington (Mount Rainier, Washington), ([a] ventral aspect; [b] left lateral aspect). 341. Nebria darlingtoni new species (Riverton, California), ventral aspect). Scale line = 1.0 mm. [In Figs. 337-341, stippled areas denote shape and location of distinct sclerites or moderately to markedly sclerotized, but less clearly defined, areas].

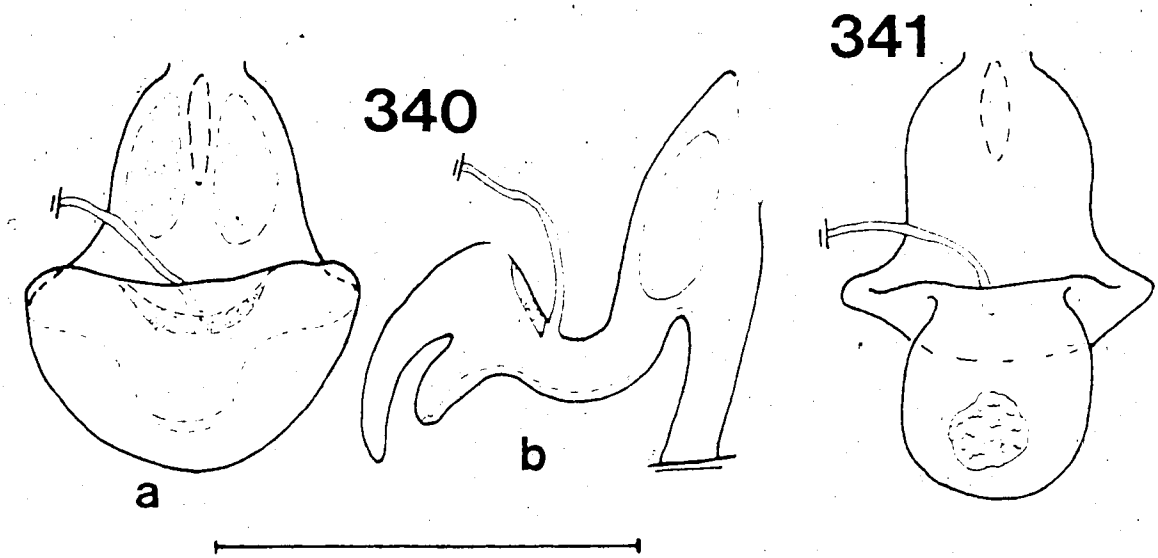




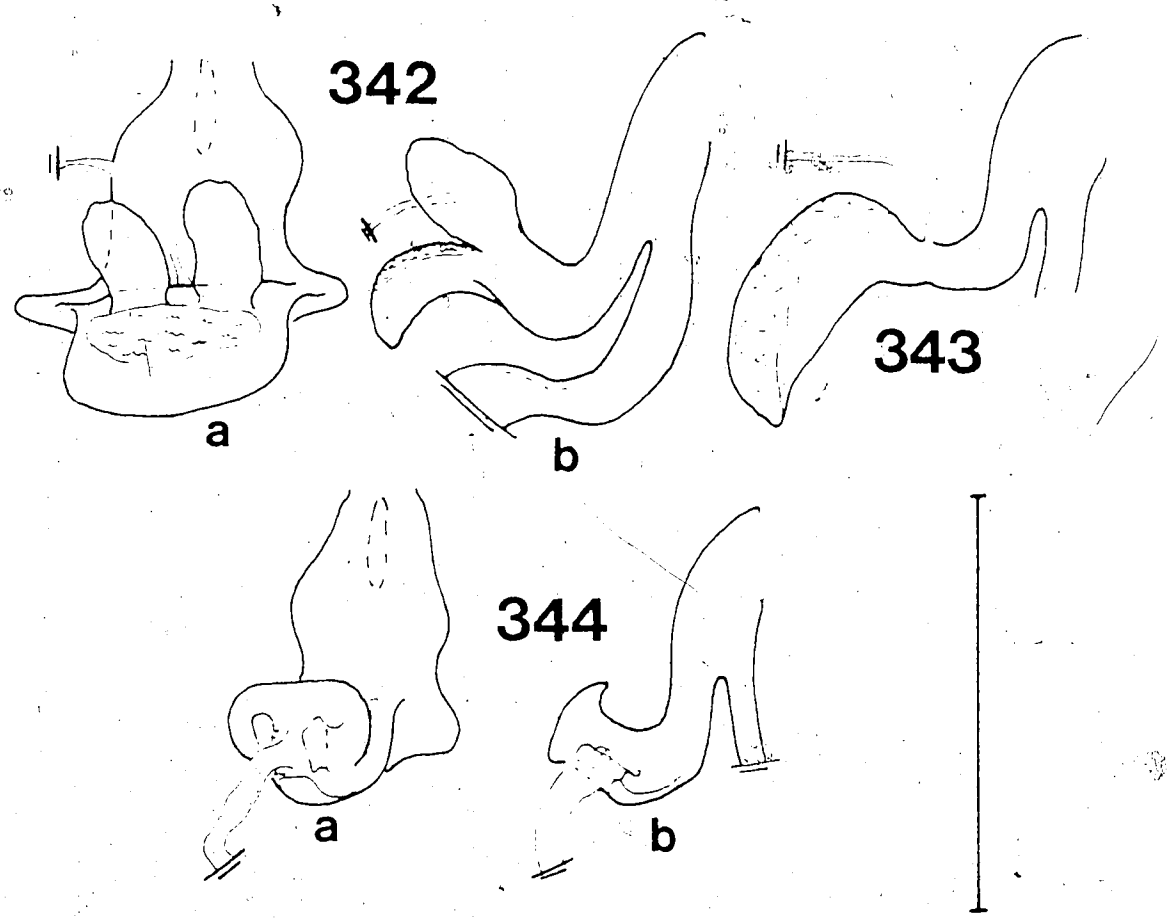
338

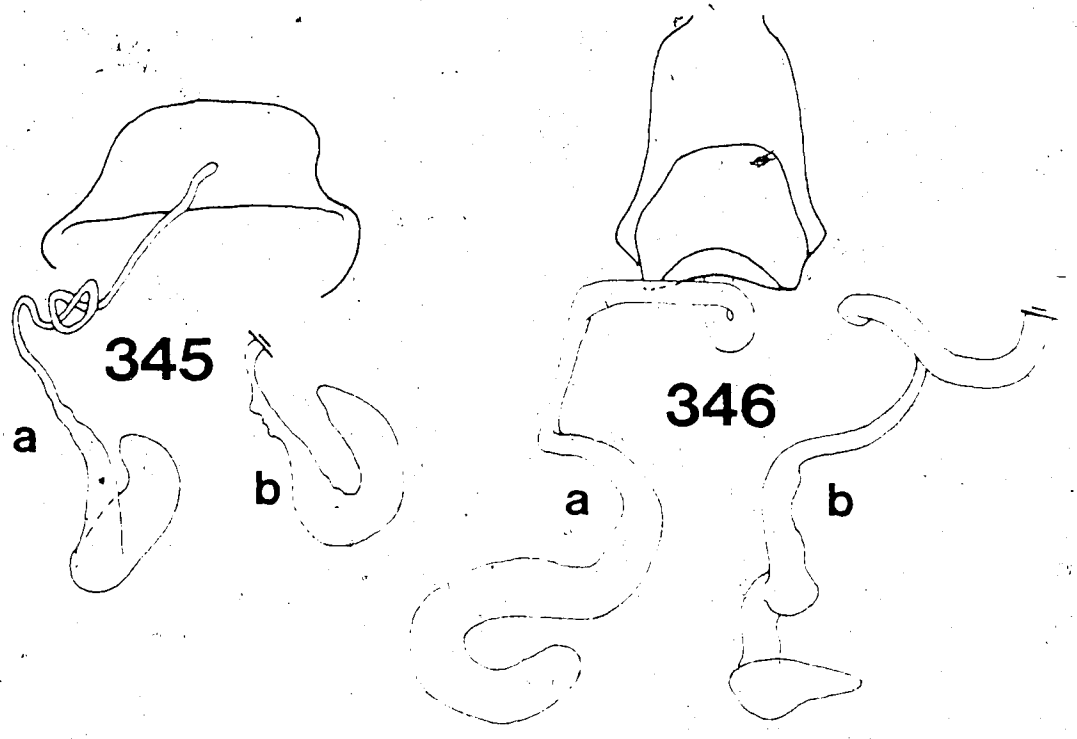


339



Figs. 342-344. Bursa copulatrix; stippled areas denote shape and location of distinct sclerites or moderately to markedly sclerotized, but less clearly defined, areas. 342. Nebria desolata Kavanaugh (11 miles southeast of Boulder, Utah), ([a] ventral aspect; [b] left lateral aspect). 343. Nebria obliqua LeConte (Athabasca River, Alberta), left lateral aspect. 344. Nebria nivalis nivalis (Paykull) (Cold Bay, Alaska), ([a] ventral aspect; [b] left lateral aspect). Figs. 345-346. Spermatheca and spermathecal duct. 345. Nebria virescens Horn (Vancouver, British Columbia), ([a] dorsal aspect; [b] left lateral aspect). 346. Nebria hudsonica LeConte (Hoback Junction, Wyoming), ([a] dorsal aspect; [b] left lateral aspect). Scale line = 1.0 mm.


342
a
b
343
344
a
b


345
a
b
346
a
b

Figs. 347-348. Spermatheca and spermathecal duct. 347. Nebria frigida Sahlberg (Eagle Summit, Alaska), ([a] dorsal aspect; [b] left lateral aspect). 348. Nebria subdilatata Motschulsky (Yakutskaya Oblast, U.S.S.R.), ([a] dorsal aspect; [b] left lateral aspect). Fig. 349. Spermatheca, bursa copulatrix, and associated structures, Notiophilus borealis Harris (Nome, Alaska), ([a] dorsal aspect; [b] left lateral aspect). Figs. 350-351. Spermatheca and spermathecal duct, dorsal aspect. 350. Nebria piperi Van Dyke (Mount Rainier, Washington). 351. Nebria pallipes Say (Bolton, Vermont). Scale line = 1.0 mm.

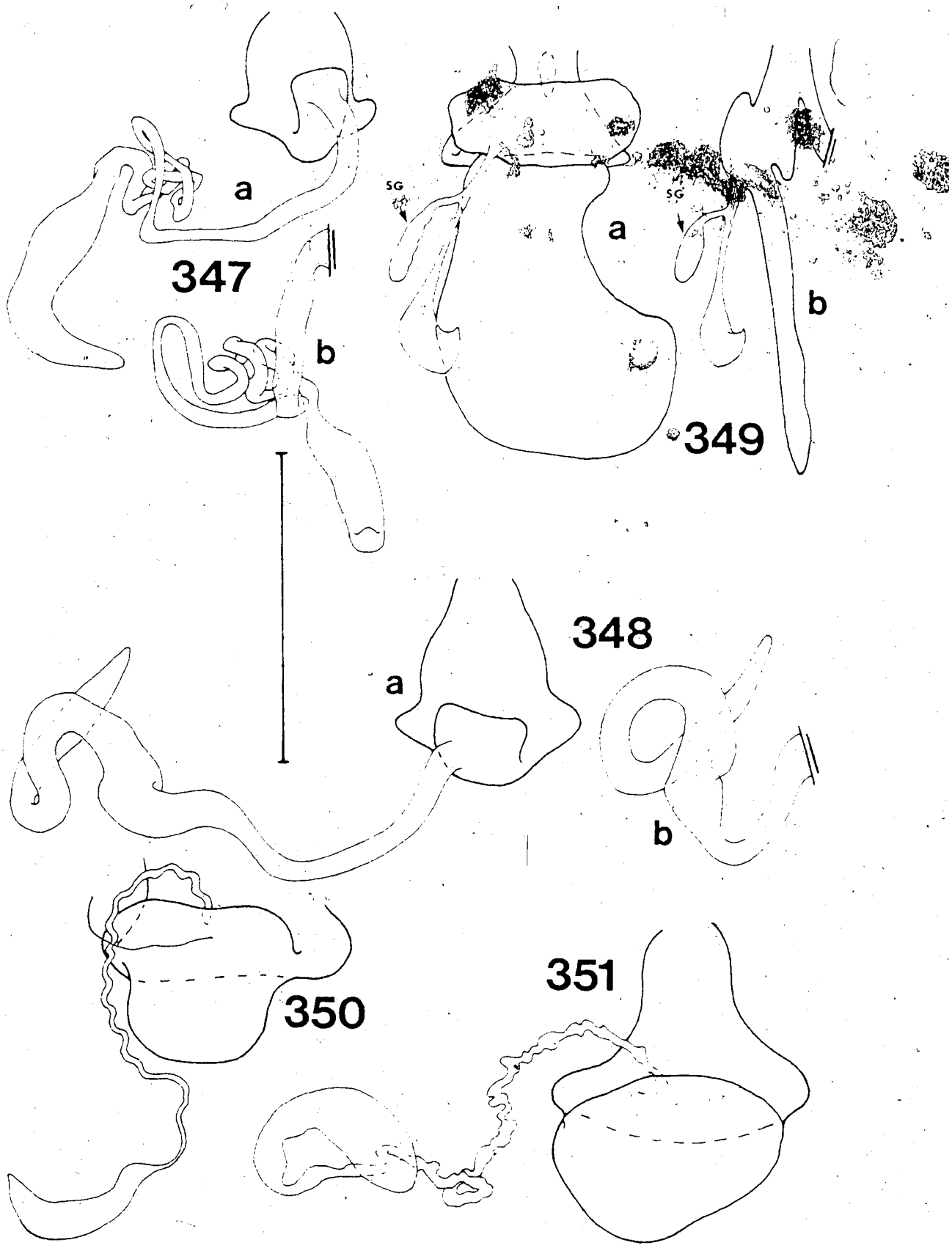
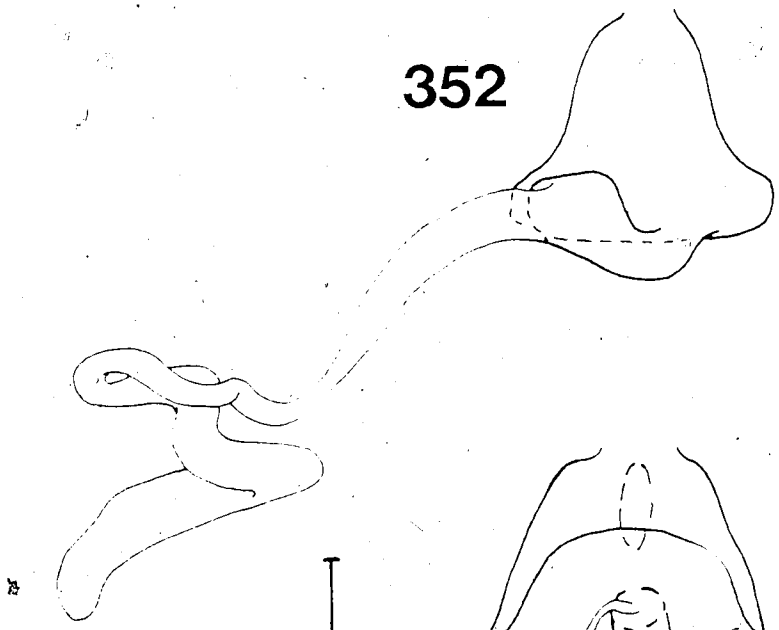
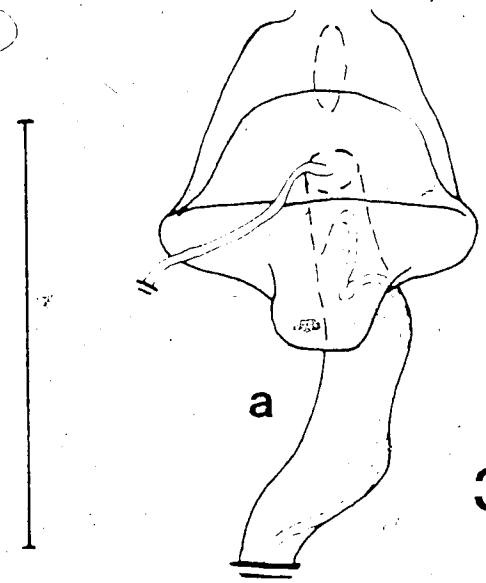

a
347
b
SG
SG
a
b
349
348
a
b
350
351

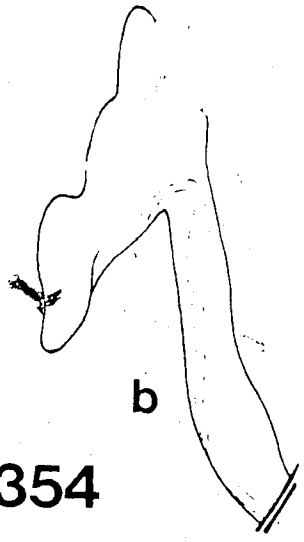
Fig. 352. Spermatheca and spermathecal duct, dorsal aspect, Nebria crassicornis intermedia Van Dyke (Logan Pass, Montana). Figs. 353-354. Bursa copulatrix and common oviduct, ([a] dorsal aspect; [b] left lateral aspect). 353. Nebria brevicollis (Fabricius) (Aviemore, Scotland). 354. Nebria virescens Horn (Vancouver, British Columbia). Scale line = 1.0 mm.



352

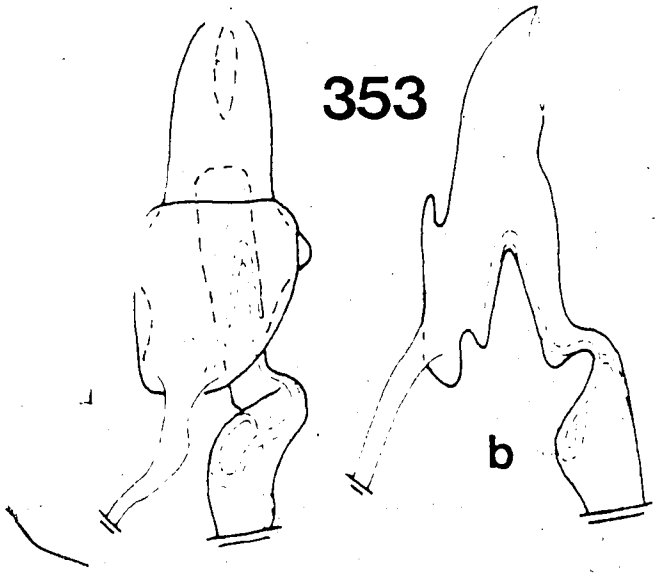


a



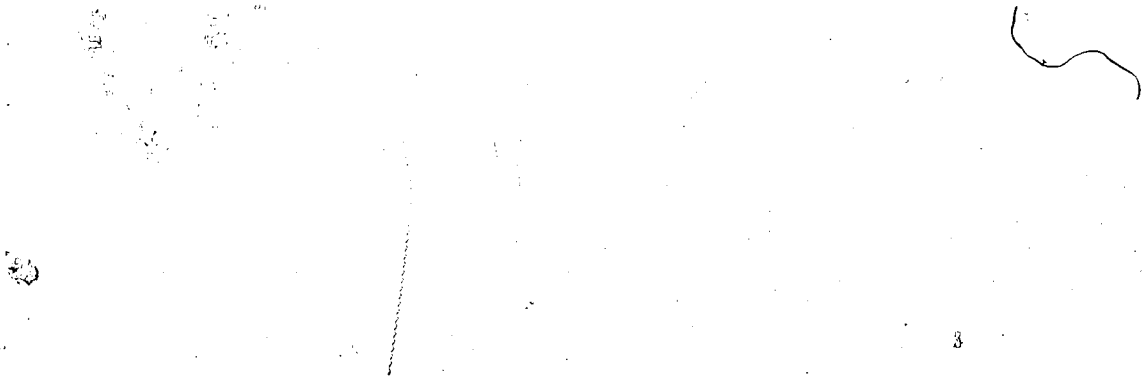
b

354

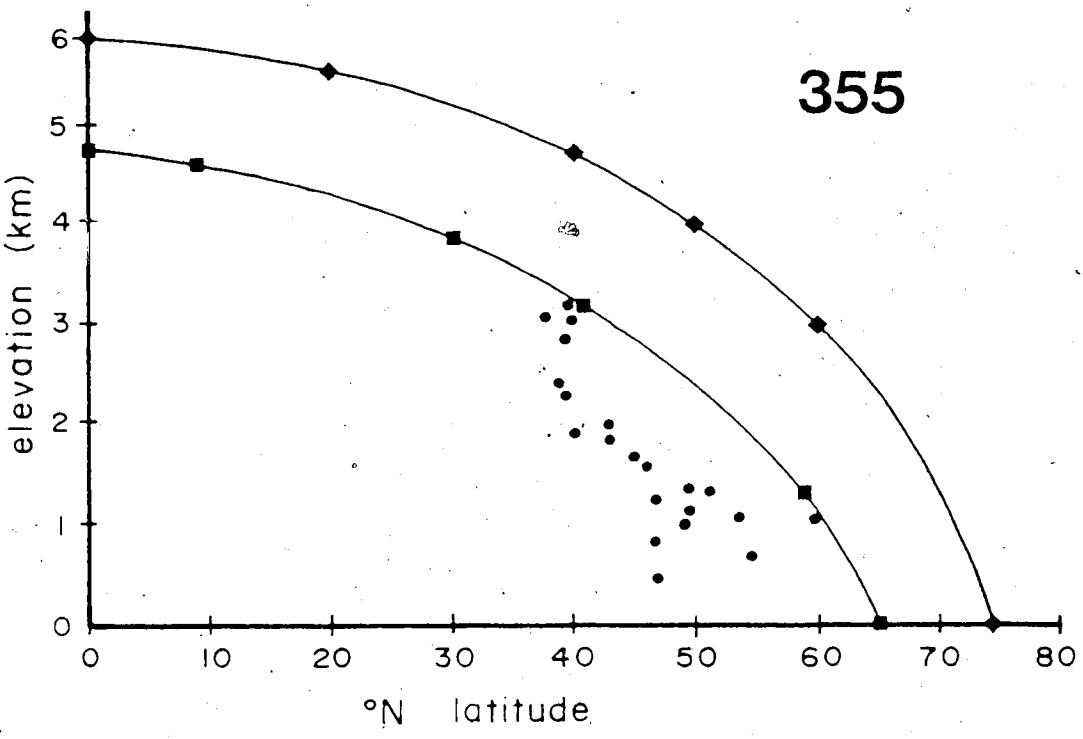


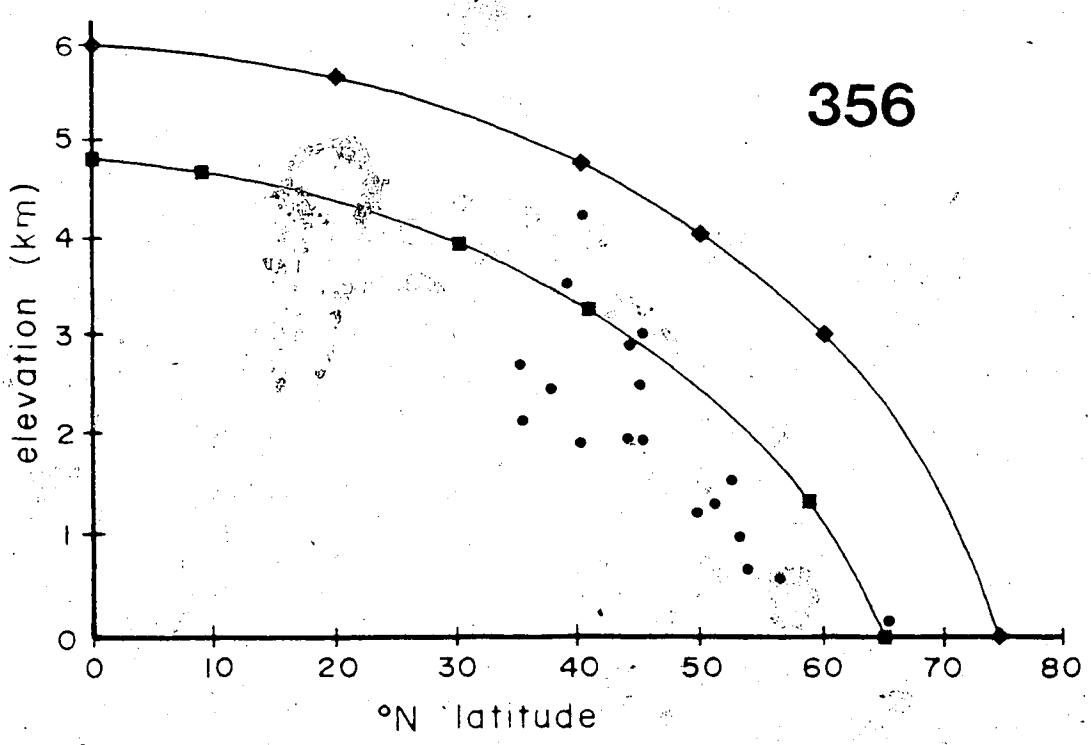
353

b

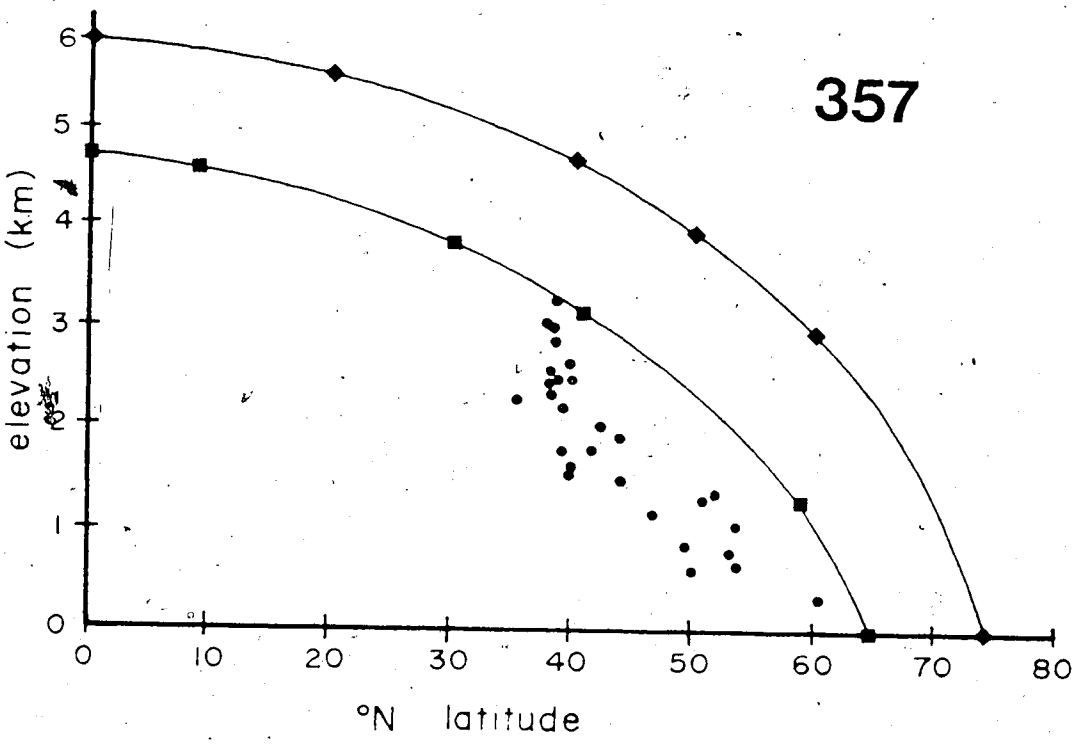


Figs. 355-356. Altitude and latitude components of distribution; curve through squares = 10° C isotherm for mean annual air temperature (approximates treeline); curve through diamonds = 0° C isotherm for mean annual air temperature (approximates line of permanent snow); isotherm data from Mani, 1962 and 1968. 355. Nebria hudsonica LeConte. 356. Nebria gyllenhali (Schönherr).


355
elevation (km)
0
1
2
3
4
5
6
0
10
20
30
40
50
60
70
80
°N latitude


356
elevation (km)
0
1
2
3
4
5
6
0
10
20
30
40
50
60
70
80
°N latitude

Figs. 357–358. Altitude and latitude components of distribution; curve through squares = 10° C isotherm for mean annual air temperature (approximates treeline); curve through diamonds = 0° C isotherm for mean annual air temperature (approximates line of permanent snow); isotherm data from Mani, 1962 and 1968. 357. Nebria obliqua LeConte. 358. Nebria purpurata LeConte.


357
elevation (km)
0
1
2
3
4
5
6
0
10
20
30
40
50
60
70
80
°N latitude

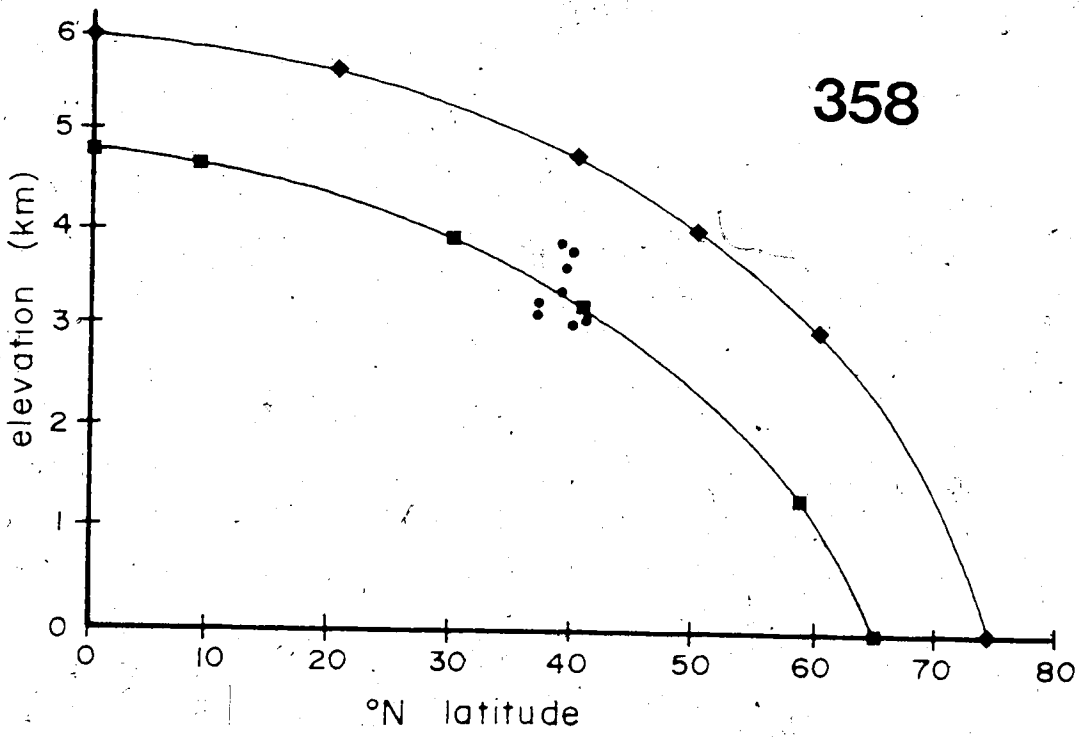

358
elevation (km)
0
1
2
3
4
5
6
0
10
20
30
40
50
60
70
80
°N latitude

Fig. 359. Relationship between proximity to water and altitude among Nebria, Front Range, Colorado; diamonds = Nebria obliqua LeConte; squares = Nebria hudsonica LeConte; circles = Nebria gyllenhali lindrothi new subspecies; lines connecting symbols denote range of distances from stream at which individuals were found at a given altitude; arrows indicate that individuals were also found at distances greater than 2.0 m from stream.

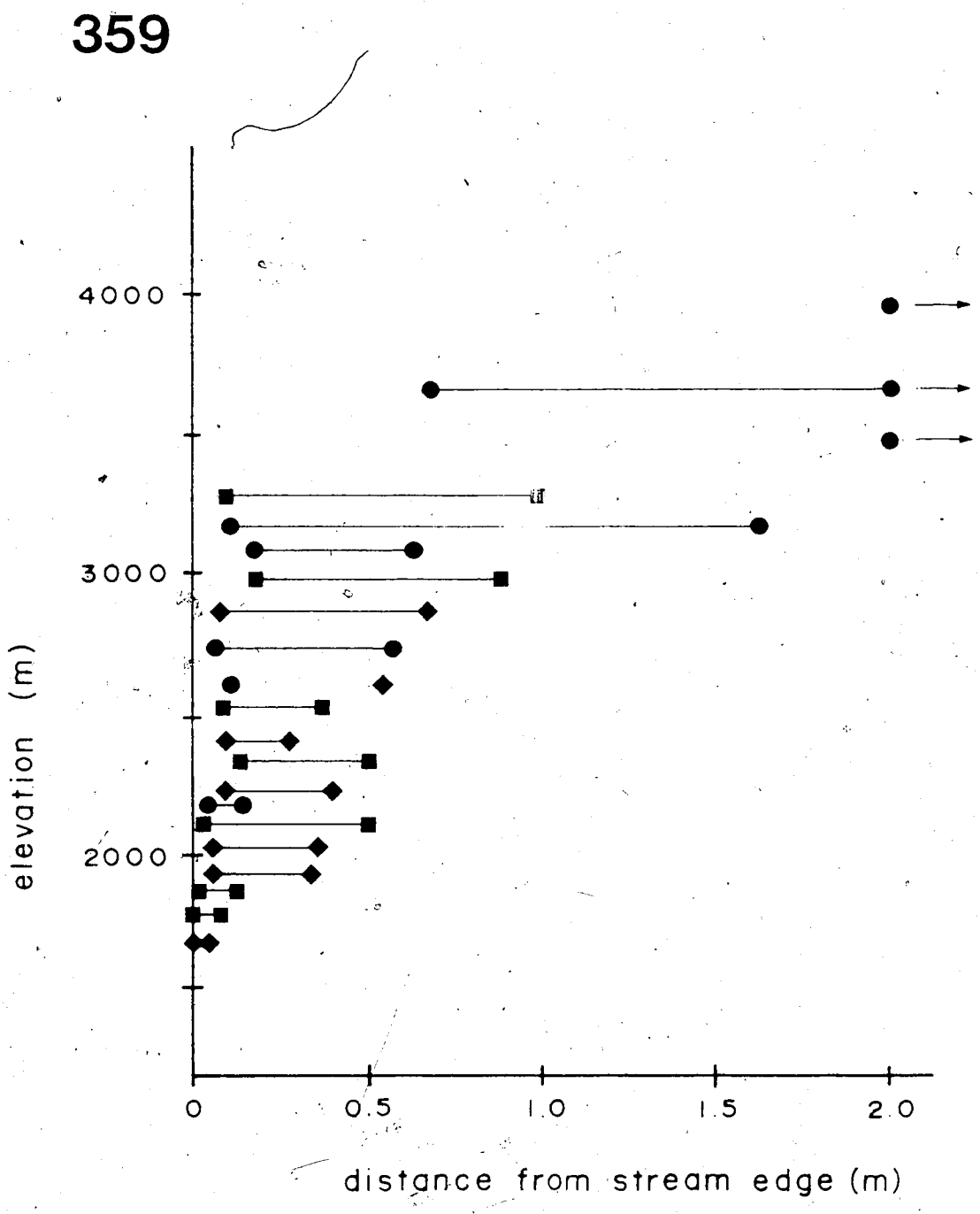
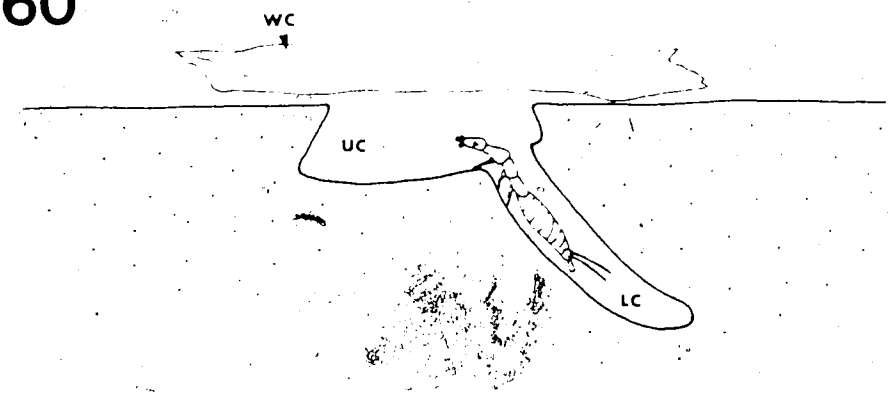

359
4000
3000
2000
elevation (m)
0
0.5
1.0
1.5
2.0
distance from stream edge (m)

Fig. 360. Cell of Nebria diversa LeConte larva (see text for discussion); LC = lower chamber; UC = upper chamber; WC = wood chip.

Fig. 361. Life cycle timing, schematic representation; solid lines denote temporal limits to frequent occurrence of individuals at a given stage of development; dashed lines denote infrequent occurence; i = adult stage; p = pupal stage; l_1, l_2, and l_3 = first, second and third larval stages, respectively; o = egg stage (see text for discussion).

360


WC
UC
LC

361

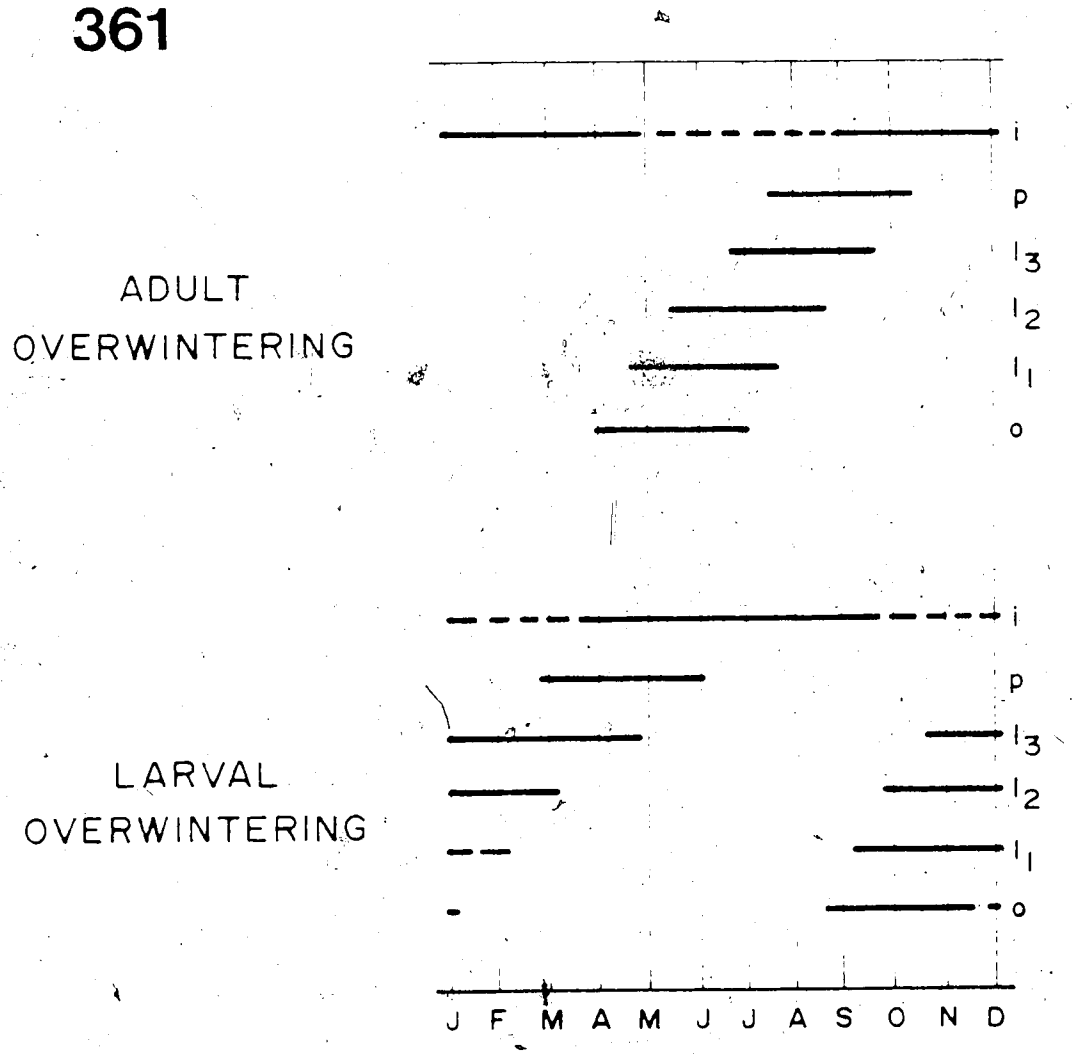
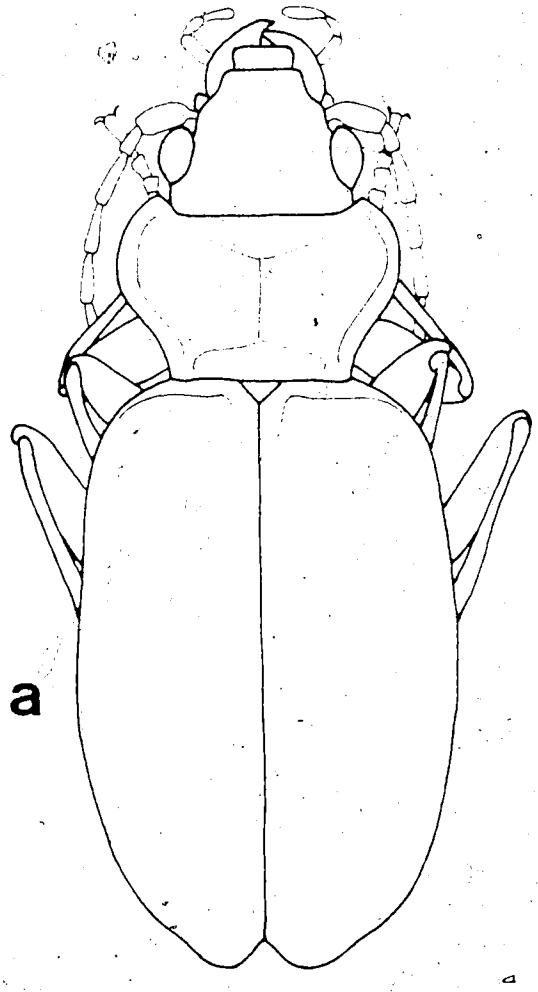

ADULT
OVERWINTERING
LARVAL
OVERWINTERING
i
p
l3
l2
l1
o
J F M A M J J A S O N D

Fig. 362. Thoracic venter, Nebria eschscholtzii Ménétriés (Rogue River, Oregon), bearing mites [scanning electron micrograph by G. Braybrook]. Scale: 1.0 cm = .250 mm. Fig. 363. Histiosoma maritimus (Oudemans) (Acarina: Anoetidae) immature on the above N. eschscholtzii specimen [mite identification by R. O. Schuster; scanning electron micrograph by G. Braybrook]. Scale: 1.0 cm = 70 .

362

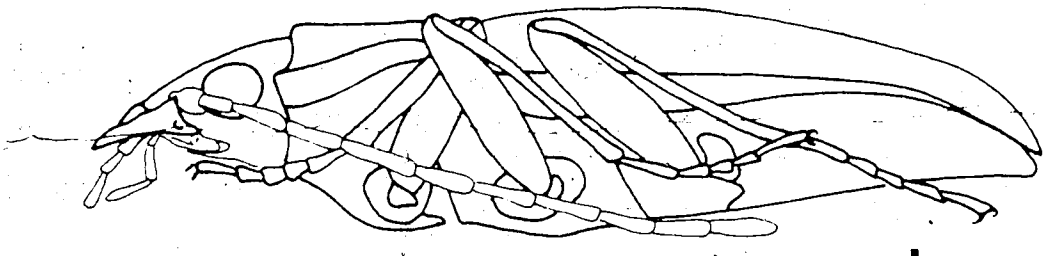
363

Fig. 364. Floating posture, Nebria piperi Van Dyke, ([a] dorsal aspect, [b] left lateral aspect).



a

364



b

Fig. 365. Comparison in species group composition between Lindroth's (1961a) classification of Nearctic taxa and two proposed earlier. Names in quotation marks in boxes refer to an author's name for a species group; numbers in parentheses in boxes refer to the number of species included by the author that are also recognized here as distinct species; lines connecting boxes indicate one or more species in common; numbers in parentheses associated with connecting lines indicate the number of species in common.

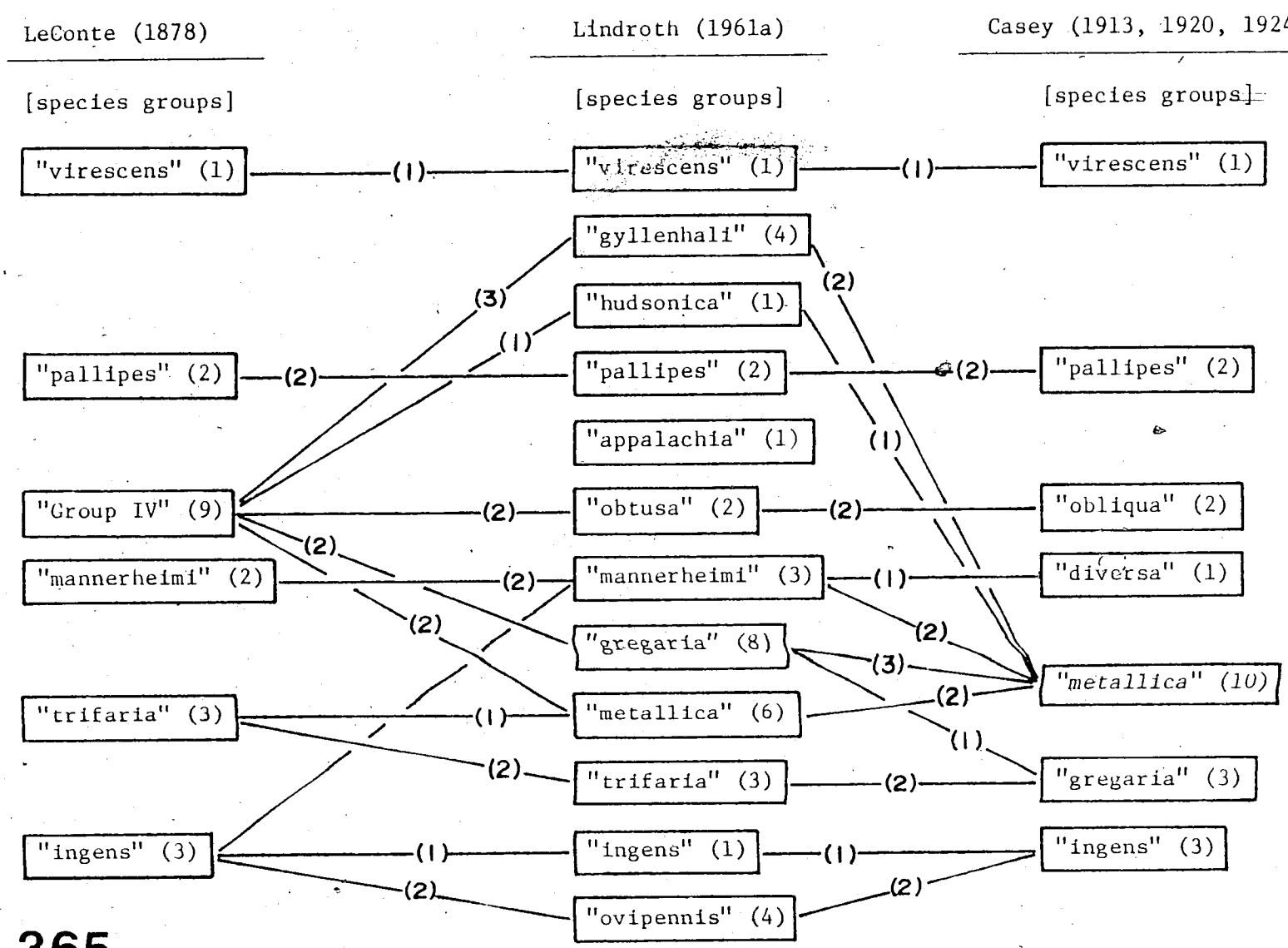

LeConte (1878)
[species groups]
"virescens" (1)
"pallipes" (2)
"Group IV" (9)
"mannerheimi" (2)
"trifaria" (3)
"ingens" (3)
Lindroth (1961a)
[species groups]
"virescens" (1)
"gyllenhali" (4)
"hudsonica" (1)
"pallipes" (2)
"appalachia" (1)
"obtusa" (2)
"mannerheimi" (3)
"gregaria" (8)
"metallica" (6)
"trifaria" (3)
"ingens" (1)
"ovipennis" (4)
Casey (1913, 1920, 1924)
[species groups]
"virescens" (1)
"pallipes" (2)
"obliqua" (2)
"diversa" (1)
"metallica" (10)
"gregaria" (3)
"ingens" (3)

Fig. 366. Comparison in species group composition between Lindroth's (1961a) classification of Nearctic taxa and three proposed later (including that proposed here). Names in quotation marks in boxes refer to an author's name for a species group; numbers in parentheses in boxes refer to the number of species included by the author that are also recognized here as distinct species; lines connecting boxes indicate one or more species in common; numbers in parentheses associated with connecting lines indicate the number of species in common.

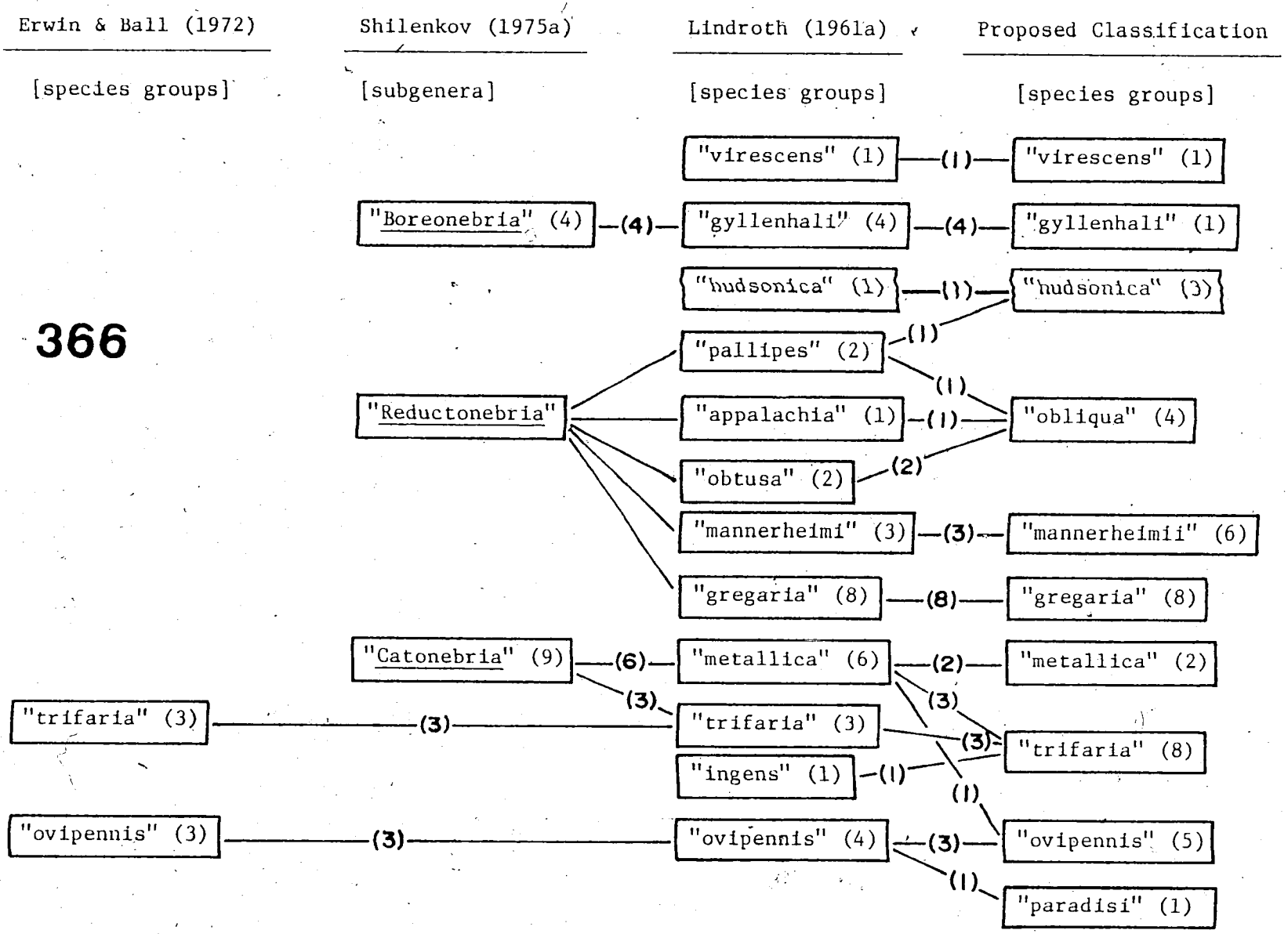
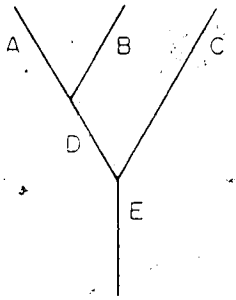
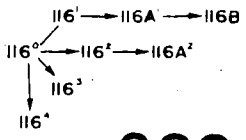

Erwin & Ball (1972)
[species groups]
Shilenkov (1975a)
[subgenera]
Lindroth (1961a)
[species groups]
Proposed Classification
[species groups]
"virescens" (1)
(1)
"virescens" (1)
"Boreonebria" (4)
(4)
"gyllenhali" (4)
(4)
"gyllenhali" (1)
"hudsonica" (1)
(1)
"hudsonica" (3)
(1)
"pallipes" (2)
(1)
"Reductonebria"
"appalachia" (1)
(1)
"obliqua" (4)
(2)
"obtusa" (2)
"mannerheimi" (3)
(3)
"mannerheimii" (6)
"gregaria" (8)
(8)
"gregaria" (8)
"Catonebria" (9)
(6)
"metallica" (6)
(2)
"metallica" (2)
(3)
(3)
"trifaria" (3)
(3)
"trifaria" (3)
(3)
"trifaria" (8)
"ingens" (1)
(1)
(1)
"ovipennis" (3)
(3)
"ovipennis" (4)
(3)
"ovipennis" (5)
(1)
"paradisi" (1)

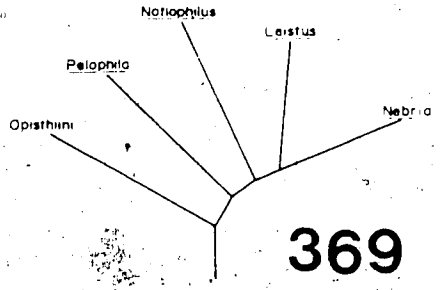
Fig. 367. Sample cladogram reflecting relationships among extant taxa, A, B, and C; D and E represent hypothetical common ancestors. Fig. 368. Hypothetical reconstruction of evolutionary sequence (transformation series) of character states of character no. 116, shape (lateral aspect) of the pre-apical shaft of the male median lobe (see Table 15 for explanation of code for character states). Fig. 369. Cladogram illustrating the hypothetical set of phylogenetic relationships among Nebria and related genera used as the basis for "ex-group" comparisons in cladistic analysis. Fig. 370. An example of use of "character correlation" in cladistic analysis. A. Circles on lines indicate distribution of character state(s) determined, with relatively high confidence, to be apotypic [representation in members of taxa A and B has been observed, that in members of D is inferred]. B. and C. Circles on lines indicate distribution of a character state evolutionary status of which is uncertain [only representation in members of A and C has been observed; alternatives for representation in D and E are inferred]. Fig. 371. Illustration of a hypothetical evolutionary sequence, including an initial pattern of geographical (clinal) variation, followed by two cycles of range fractionation which result (eventually) in speciation; vertical double bars denote geographical barriers; underlining brackets group populations considered conspecific.



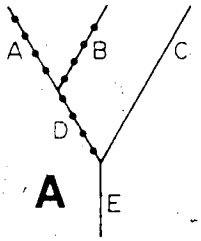
367



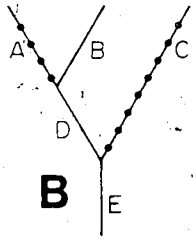
368



369

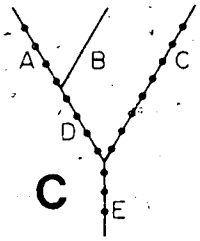


A

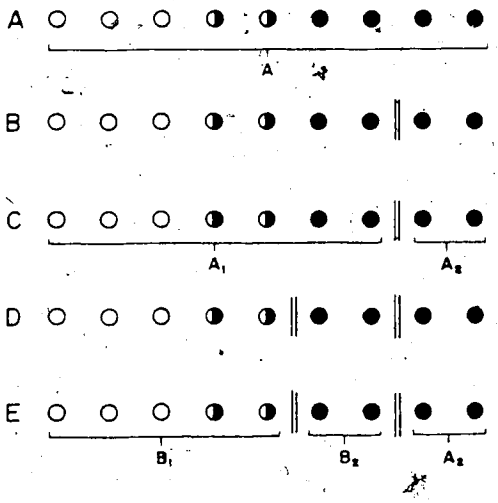


B

370



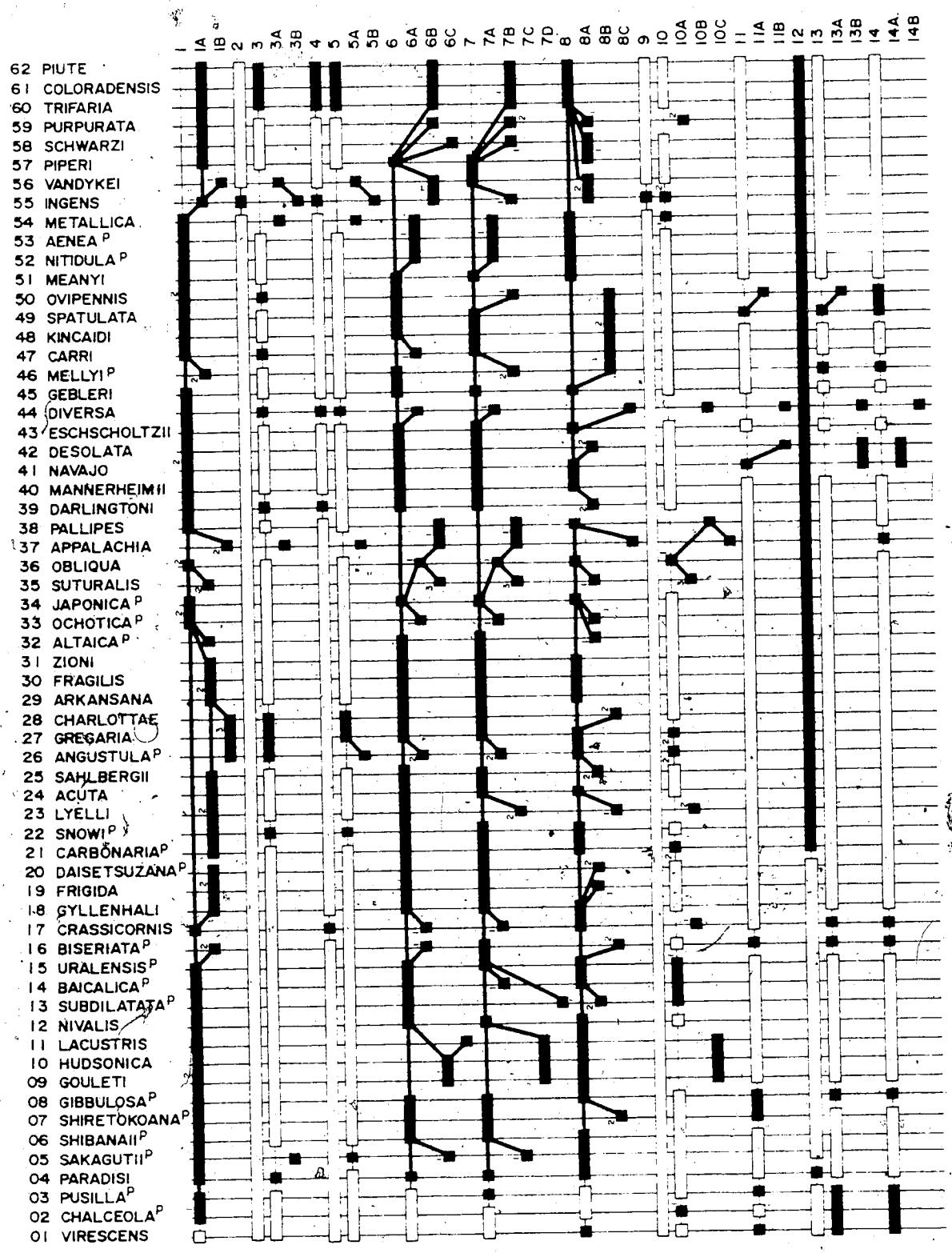
C



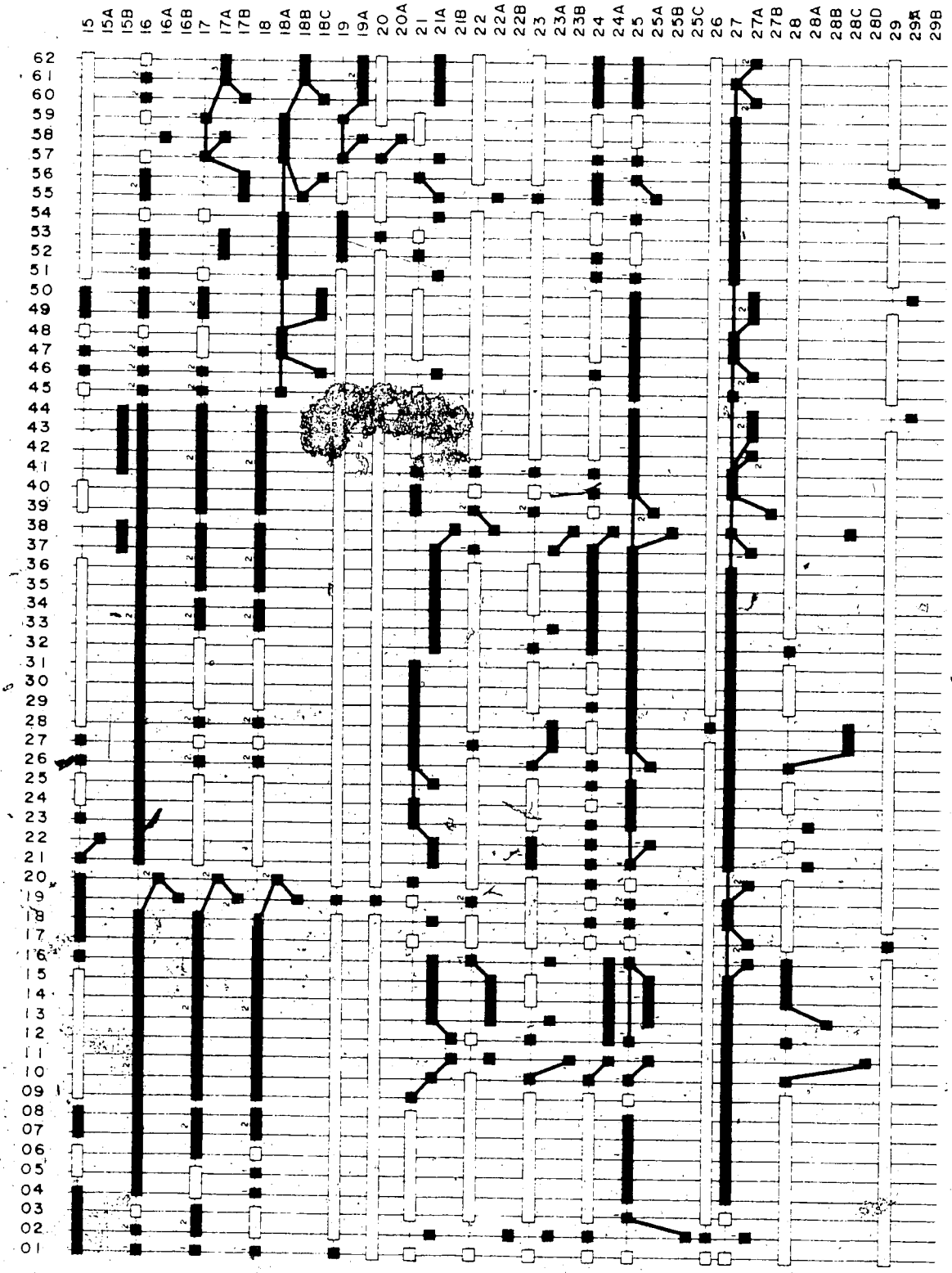
371

Fig. 372. Distribution of character states among Nearctic Nebria species and their Palaearctic relatives (designated by superscript "p"). This figure is presented in lieu of a narrative report on character state distributions; and it is to be used in concert with Tables 14 and 15, the latter of which explains the alpha-numeric code used here for characters and character states. Reference to the figure and tables should permit the reader to retrieve data on single taxa or groups of same, or on given characters or distributions of given character states. Various characters for which the only apotypic states represented are those autapotypic for members of single species have been omitted from both figure and tables. Black rectangles indicate representation of states interpreted as apotypic; white rectangles denote pleisiotypic states. Where apotypic states are shared AND this synapotypy is interpreted as due to inheritance from a common ancestor, a continuous black rectangle appears, linking columns for species concerned. Further evolutionary modifications of primary apotypic character states (i.e. secondary, tertiary, etc. apotypic states) are presented on subsequent rows designated, sequentially, as A, B, C etc. Rectangles representing all apotypic states interpreted as synapotypic at a primary level (i.e. derived from a common apotypic [but relatively pleisiotypic] state) are linked to rectangles representing the stem state by thick lines if they are in different rows (equivalent to continuous rectangles in the same row). Where two or more relatively apotypic states have developed from one relatively pleisiotypic state, each of the former is designated by a superscript number over appropriate rectangles. Question marks ("?") denote state representations yet unknown.

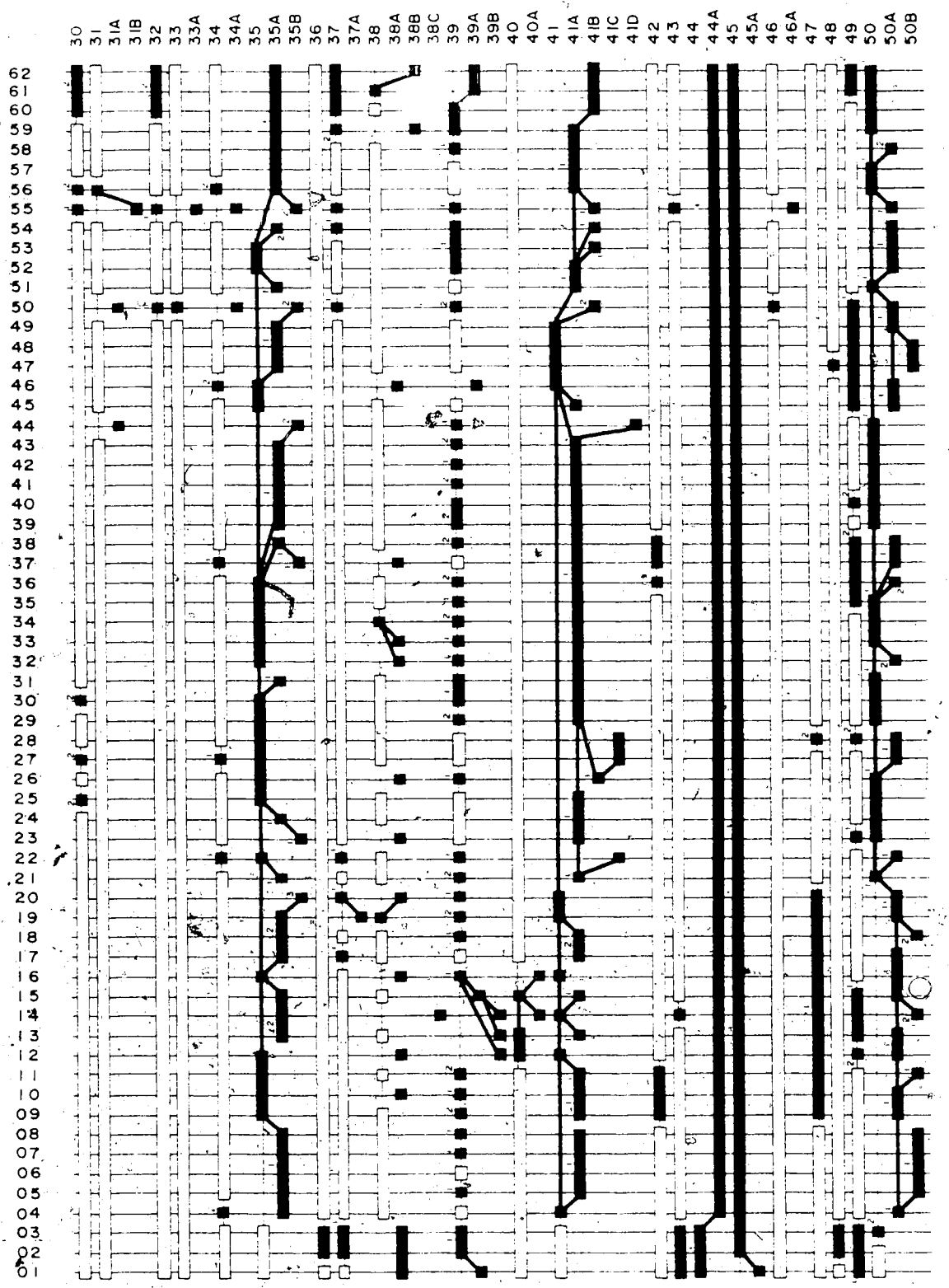
372


1 1A 1B 2 3 3A 3B 4 5 5A 5B 6 6A 6B 6C 7 7A 7B 7C 7D 8 8A 8B 8C 9 10 10A 10B 10C 11 11A 11B 12 13 13A 13B 14 14A 14B
62 PIUTE
61 COLORADENSIS
60 TRIFARIA
59 PURPURATA
58 SCHWARZI
57 PIPERI
56 VANDYKEI
55 INGENS
54 METALLICA
53 AENEA P
52 NITIDULA P
51 MEANYI
50 OVIPENNIS
49 SPATULATA
48 KINCAIDI
47 CARRI
46 MELLYI P
45 GEBLERI
44 DIVERSA
43 ESCHSCHOLTZII
42 DESOLATA
41 NAVAJO
40 MANNERHEIMII
39 DARLINGTONI
38 PALLIPES
37 APPALACHIA
36 OBLIQUA
35 SUTURALIS
34 JAPONICA P
33 OCHOTICA P
32 ALTAICA P
31 ZIONI
30 FRAGILIS
29 ARKANSANA
28 CHARLOTTAE
27 GREGARIA
26 ANGUSTULA P
25 SAHLBERGII
24 ACUTA
23 LYELLI
22 SNOWI P
21 CARBONARIA P
20 DAISETSUZANA P
19 FRIGIDA
18 GYLLENHALI
17 CRASSICORNIS
16 BISERIATA P
15 URALENSIS P
14 BAICALICA P
13 SUBDILATATA P
12 NIVALIS
11 LACUSTRIS
10 HUDSONICA
09 GOULETI
08 GIBBULOSA P
07 SHIRETOKOANA P
06 SHIBANAII P
05 SAKAGUTII P
04 PARADISI
03 PUSILLA P
02 CHALCEOLA P
01 VIRESCENS

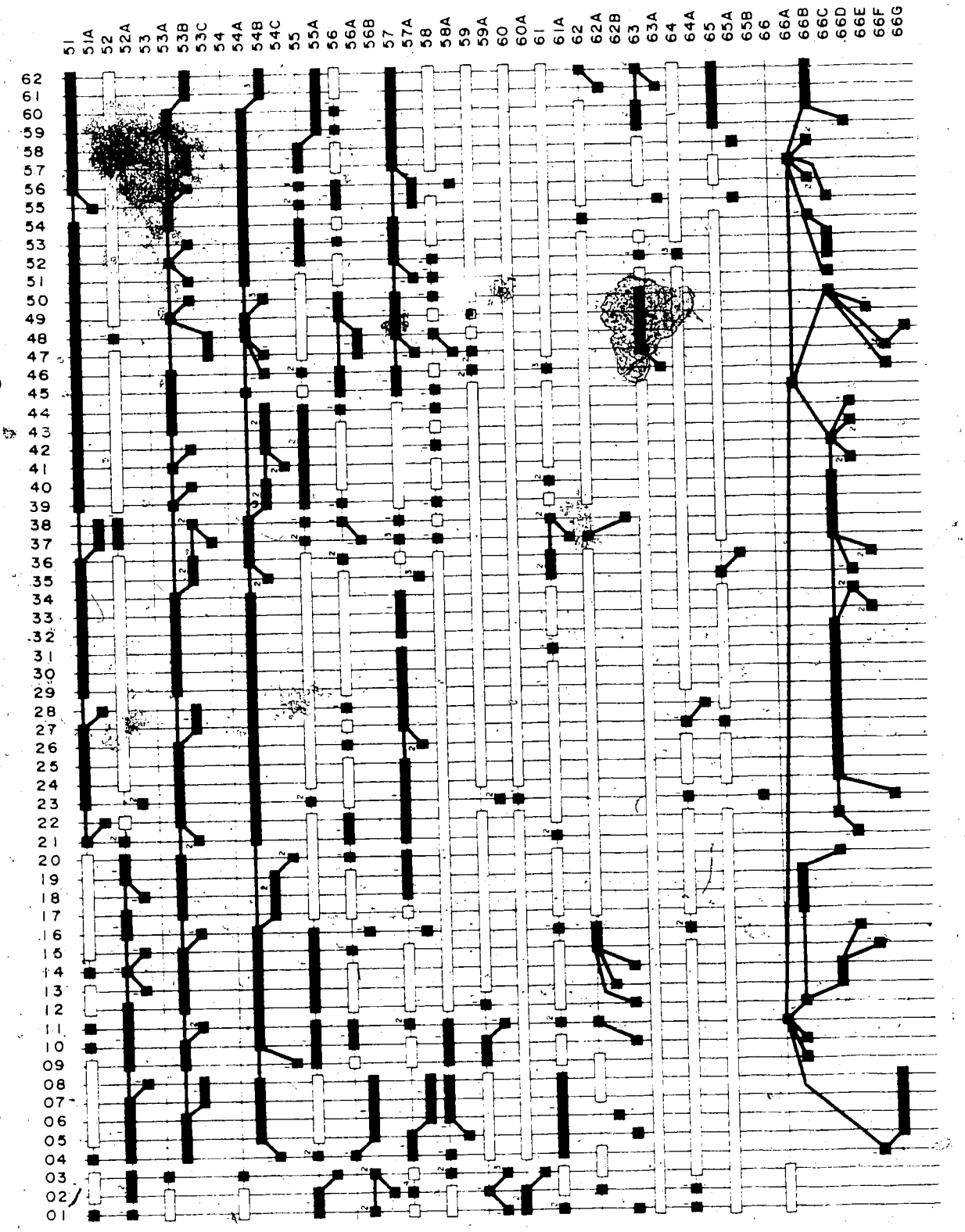
372 cont.


15
15A
15B
16
16A
16B
17
17A
17B
18
18A
18B
18C
19
19A
20
20A
21
21A
21B
22
22A
22B
23
23A
23B
24
24A
25
25A
25B
25C
26
27
27A
27B
28
28A
28B
28C
28D
29
29A
29B
62
61
60
59
58
57
56
55
54
53
52
51
50
49
48
47
46
45
44
43
42
41
40
39
38
37
36
35
34
33
32
31
30
29
28
27
26
25
24
23
22
21
20
19
18
17
16
15
14
13
12
11
10
09
08
07
06
05
04
03
02
01

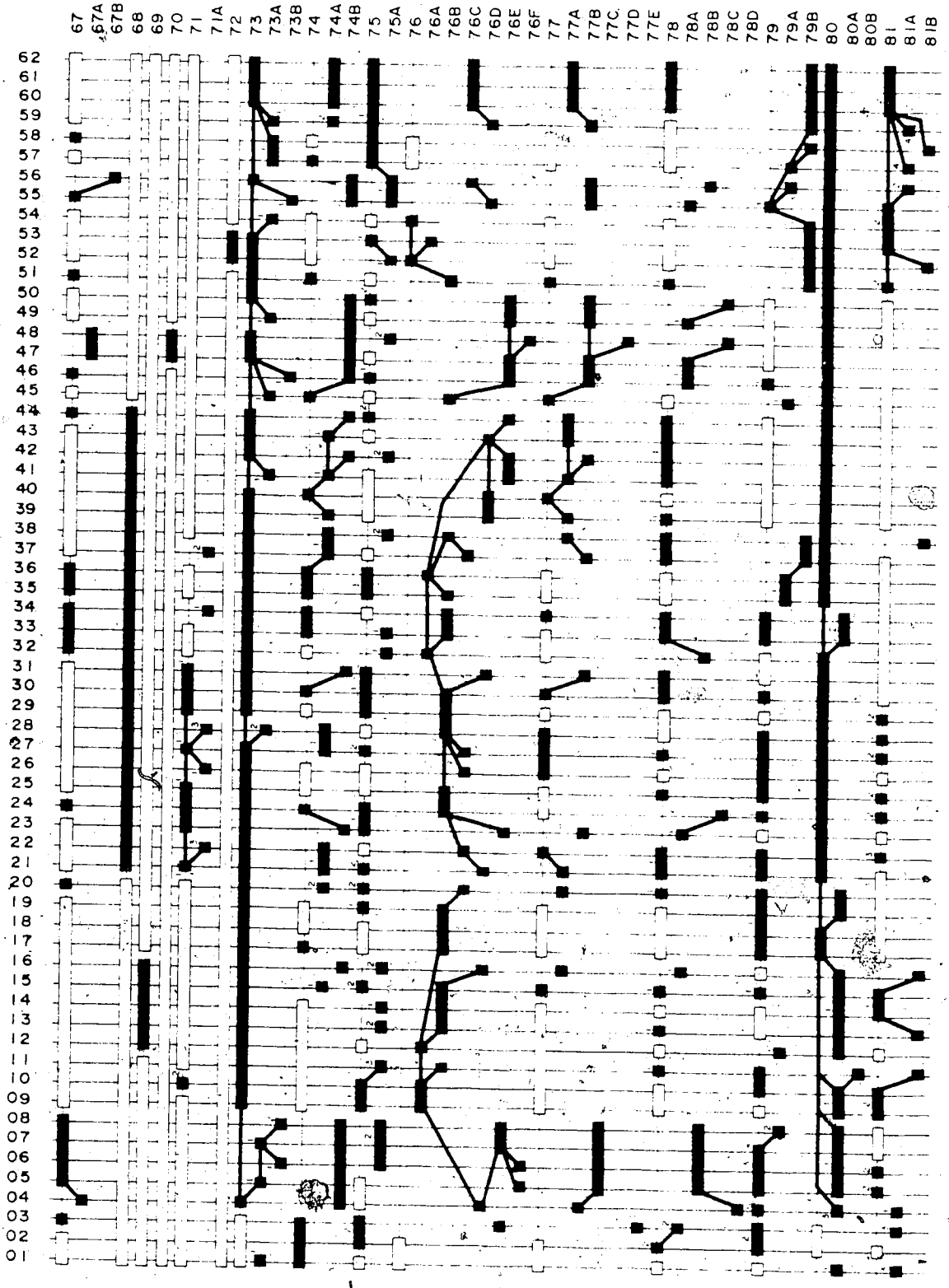
372 cont.


30
31
31A
31B
32
33
33A
34
34A
35
35A
35B
36
37
37A
38
38A
38B
38C
39
39A
39B
40
40A
41
41A
41B
41C
41D
42
43
44
44A
45
45A
46
46A
47
48
49
50
50A
50B
62
61
60
59
58
57
56
55
54
53
52
51
50
49
48
47
46
45
44
43
42
41
40
39
38
37
36
35
34
33
32
31
30
29
28
27
26
25
24
23
22
21
20
19
18
17
16
15
14
13
12
11
10
09
08
07
06
05
04
03
02
01

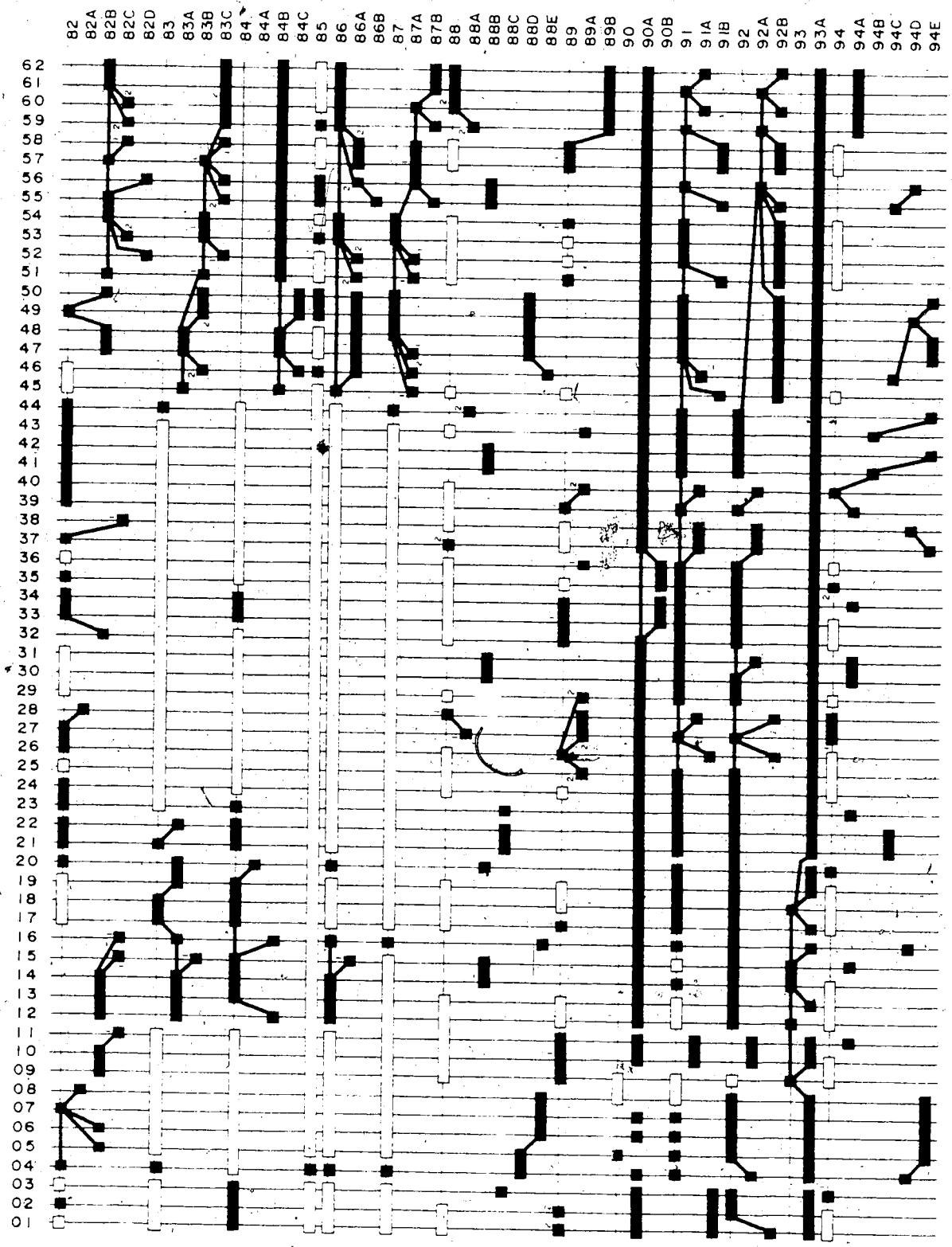
372 cont.


51
51A
52
52A
53
53A
53B
53C
54
54A
54B
54C
55
55A
56
56A
56B
57
57A
58
58A
59
59A
60
60A
61
61A
62
62A
62B
63
63A
64
64A
65
65A
65B
66
66A
66B
66C
66D
66E
66F
66G
62
61
60
59
58
57
56
55
54
53
52
51
50
49
48
47
46
45
44
43
42
41
40
39
38
37
36
35
34
33
32
31
30
29
28
27
26
25
24
23
22
21
20
19
18
17
16
15
14
13
12
11
10
09
08
07
06
05
04
03
02
01

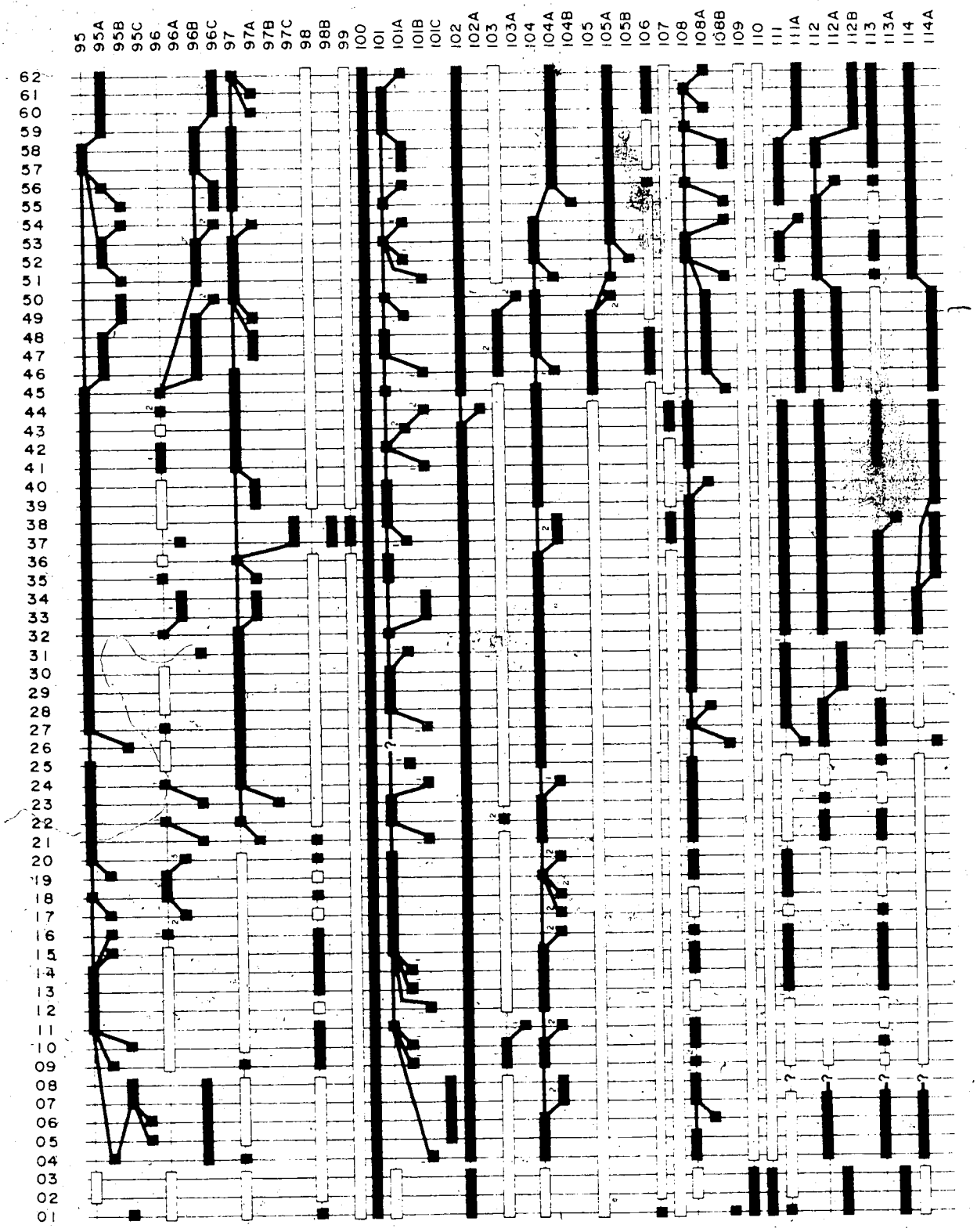
372 cont.


67
67A
67B
68
69
70
71
71A
72
73
73A
73B
74
74A
74B
75
75A
76
76A
76B
76C
76D
76E
76F
77
77A
77B
77C
77D
77E
78
78A
78B
78C
78D
79
79A
79B
80
80A
80B
81
81A
81B
62
61
60
59
58
57
56
55
54
53
52
51
50
49
48
47
46
45
44
43
42
41
40
39
38
37
36
35
34
33
32
31
30
29
28
27
26
25
24
23
22
21
20
19
18
17
16
15
14
13
12
11
10
09
08
07
06
05
04
03
02
01

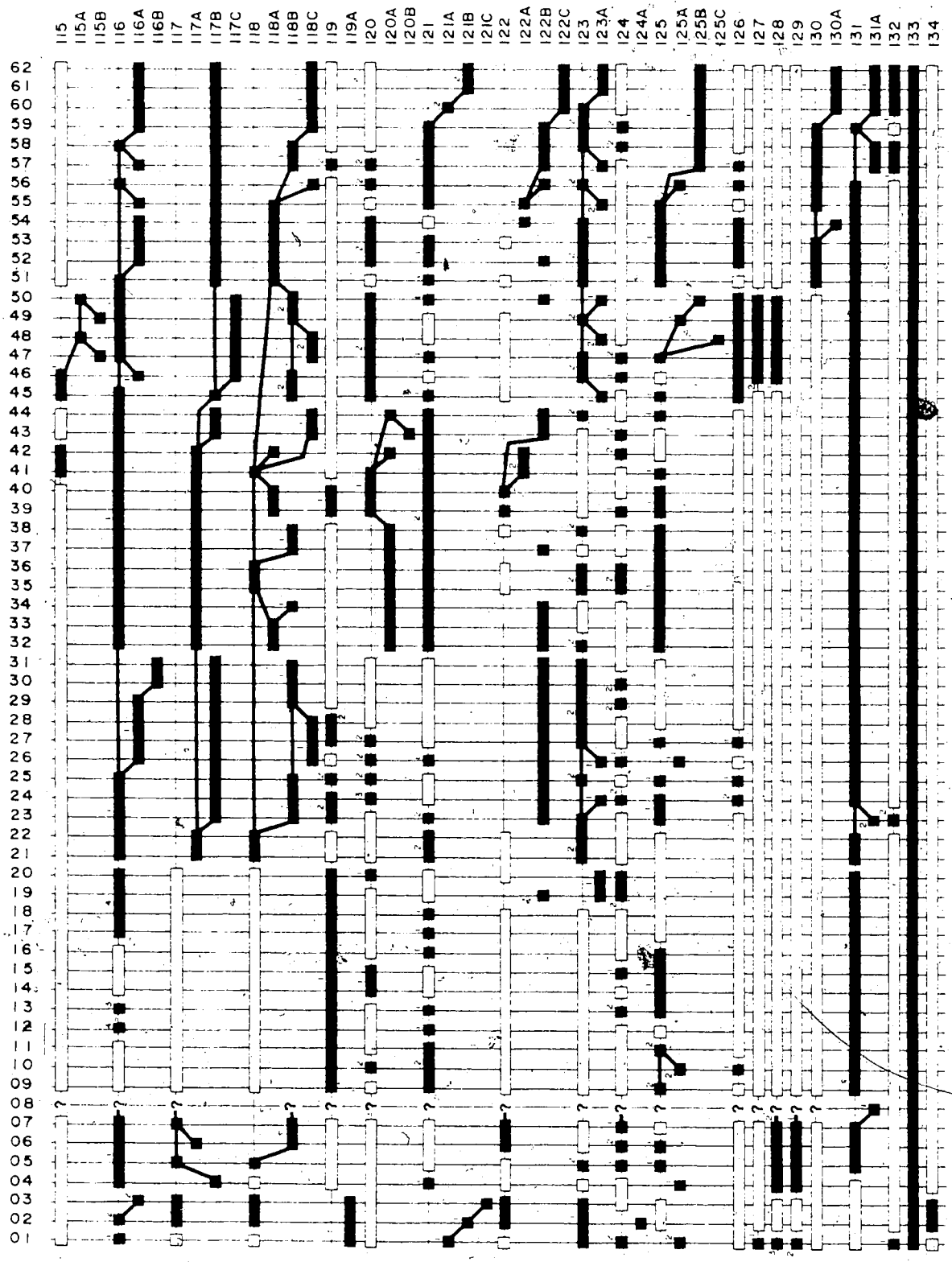
372 cont.


82
82A
82B
82C
82D
83
83A
83B
83C
84
84A
84B
84C
85
86
86A
86B
87
87A
87B
88
88A
88B
88C
88D
88E
89
89A
89B
90
90A
90B
91
91A
91B
92
92A
92B
93
93A
94
94A
94B
94C
94D
94E
62
61
60
59
58
57
56
55
54
53
52
51
50
49
48
47
46
45
44
43
42
41
40
39
38
37
36
35
34
33
32
31
30
29
28
27
26
25
24
23
22
21
20
19
18
17
16
15
14
13
12
11
10
09
08
07
06
05
04
03
02
01

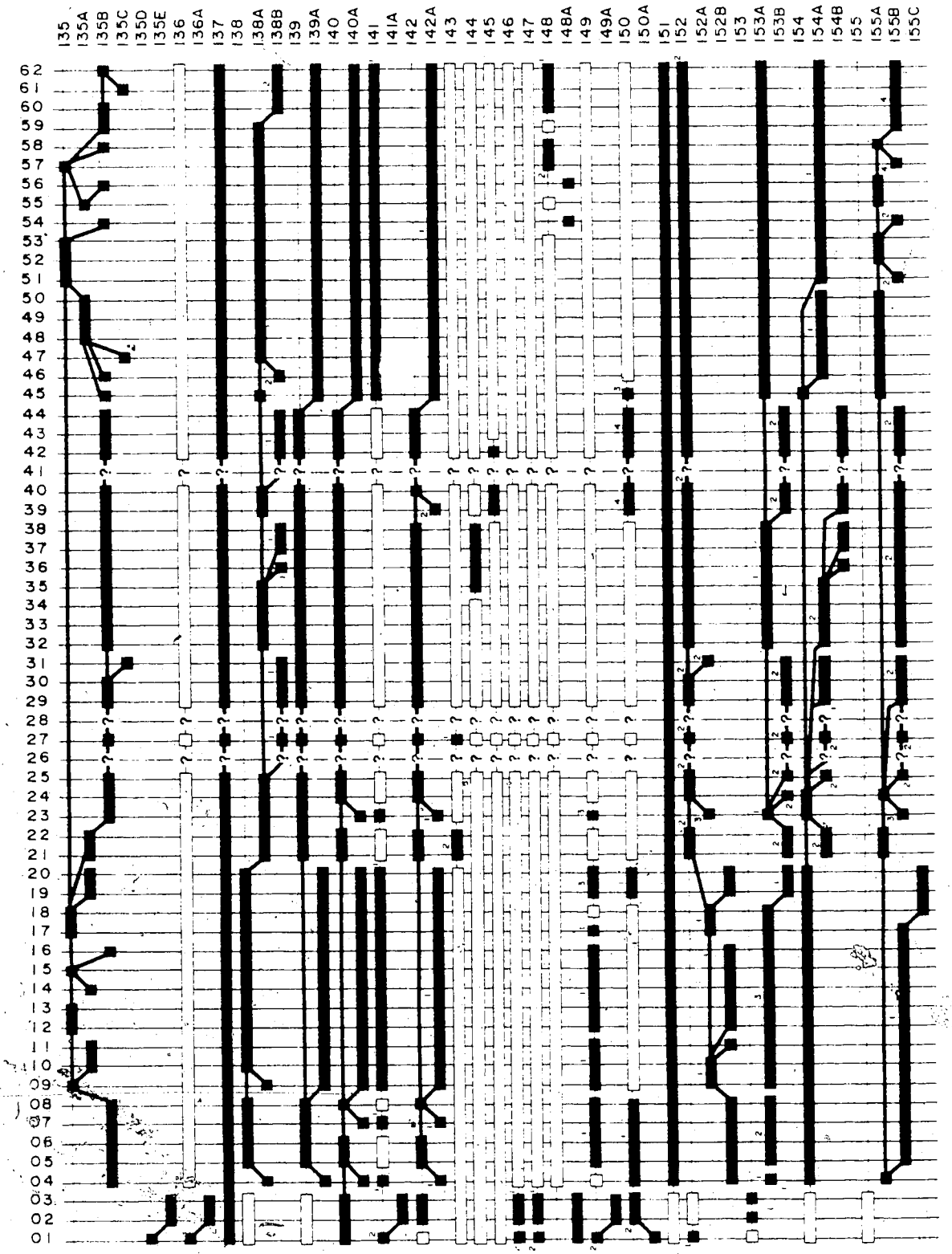
372 cont.


95
95A
95B
95C
96
96A
96B
96C
97
97A
97B
97C
98
98B
99
100
101
101A
101B
101C
102
102A
103
103A
104
104A
104B
105
105A
105B
106
107
108
108A
108B
109
110
111
111A
112
112A
112B
113
113A
114
114A
62
61
60
59
58
57
56
55
54
53
52
51
50
49
48
47
46
45
44
43
42
41
40
39
38
37
36
35
34
33
32
31
30
29
28
27
26
25
24
23
22
21
20
19
18
17
16
15
14
13
12
11
10
09
08
07
06
05
04
03
02
01

372cont.


115
115A
115B
116
116A
116B
117
117A
117B
117C
118
118A
118B
118C
119
119A
120
120A
120B
121
121A
121B
121C
122
122A
122B
122C
123
123A
124
124A
125
125A
125B
125C
126
127
128
129
130
130A
131
131A
132
133
134
62 61 60 59 58 57 56 55 54 53 52 51 50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21 20 19 18 17 16 15 14 13 12 11 10 09 08 07 06 05 04 03 02 01

372 cont.


135
135A
135B
135C
135D
135E
136
136A
137
138
138A
138B
139
139A
140
140A
141
141A
142
142A
143
144
145
146
147
148
148A
149
149A
150
150A
151
152
152A
152B
153
153A
153B
154
154A
154B
155
155A
155B
155C
62
61
60
59
58
57
56
55
54
53
52
51
50
49
48
47
46
45
44
43
42
41
40
39
38
37
36
35
34
33
32
31
30
29
28
27
26
25
24
23
22
21
20
19
18
17
16
15
14
13
12
11
10
09
08
07
06
05
04
03
02
01

372 cont.

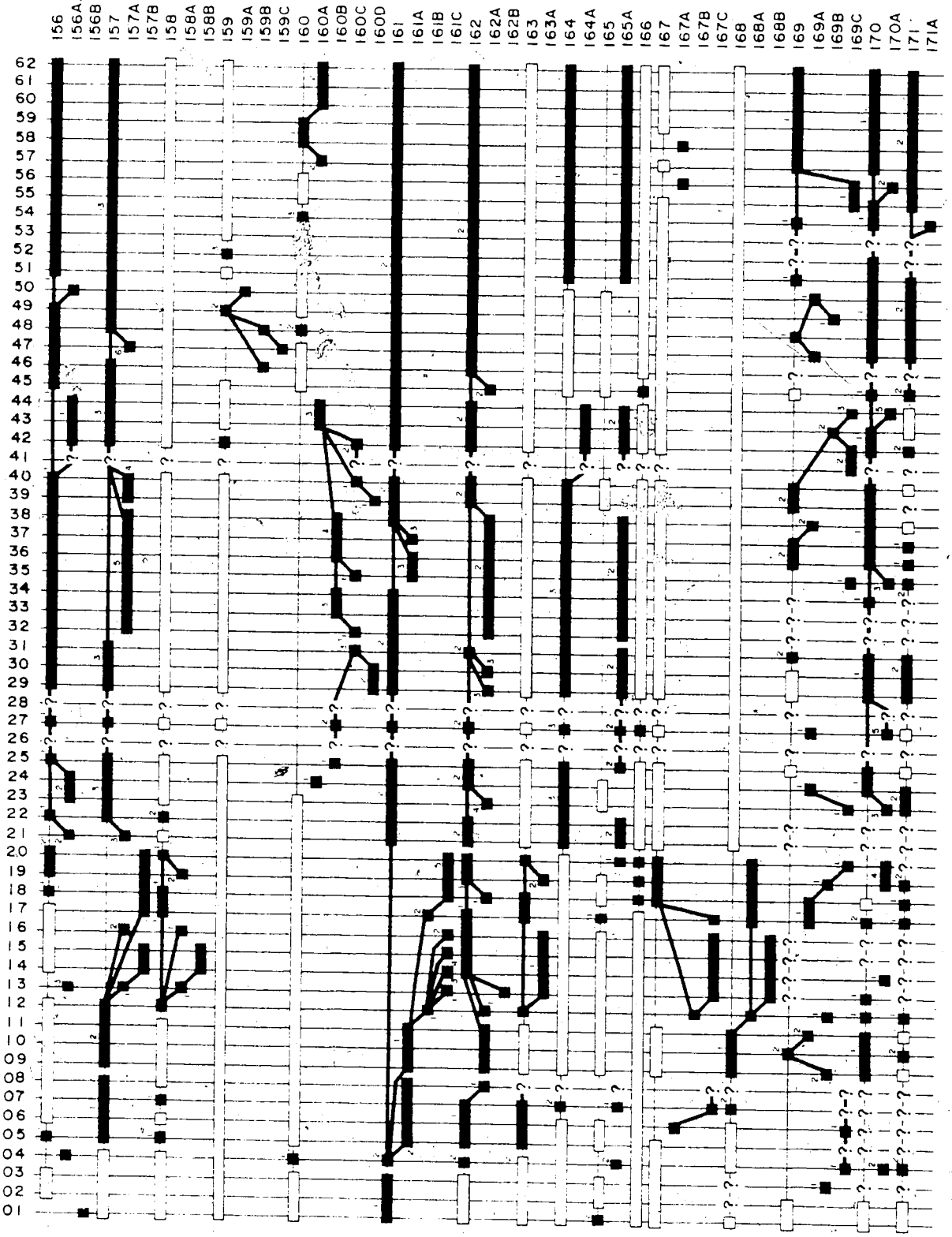
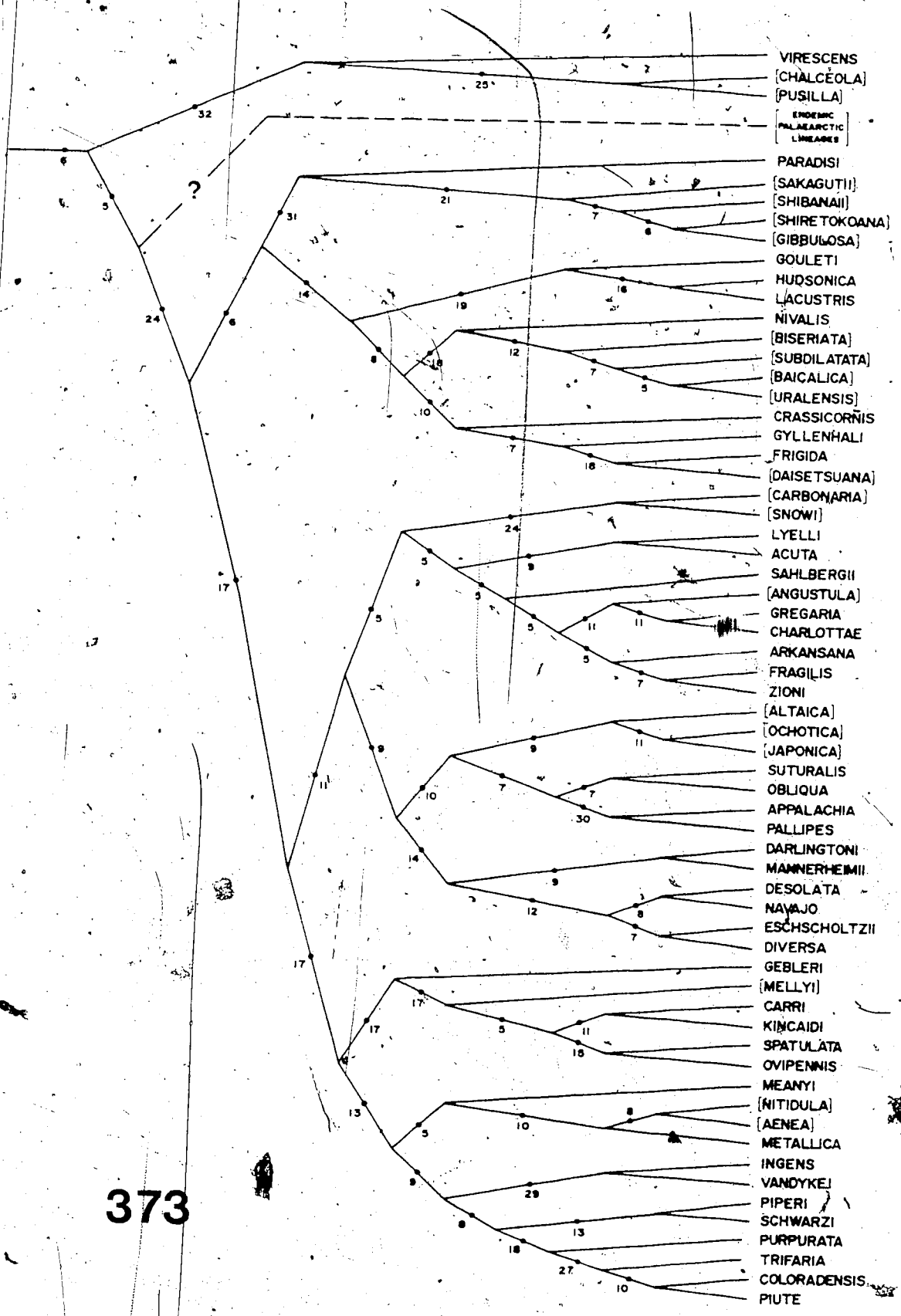
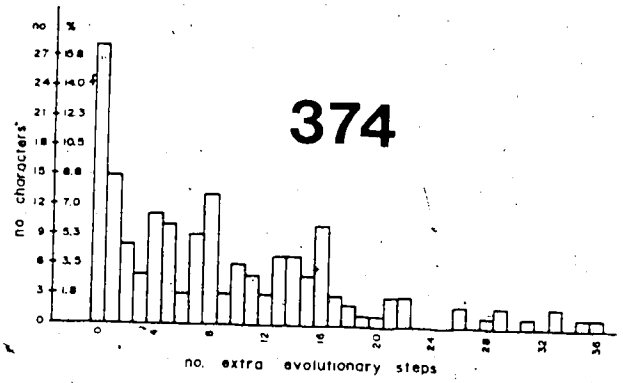

156
156A
156B
157
157A
157B
158
158A
158B
159
159A
159B
159C
160
160A
160B
160C
160D
161
161A
161B
161C
162
162A
162B
163
163A
164
164A
165
165A
166
167
167A
167B
167C
168
168A
168B
169
169A
169B
169C
170
170A
171
171A
62
61
60
59
58
57
56
55
54
53
52
51
50
49
48
47
46
45
44
43
42
41
40
39
38
37
36
35
34
33
32
31
30
29
28
27
26
25
24
23
22
21
20
19
18
17
16
15
14
13
12
11
10
09
08
07
06
05
04
03
02
01

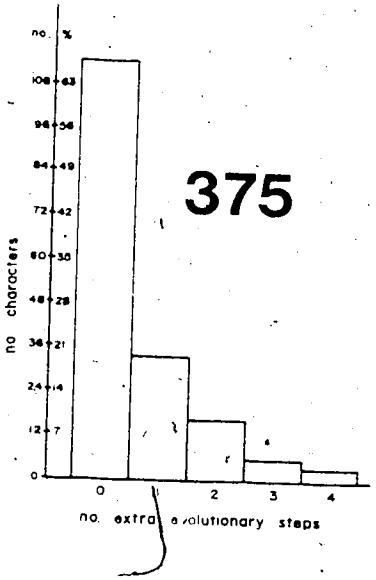
Fig. 373. Cladogram illustrating proposed phylogenetic relationships among Nearctic Nebria species and their Palaearctic relatives (names of the latter appear in brackets). Numbers beside solid dots on line segments denote the number of synapotypic character states shared by members of the monophyletic group including the hypothetical stem species (represented by the line segment) and all its descendant (extant) species.

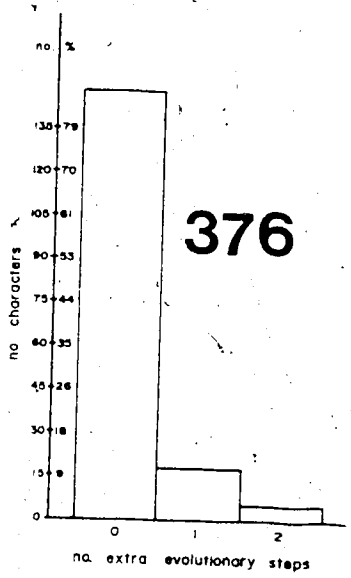

VIRESCENS
[CHALCEOLA]
[PUSILLA]
[ENDEMIC PALAEARCTIC LINEAGES]
PARADISI
[SAKAGUTII]
[SHIBANAII]
[SHIRETOKOANA]
[GIBBULOSA]
GOULETI
HUDSONICA
LACUSTRIS
NIVALIS
[BISERIATA]
[SUBDILATATA]
[BAICALICA]
[URALENSIS]
CRASSICORNIS
GYLLENHALI
FRIGIDA
[DAISETSUANA]
[CARBONARIA]
[SNOWI]
LYELLI
ACUTA
SAHLBERGII
[ANGUSTULA]
GREGARIA
CHARLOTTAE
ARKANSANA
FRAGILIS
ZIONI
[ALTAICA]
[OCHOTICA]
[JAPONICA]
SUTURALIS
OBLIQUA
APPALACHIA
PALLIPES
DARLINGTONI
MANNERHEIMII
DESOLATA
NAVAJO
ESCHSCHOLTZII
DIVERSA
GEBLERI
[MELLYI]
CARRI
KINCAIDI
SPATULATA
OVIPENNIS
MEANYI
[NITIDULA]
[AENEA]
METALLICA
INGENS
VANDYKEI
PIPERI
SCHWARZI
PURPURATA
TRIFARIA
COLORADENSIS
PIUTE

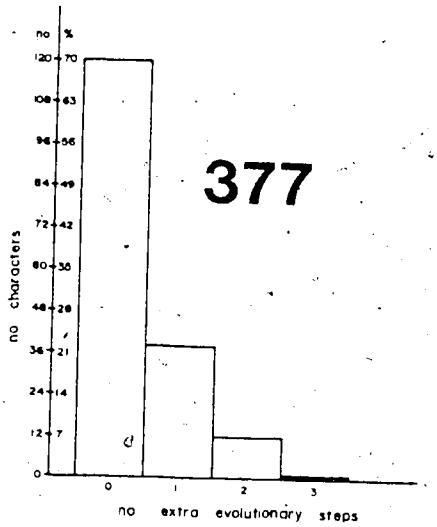
373

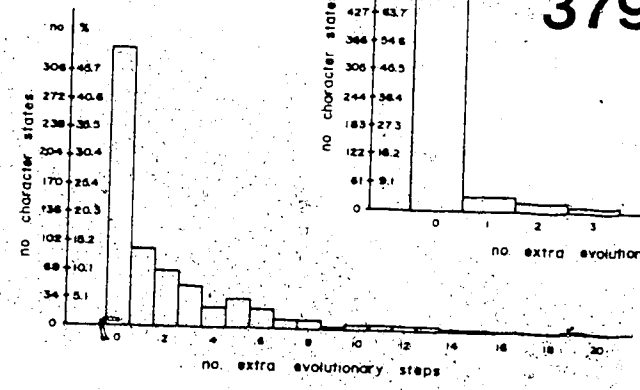
Fig. 374. Frequency distribution of characters in which a given total number of extra evolutionary steps (including both intrinsic and extrinsic steps) are required by the proposed phylogeny. Fig. 375. Frequency distribution of characters in which a given number of intrinsic extra evolutionary steps are required. Fig. 376. Frequency distribution of characters in which a given number of convergent, intrinsic steps are required. Fig. 377. Frequency distribution of characters in which a given number of reversed, intrinsic steps are required. Fig. 378. Frequency distribution of character states in which a given number of convergent, extrinsic steps are required by the proposed phylogeny. Fig. 379. Frequency distribution of character states in which a given number of reversed, extrinsic steps are required.

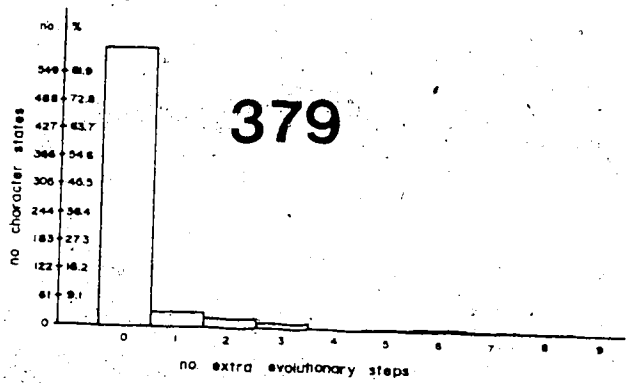

374
no characters
no. extra evolutionary steps


375
no characters
no. extra evolutionary steps


376
no characters
no. extra evolutionary steps

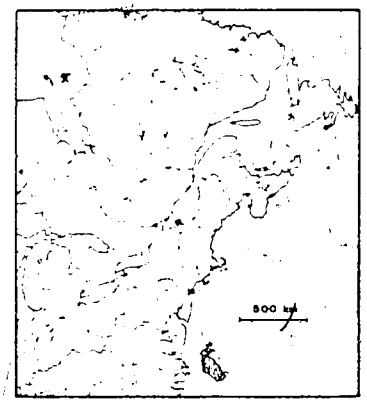

377
no characters
no extra evolutionary steps


no character states
no. extra evolutionary steps

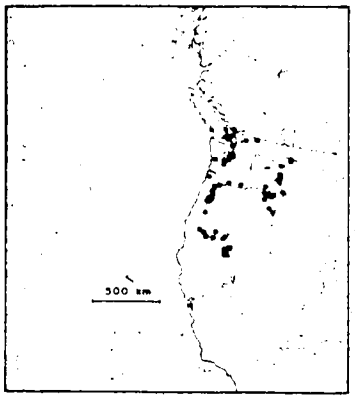

379
no character states
no. extra evolutionary steps

378

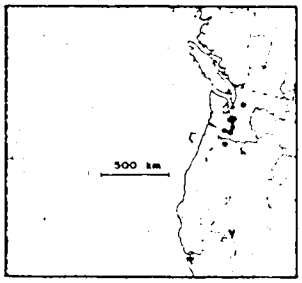
Figs. 380 - 384. Geographical distribution maps. 380. Nebria brevicollis (Fabricius). 381. Nebria virescens Horn. 382. Nebria paradisi Darlington. 383. Nebria gouleti new species. 384. Nebria hudsonica LeConte (solid circles), N. lacustris lacustris Casey (open circles), and N. lacustris bellorum new subspecies (solid triangles).



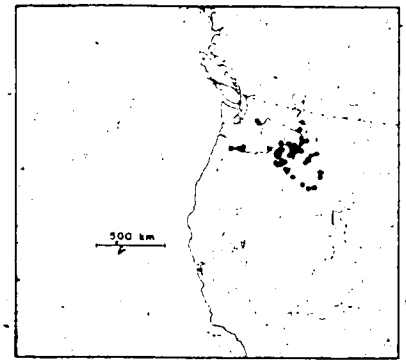
380



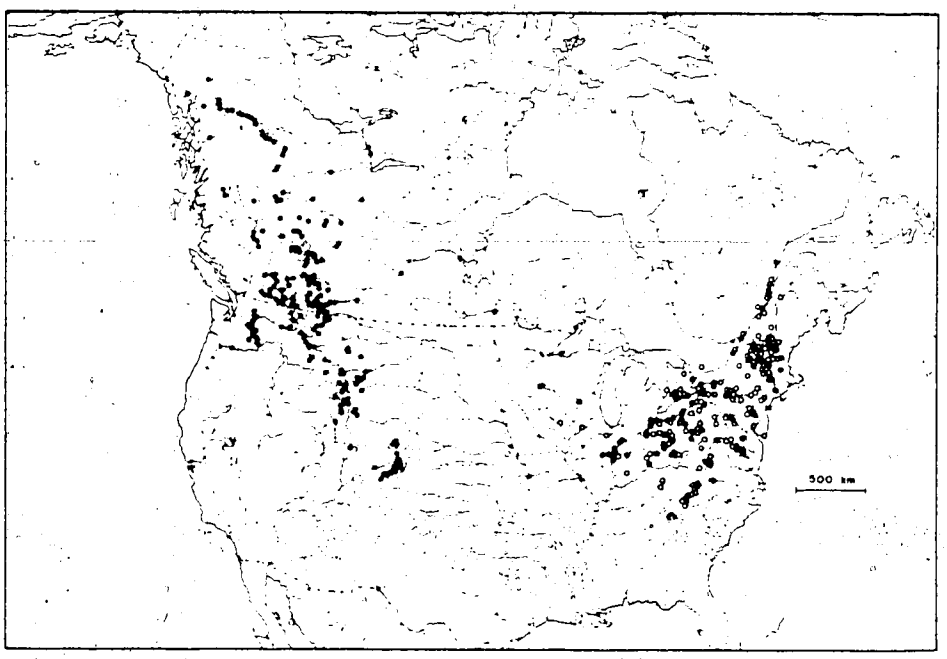
381



382



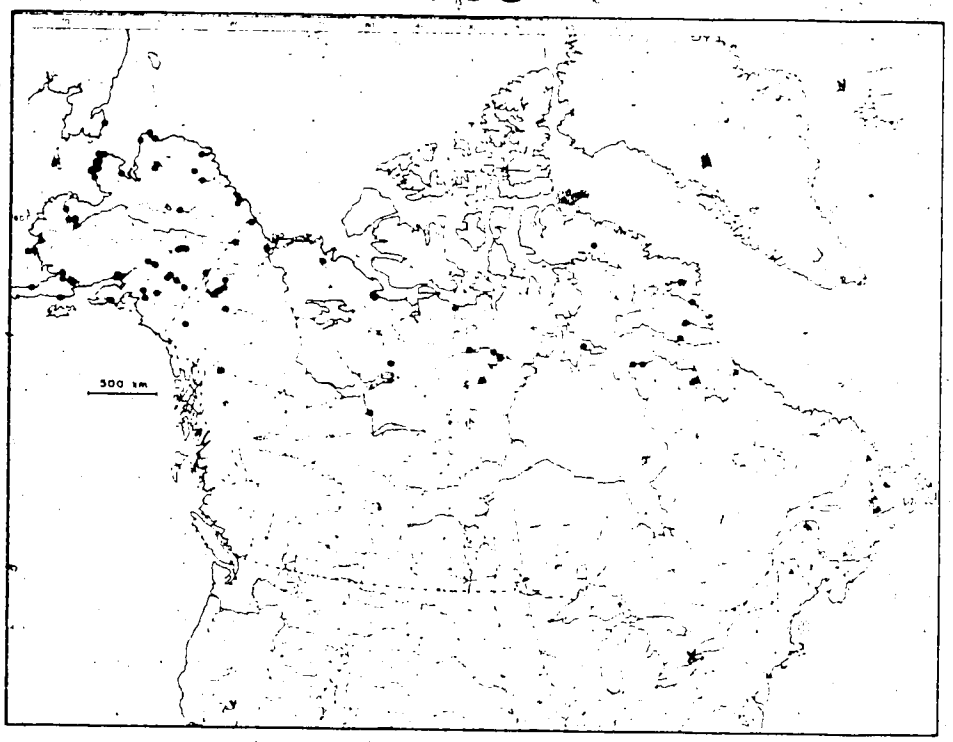
383

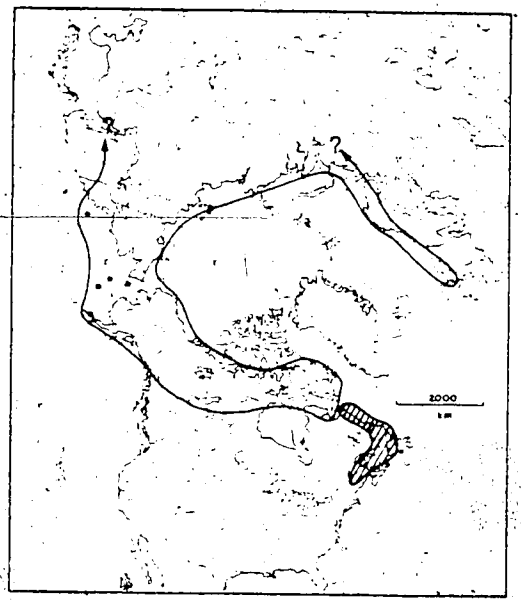


384

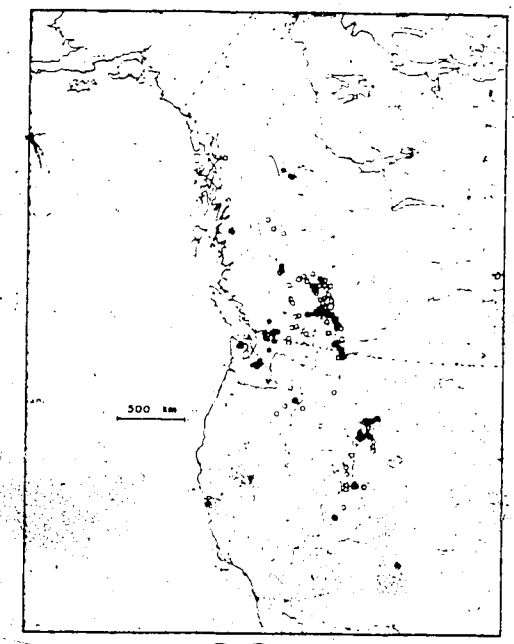
Figs. 385 - 387. Geographical distribution maps. 385. Nebria nivalis nivalis (Paykull) (solid circles) and N. nivalis gaspesiana new subspecies (solid triangles); "X" denotes location of deposits yeilding N. nivalis fossils. 386. Nebria nivalis nivalis (Paykull) (open area; southern range limits in Asia unknown) and N. nivalis gaspesiana new subspecies (cross-hatched area). 387. Nebria crassicornis crassicornis Van Dyke (solid circles) and N. crassicornis intermedia Van Dyke (open circles).

385





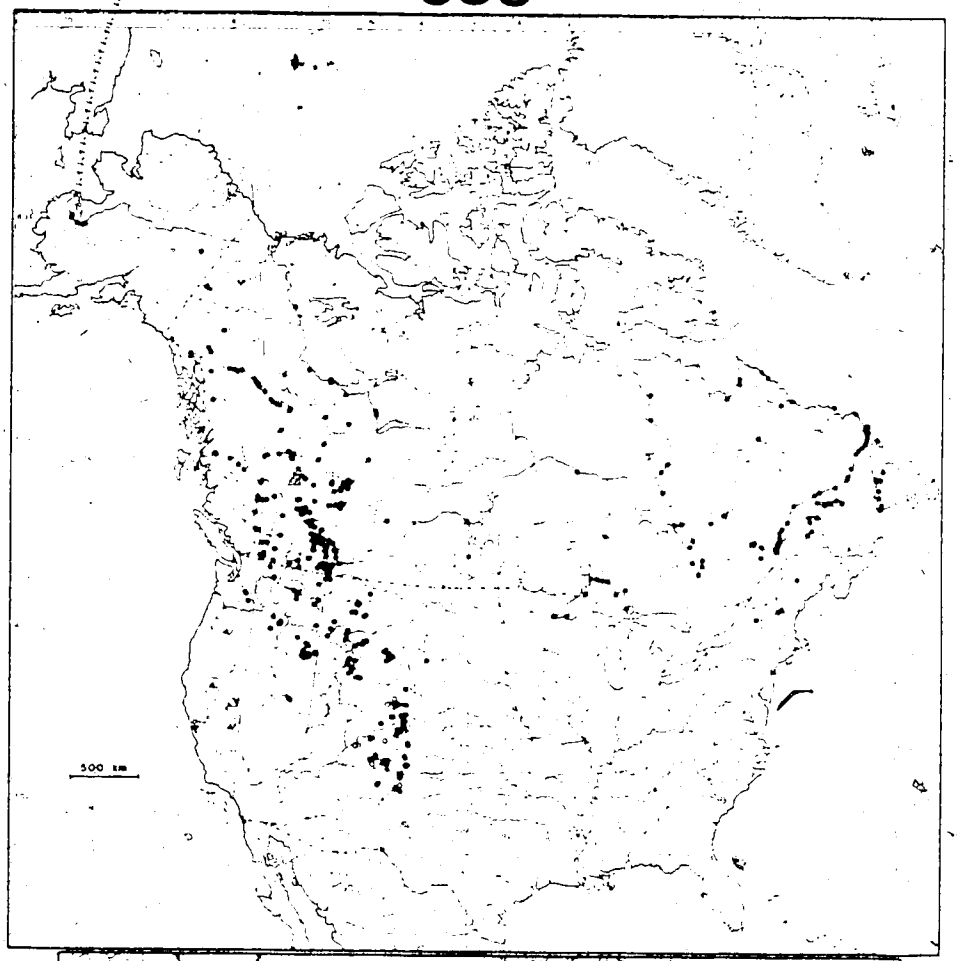
386

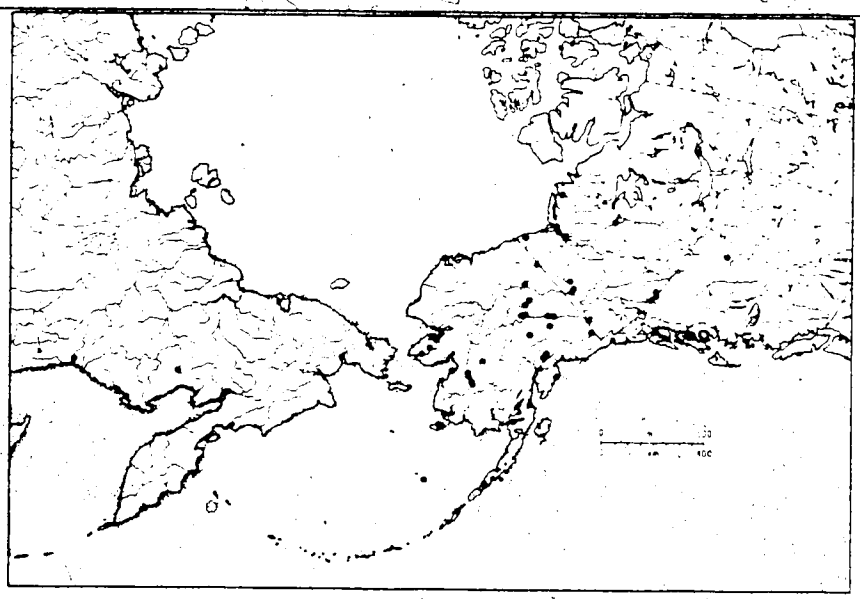


387

Figs. 388 - 389. Geographical distribution maps. 388. Nebria gyllenhali castanipes (Kirby) (solid circles), N. gyllenhali lassenensis new subspecies (solid triangles), and N. gyllenhali lindrothi new subspecies (open circles). 389. Nebria frigida Sahlberg.

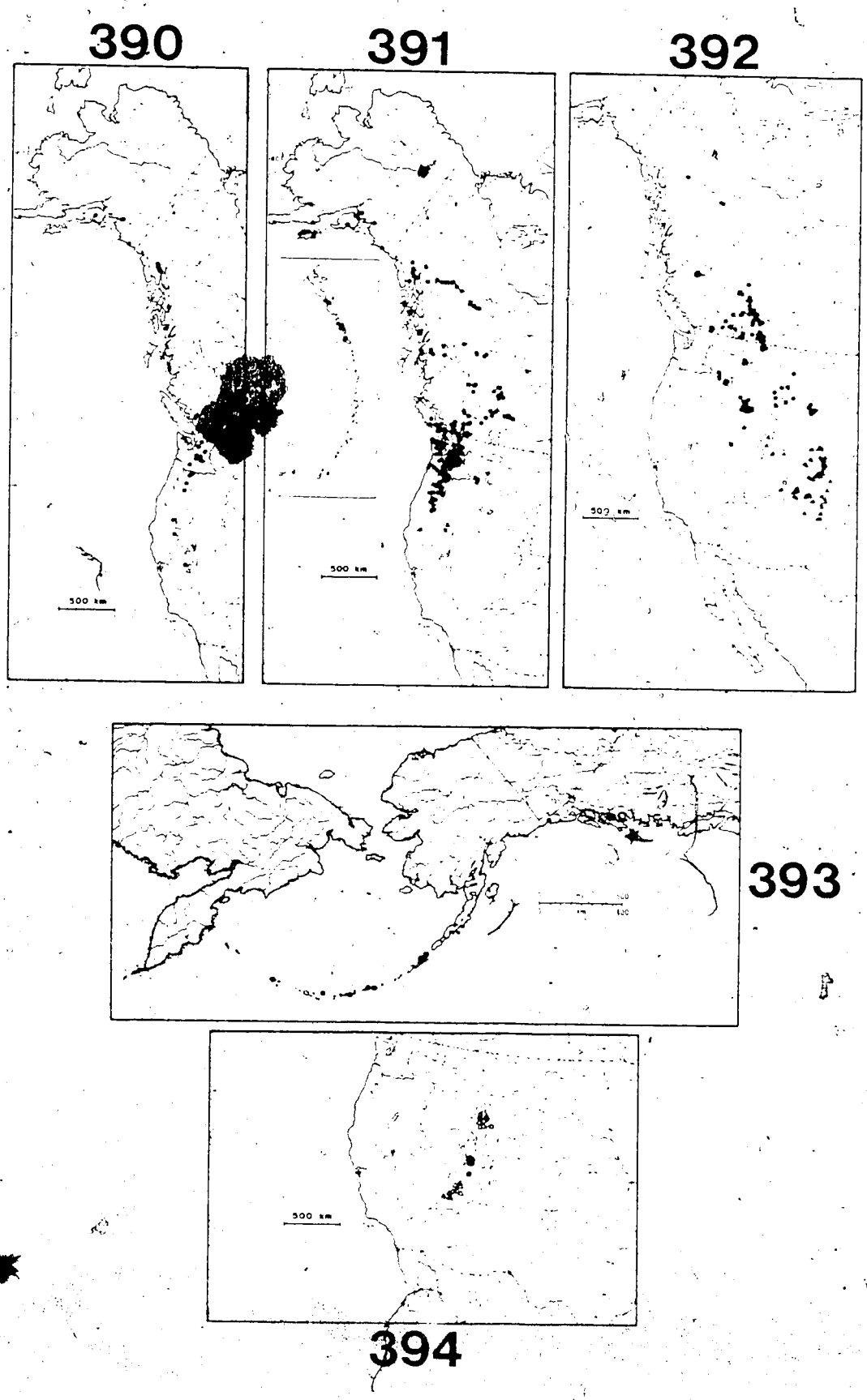
388





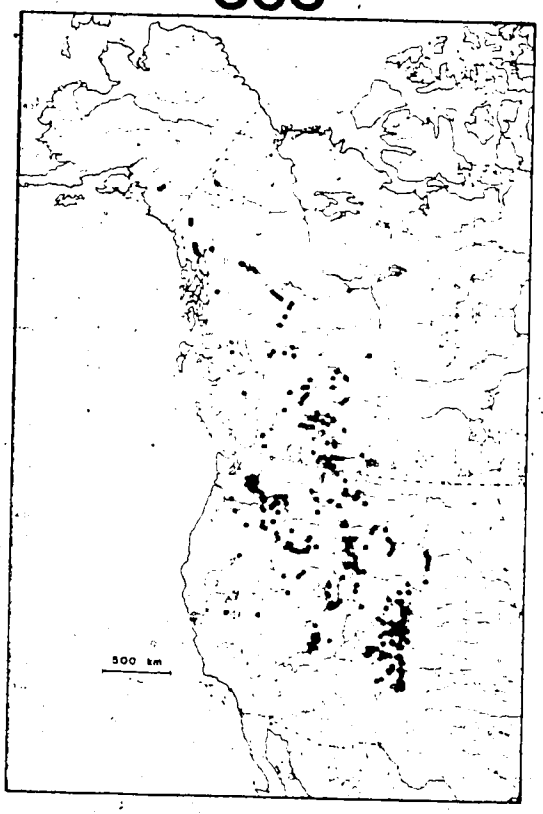
389

Figs. 390 - 394. Geographical distribution maps. 390. Nebria acuta acuta Lindroth (solid circles), N. acuta quileute new subspecies (solid triangles), and N. lyelli Van Dyke (open triangle). 391. Nebria sahlbergii sahlbergii Fischer von Waldheim (solid circles), N. sahlbergii modoc new subspecies (open triangles), and N. sahlbergii triad new subspecies (solid triangles). 392. Nebria arkansana arkansana Casey (solid triangles), N. arkansana edwardsi new subspecies (solid circles), N. arkansana oowah new subspecies (open square), and N. arkansana uinta new subspecies (open triangles). 393. Nebria gregaria Fischer von Waldheim (solid circles) and N. charlottae Lindroth (solid star). 394. Nebria fragilis fragilis Casey (solid circles), N. fragilis teewinot new subspecies (open circles), N. zioni zioni Van Dyke (open triangles), and N. zioni oasis new subspecies (solid triangle).

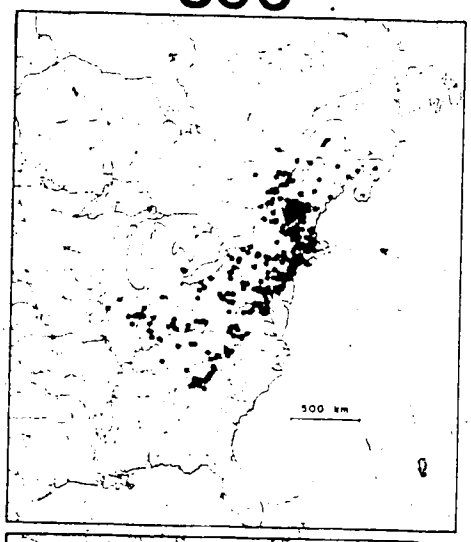

390
391
392
393
394
500 km

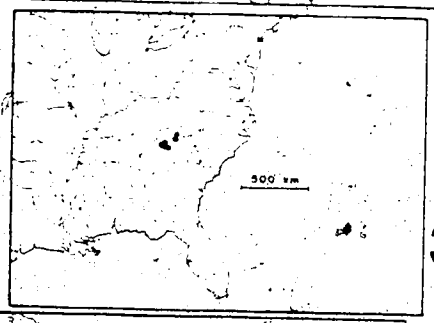
Figs. 395 - 398. Geographical distribution maps. 395. Nebria obliqua LeConte. 396. Nebria pallipes Say. 397. Nebria appalachia Darlington. 398. Nebria suturalis LeConte; "X" denotes location of deposits yielding N. suturalis fossils.

395

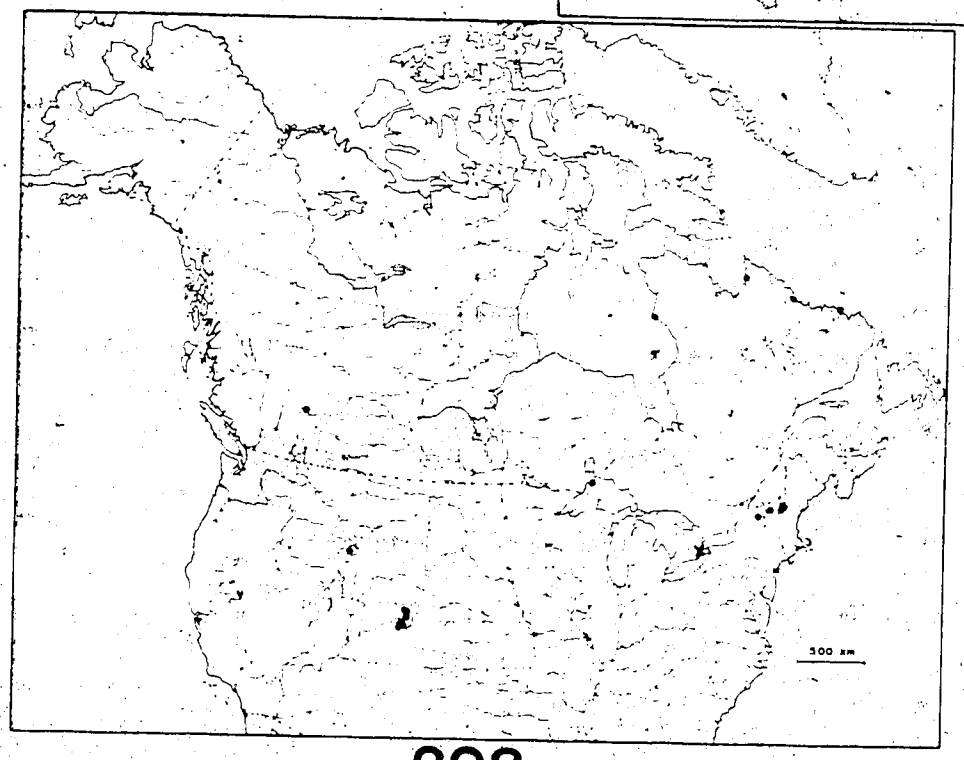


396



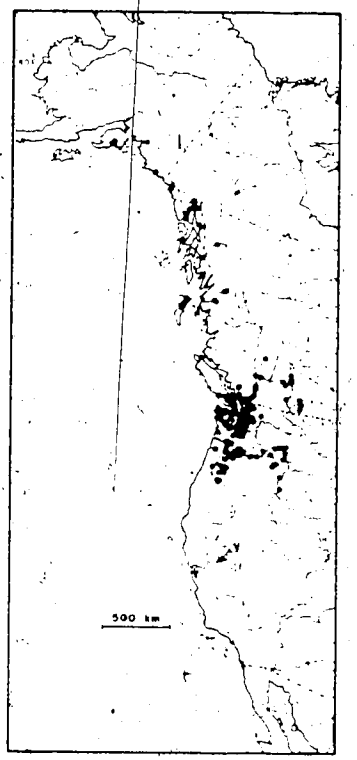


397



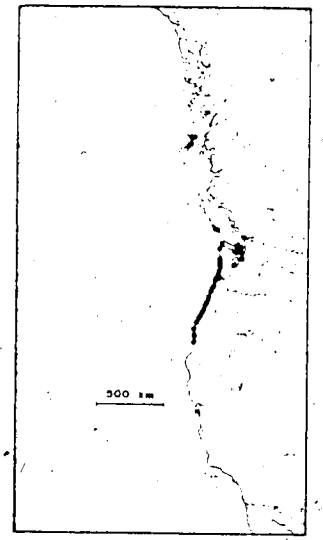
398

Figs. 399 - 405. Geographical distribution maps. 399. Nebria mannerheimii Fischer von Waldheim (solid circles) and N. darlingtoni new species (solid triangles). 400. Nebria eschscholtzii Ménétriés (solid circles), N. desolata Kavanaugh (open triangles), and N. navajo new species (solid triangles). 401. Nebria diversa LeConte. 402. Nebria gebleri gebleri Dejean (solid circles), N. gebleri cascadensis new subspecies (open triangles), N. gebleri strawberryensis new subspecies (open square), N. gebleri rathvoni LeConte (solid triangles), and N. gebleri siskiyouensis new subspecies (solid squares). 403. Nebria spatulata spatulata Van Dyke (solid circles) and N. spatulata sierrae new subspecies (solid squares). 404. Nebria ovipennis LeConte. 405. Nebria kincaidi kincaidi Schwarz (solid circles), N. kincaidi balli new subspecies (solid triangles), and N. carri new species (solid squares).

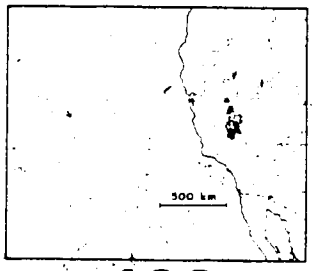


399

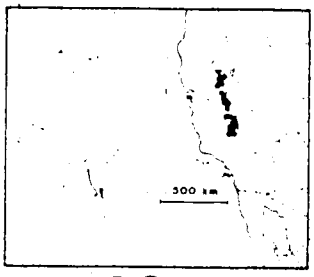
400



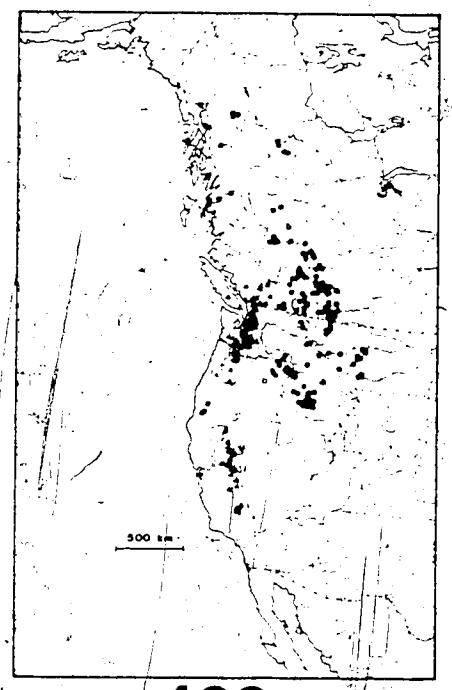
401



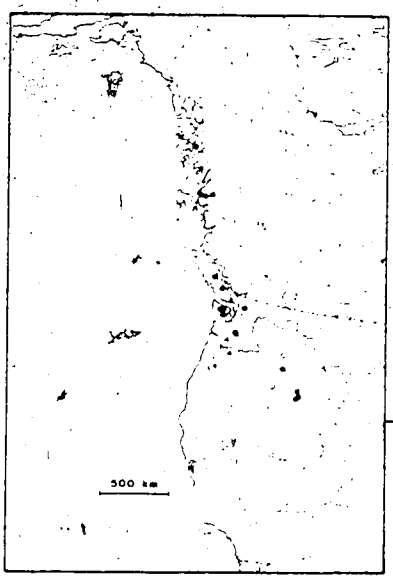
403



404

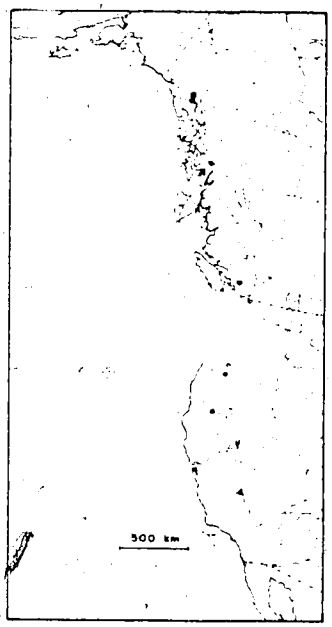


402

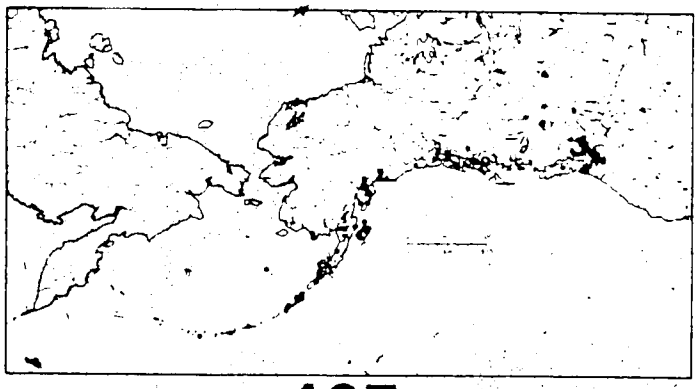


405

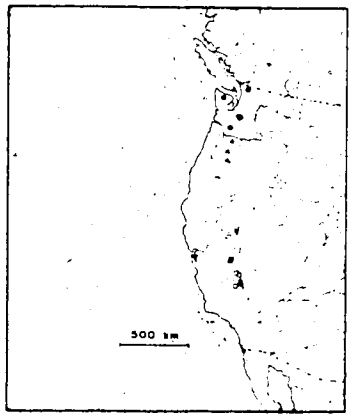
Figs. 406 – 411. Geographical distribution maps. 406. Nebria meanyi meanyi Van Dyke (solid circles), N. meanyi lamarckensis new subspecies (solid triangles), and N. meanyi sylvatica new subspecies (open triangles). 407. Nebria metallica Fischer von Waldheim. 408. Nebria vandykei vandykei Banninger (solid circles), N. vandykei wyeast new subspecies (open triangles), N. ingens ingens Horn (open circles), and N. ingens riversi Van Dyke (solid squares). 409. Nebria piperi Van Dyke (solid circles), N. schwarzi schwarzi Van Dyke (solid triangles), N. schwarzi beverlianna new subspecies (solid square), and N. purpurata LeConte (open circles). 410. Nebria coloradensis Van Dyke (solid circles) and N. piute Erwin and Ball (solid triangles). 411. Nebria trifaria trifaria LeConte (solid circles), N. trifaria catenata Casey (open triangles), and N. trifaria utahensis new subsp (solid triangle).



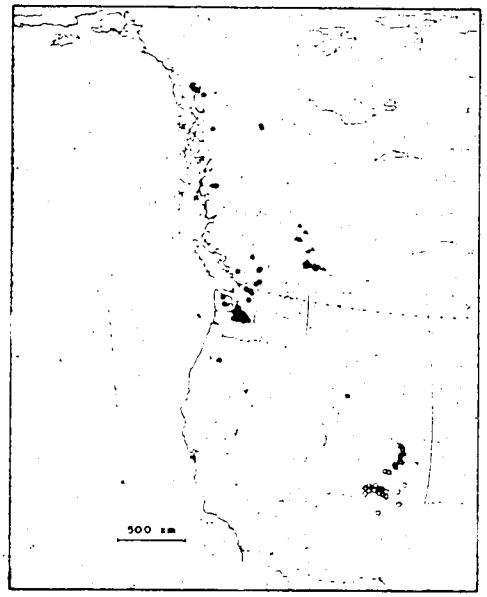
406



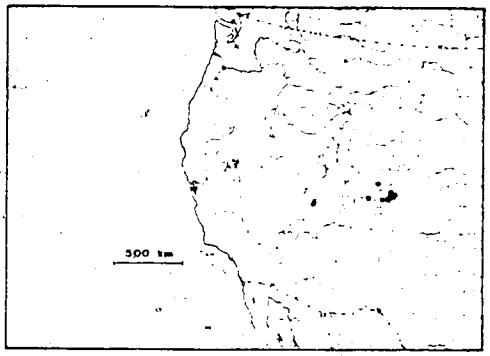
407



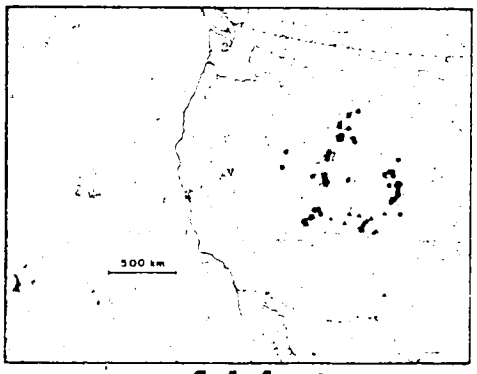
408



409

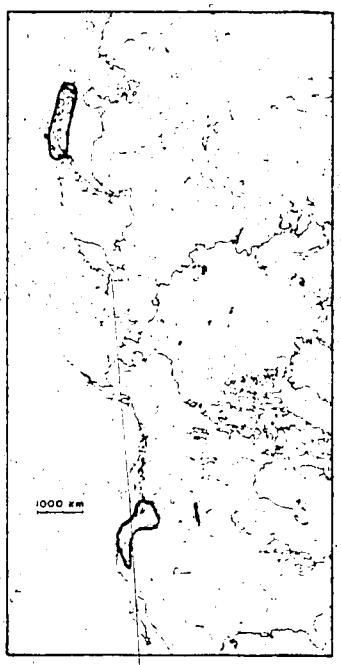


410

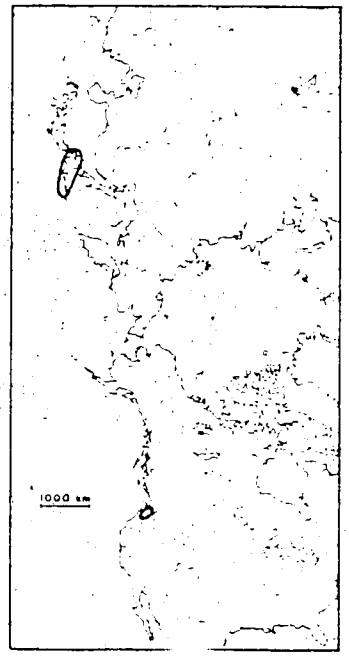


411

Figs. 412 - 416. Geographical distribution maps. 412. The virescens species group. 413. The paradisi species group. 414. The gregaria species group. 415. The hudsonica species group. 416. The gyllenhali species group.

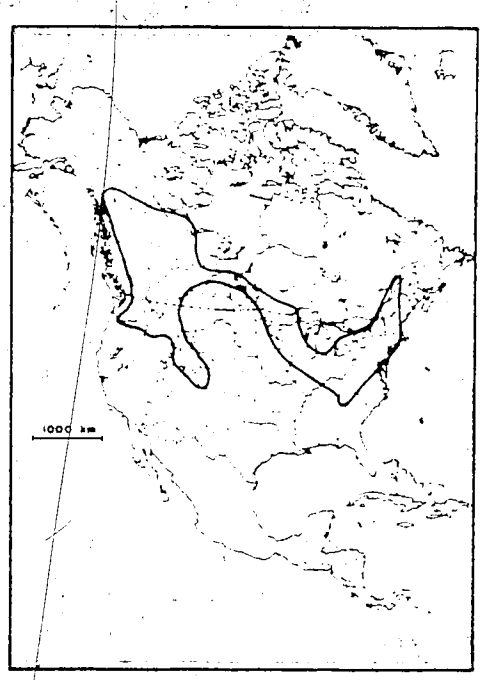


412



413

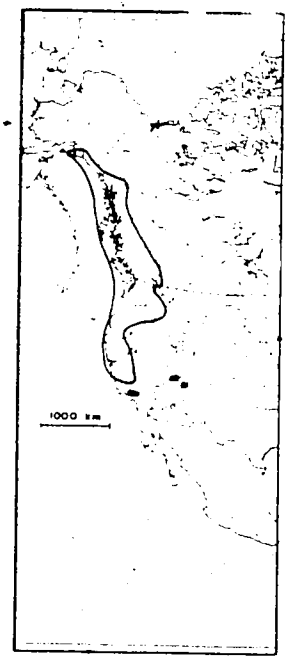
414



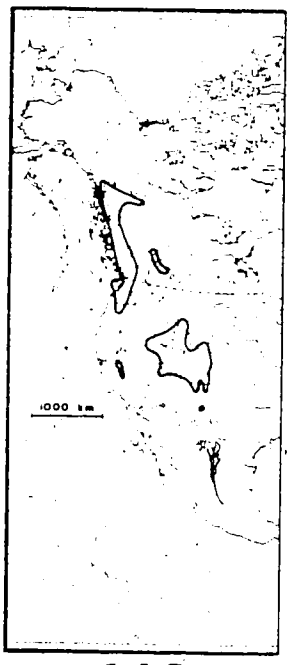
415

416

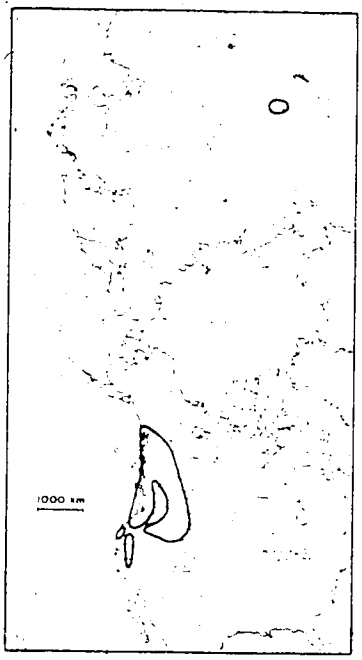
Figs. 417 – 421. Geographical distribution maps. 417. The mannerheimii species group. 418. The trifaria species group. 419. The ovipennis species group. 420. The obliqua species group. 421. The metallica species group.



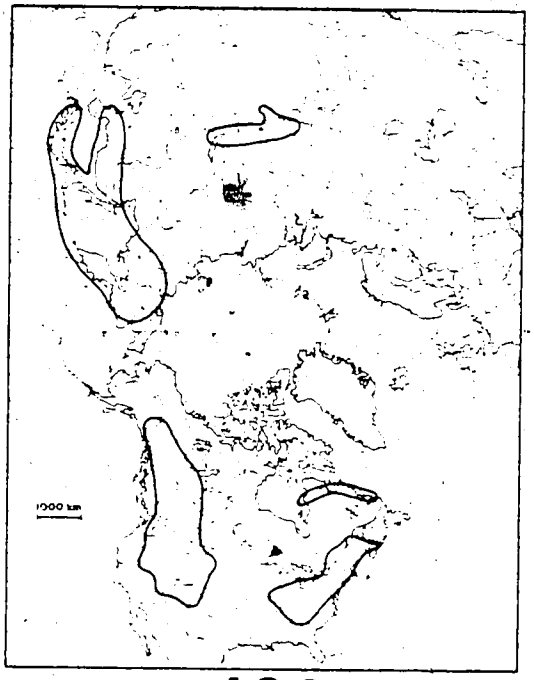
417



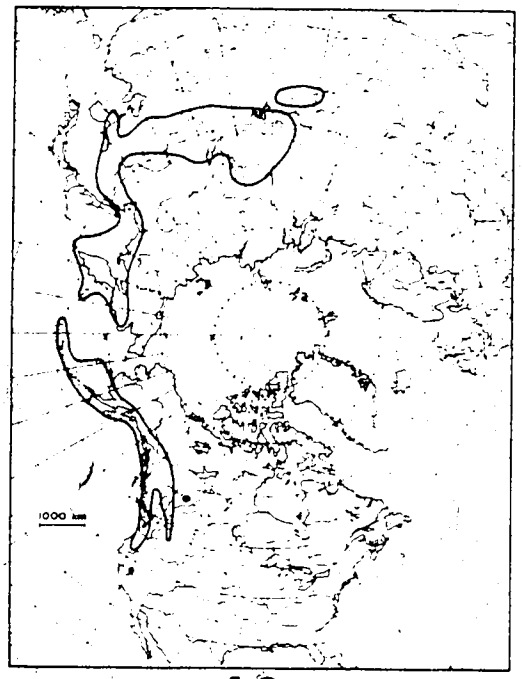
418



419

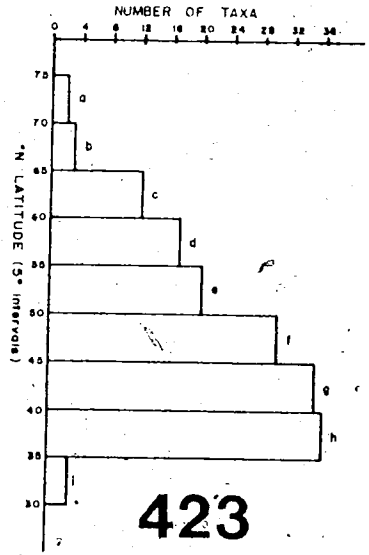


420

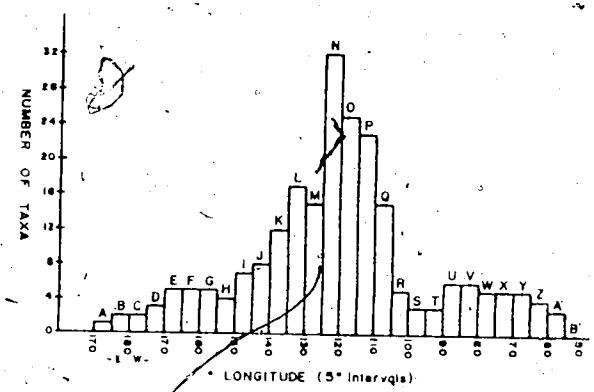


421

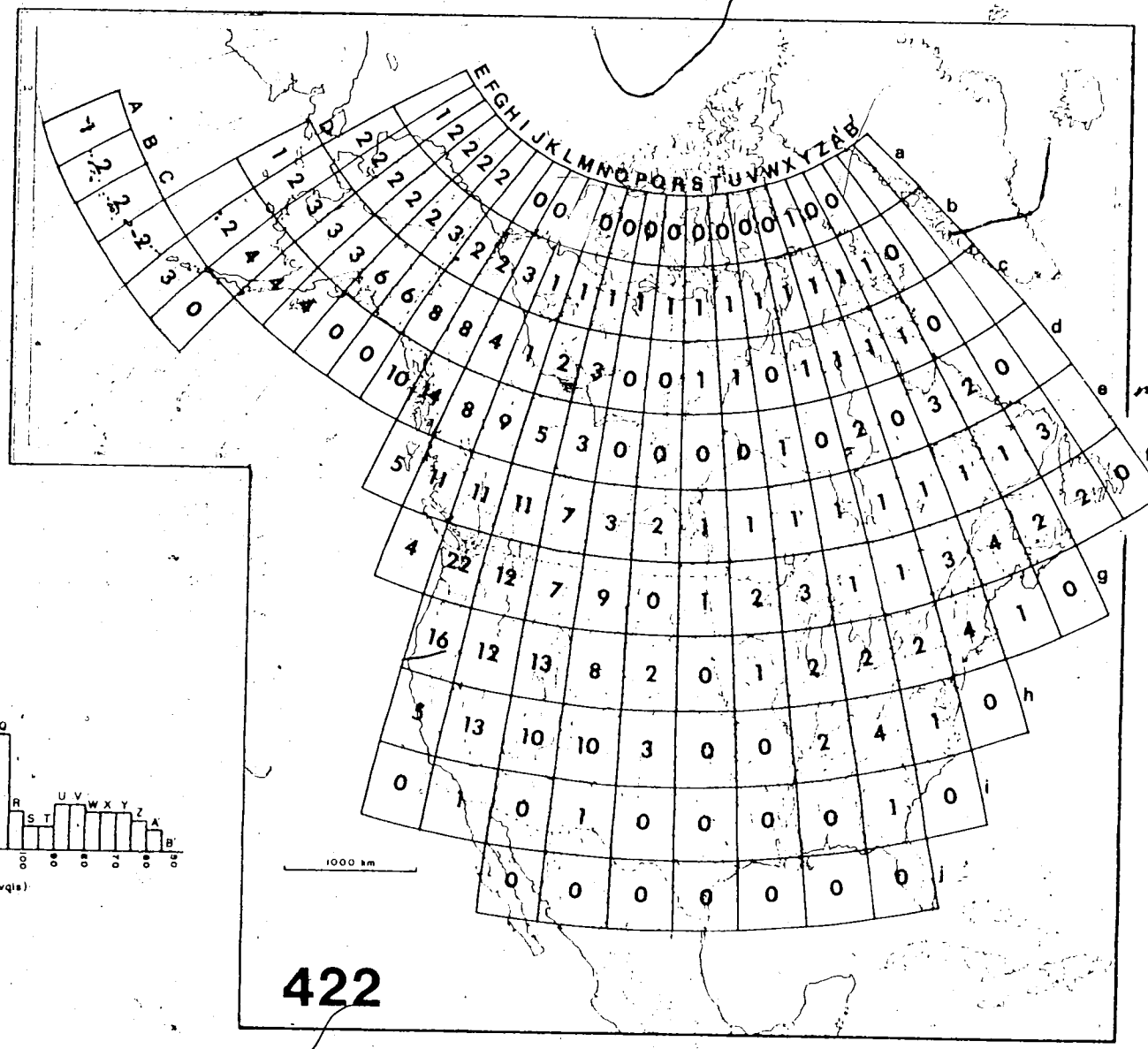
Fig. 422. Numbers of Nebria species and subspecies represented in 5° latitude and longitude intervals; capital and lower case letters refer to intervals used in Table 16. Fig. 423. Histogram illustrating Nearctic Nebria diversity in relation to latitude. Fig. 424. Histogram illustrating Nearctic Nebria diversity in relation to longitude.


NUMBER OF TAXA
°N LATITUDE (5° intervals)

423

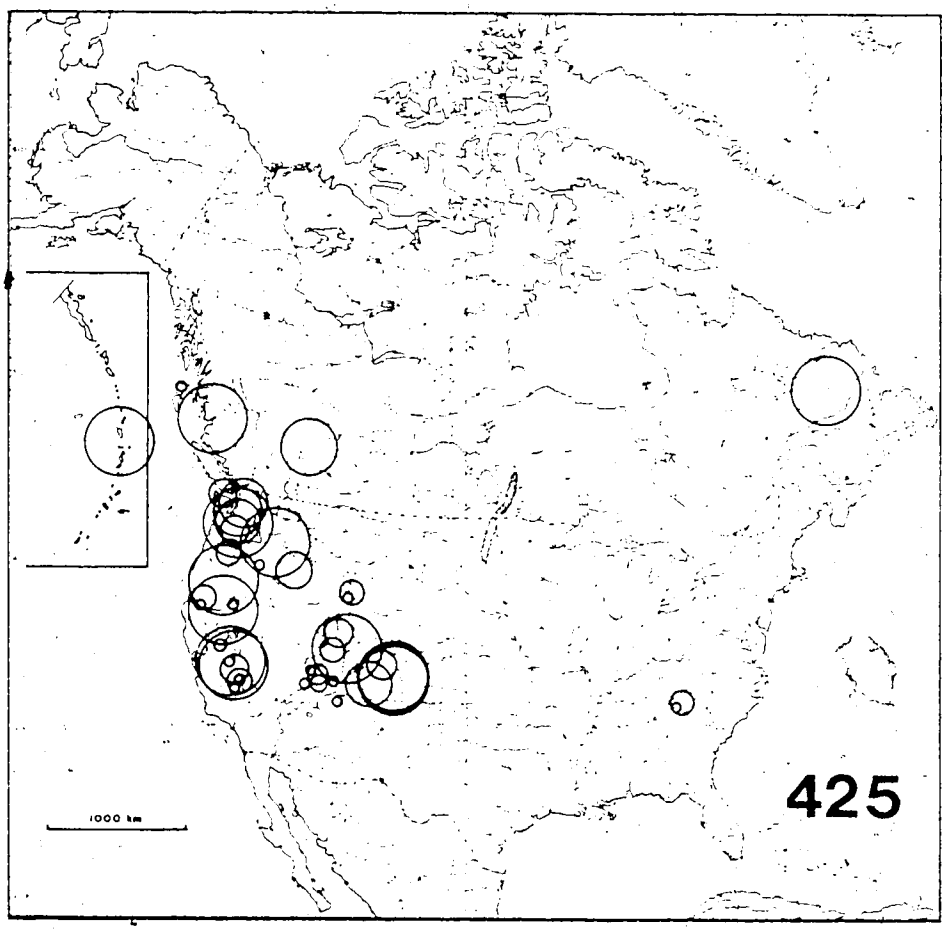

NUMBER OF TAXA
° LONGITUDE (5° intervals)

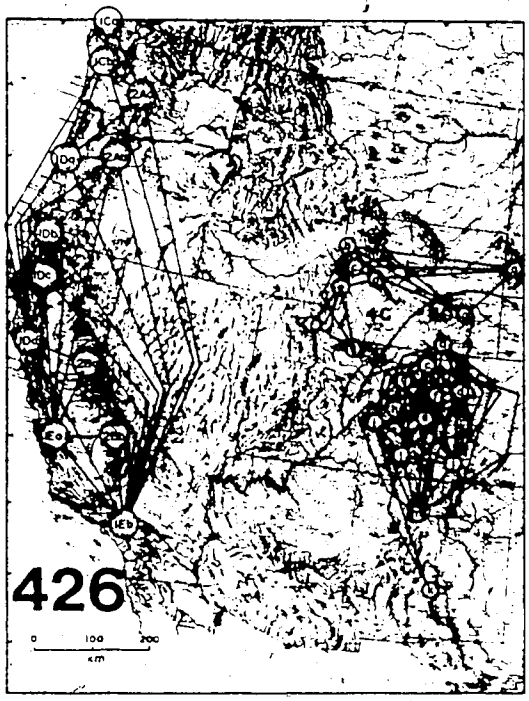
424


1000 km

422

Fig. 425. Centers of endemism among Nearctic species and subspecies of Nebria. Circles are placed around centers of distribution of all taxa for which maximum linear extent of geographical range (= m.e.r.) is 1600 km or less. Radii of circles reflect respective range sizes, except that maximum radius plotted is 250 km (i.e. for all taxa with m.e.r.= 250 km or more, up to 1600 km) and minimum radius plotted is about 50 km (i.e. for all taxa with m.e.r. less than or equal to 100 km). Fig. 426. Diagrammatic representation of Nebria faunal similarities, based on Simpson coefficients (Simpson, 1960), among mountain ranges of the southern and central Rocky Mountain regions and among mountain ranges of the central and southern Pacific Coast regions (see Table 1 for alpha-numeric code used for mountain ranges); lines link only those areas between which coefficients of similarity are greater than or equal to 75. Fig. 427. Same as Fig. 426, but Jaccard coefficients (Braun-Blanquet, 1932) are instead used in similarity measures.


1000 km
425


426
0 100 200
km

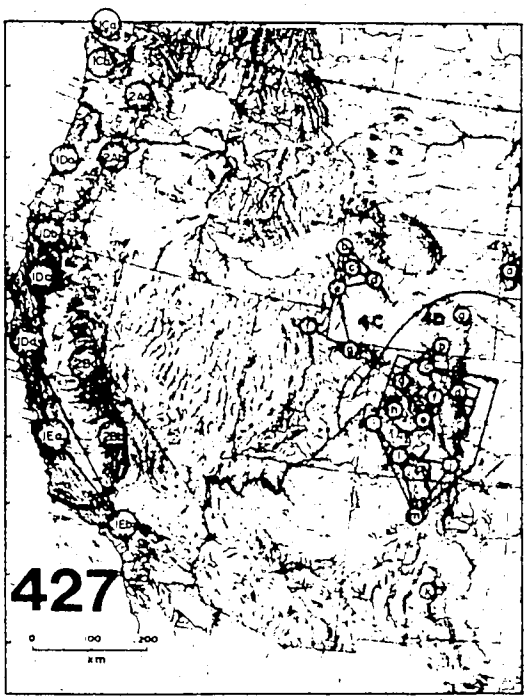
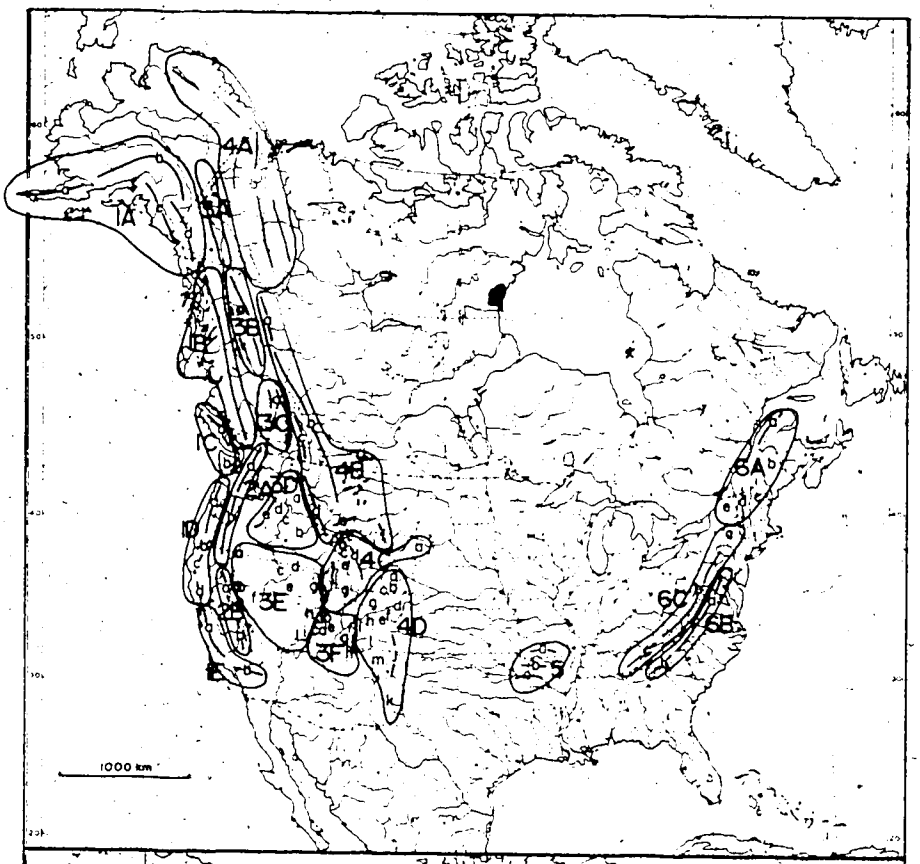
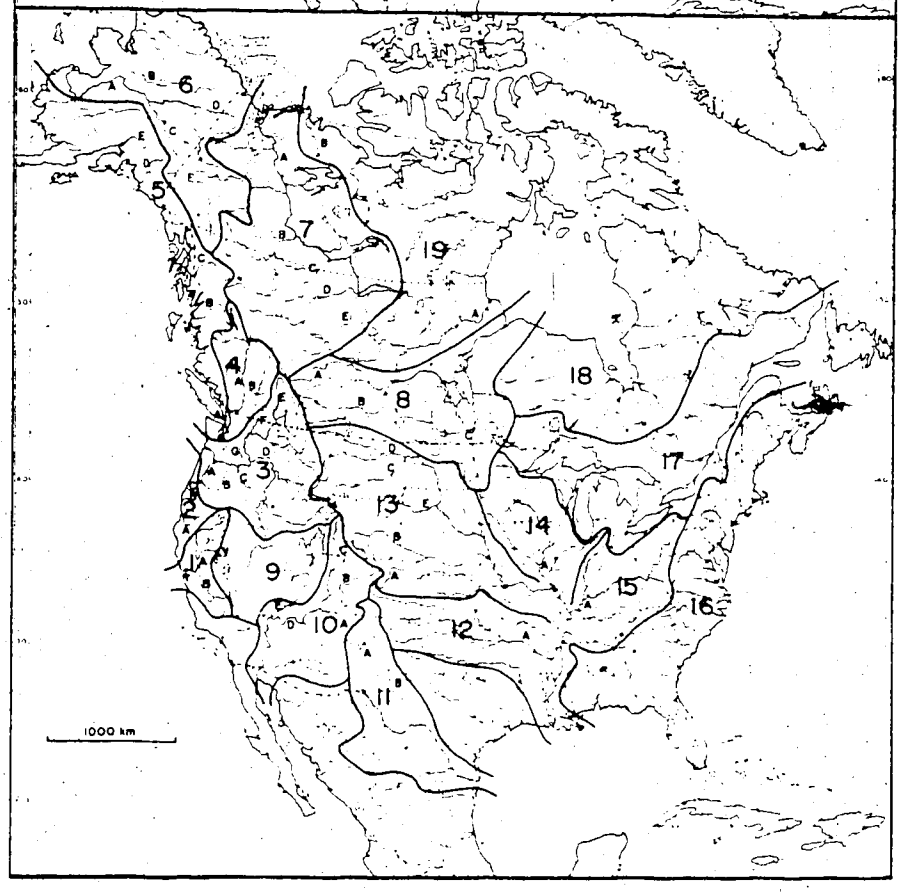

427
0 100 200
km

Fig. 428. Mountain systems and ranges of North America (see Table 1 for explanation of alpha-numeric code used). Fig. 429. Principal drainage systems of North America (see Table 3 for explanation of alpha-numeric code used).

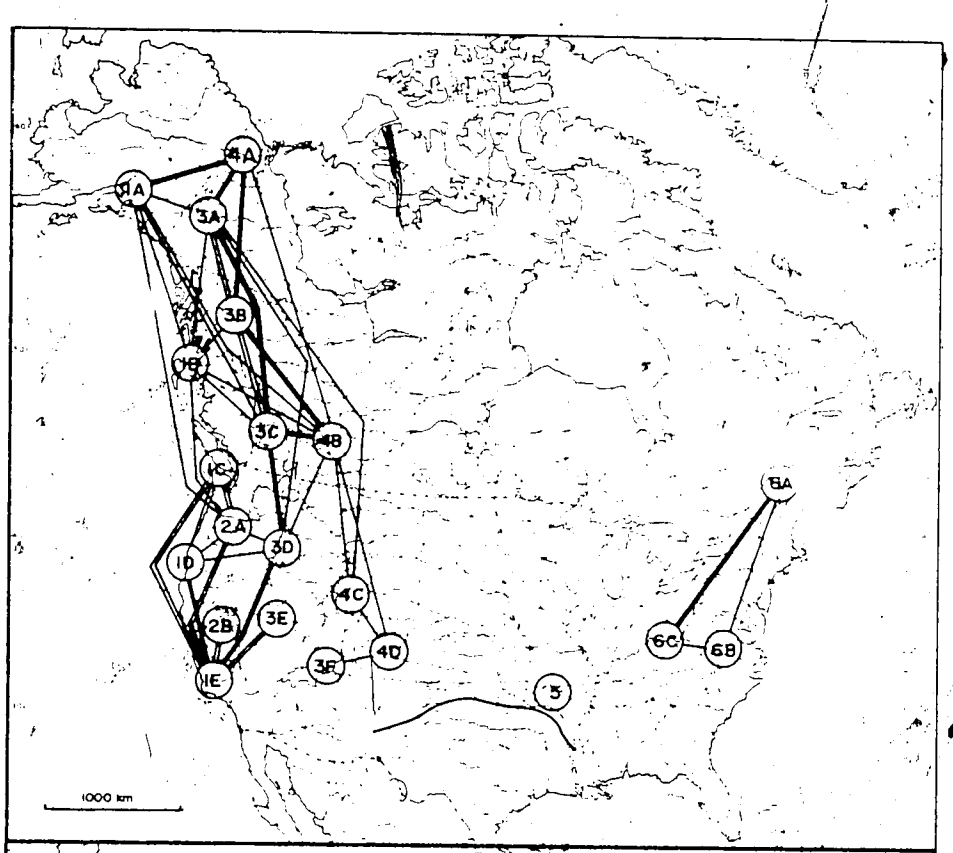


428

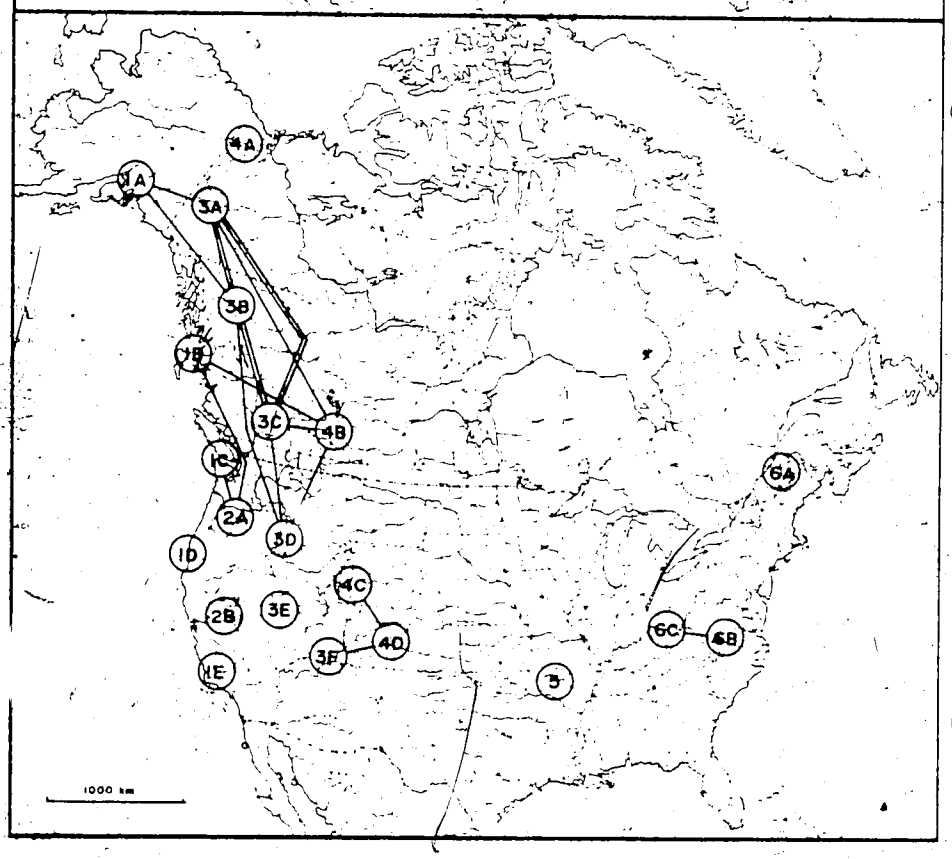


429

Fig. 430. Diagrammatic representation of Nebria faunal similarities, based on Simpson coefficients (Simpson, 1960), among major montane regions (physiographic units) (see Table 1 for alpha-numeric code used for montane regions); single lines link those areas between which coefficients of similarity are greater than or equal to 50; double lines indicate similarity values greater than or equal to 75 between areas linked. Fig. 431. Same as Fig. 430, but Jaccard coefficients (Braun-Blanquet, 1932) are instead used in similarity measures.


4A
1A
3A
3B
1B
3C
4B
1C
2A
3D
1D
4C
2B
3E
1E
3F
4D
5
6A
6C
6B
1000 km

430


4A
1A
3A
3B
1B
3C
4B
1C
2A
3D
1D
4C
2B
3E
1E
3F
4D
5
6A
6C
6B
1000 km

431

Fig. 432. Eastern geographical range patterns; pattern 1 = line with solid beads; pattern 2 = solid line; pattern 3 = broken line.

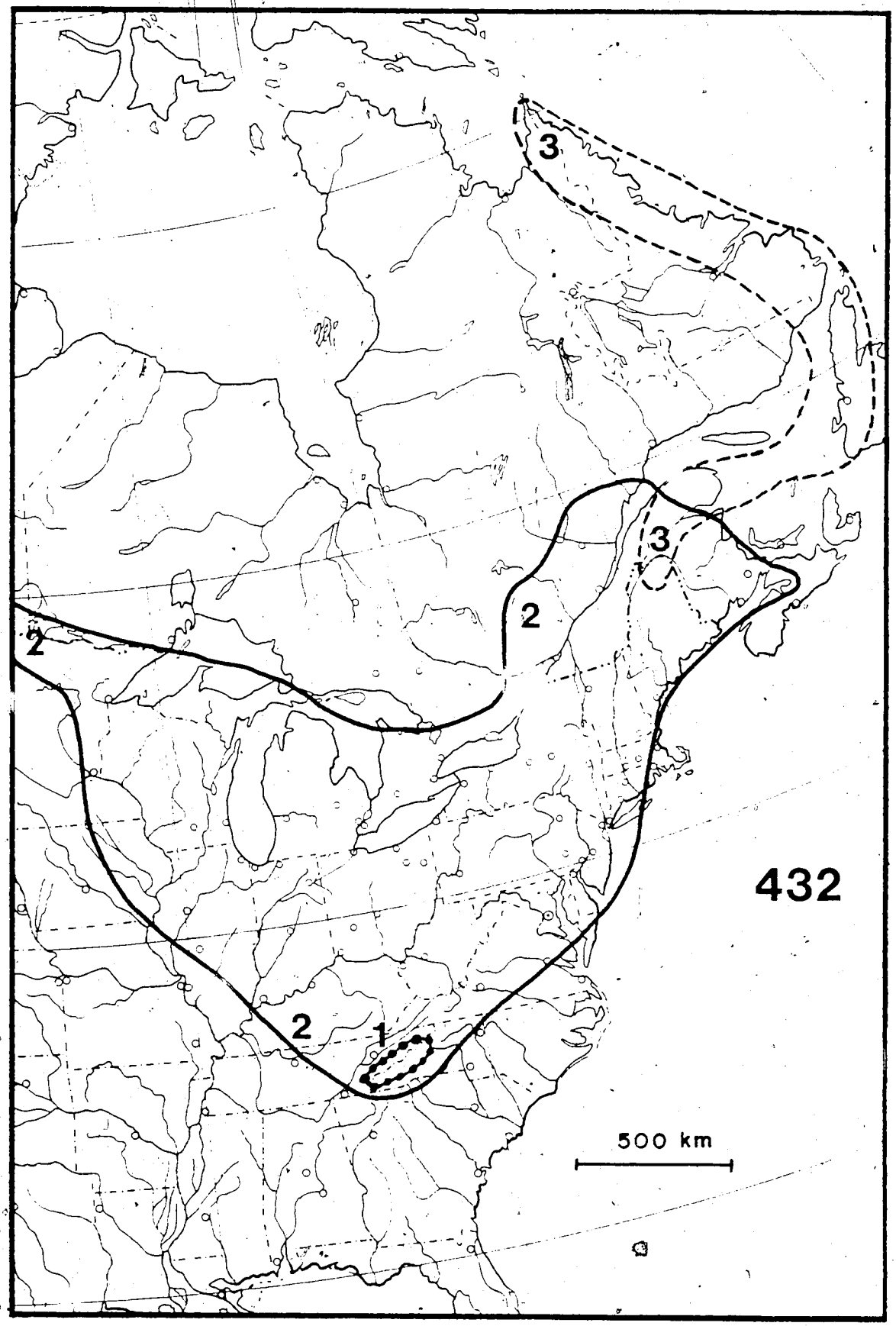

3
3
2
2
2
1
432
500 km

Fig. 433. Rock Mountain geographical range patterns; pattern 4 = dotted line; pattern 5 = line alternating a single dot with a single dash; pattern 6 = broken (dashed) line; pattern 7 = line of oblique slash marks; pattern 8 = line of small open circles; pattern 9 is not illustrated; pattern 10 = solid line.

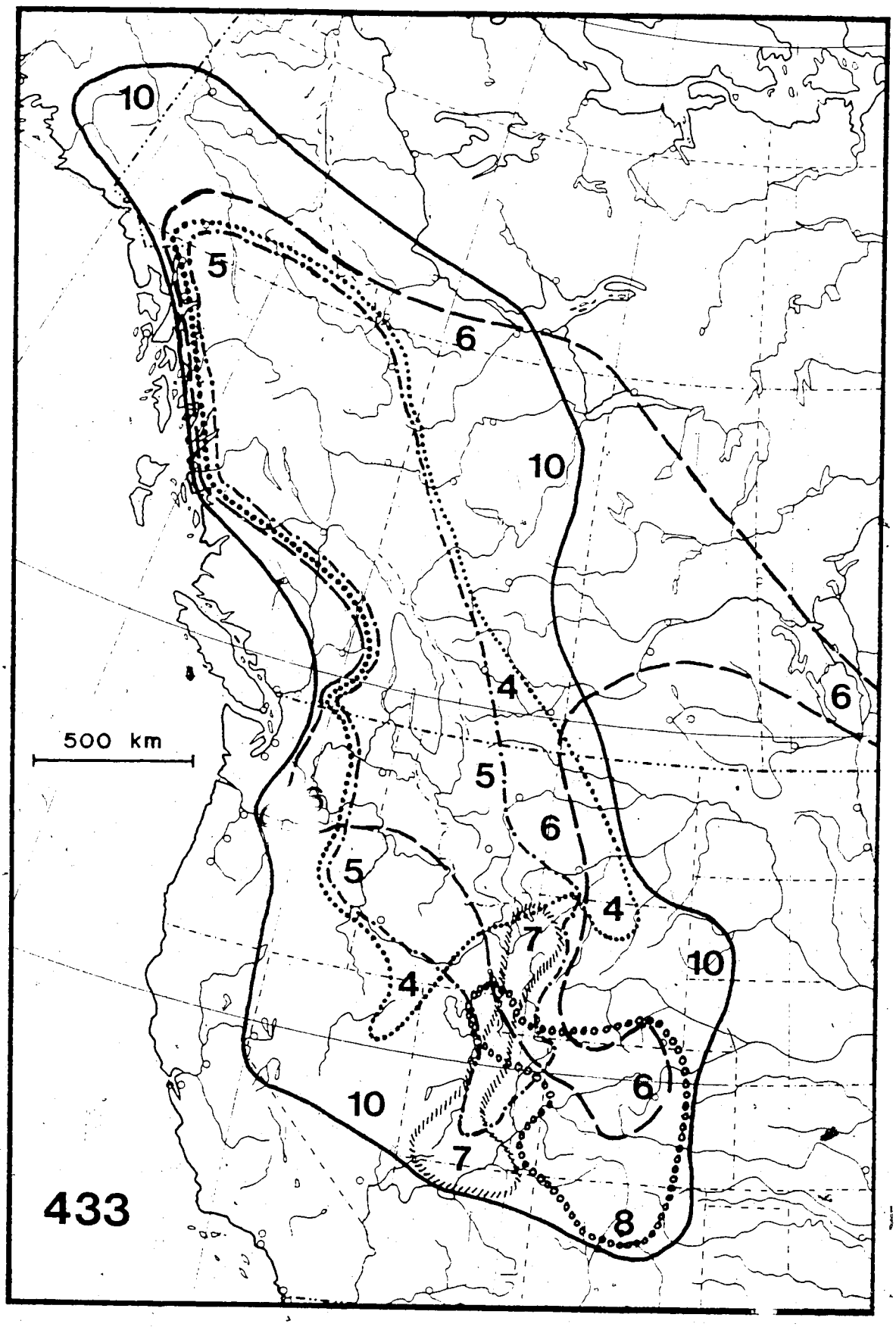

10
5
6
10
4
6
500 km
5
6
5
4
7
10
4
6
10
7
8
433

Fig. 434. Pacific coastal geographical range patterns; pattern 11 = line alternating a single dot with a single dash; pattern 12 = line of small open circles; pattern 13 = dotted line; pattern 14 is not illustrated; pattern 15 = broken line of short dashes; pattern 16 = line alternating two dots with a single dash; pattern 17 = broken line of long dashes; pattern 18 = solid line; pattern 19 = line of oblique slash marks.

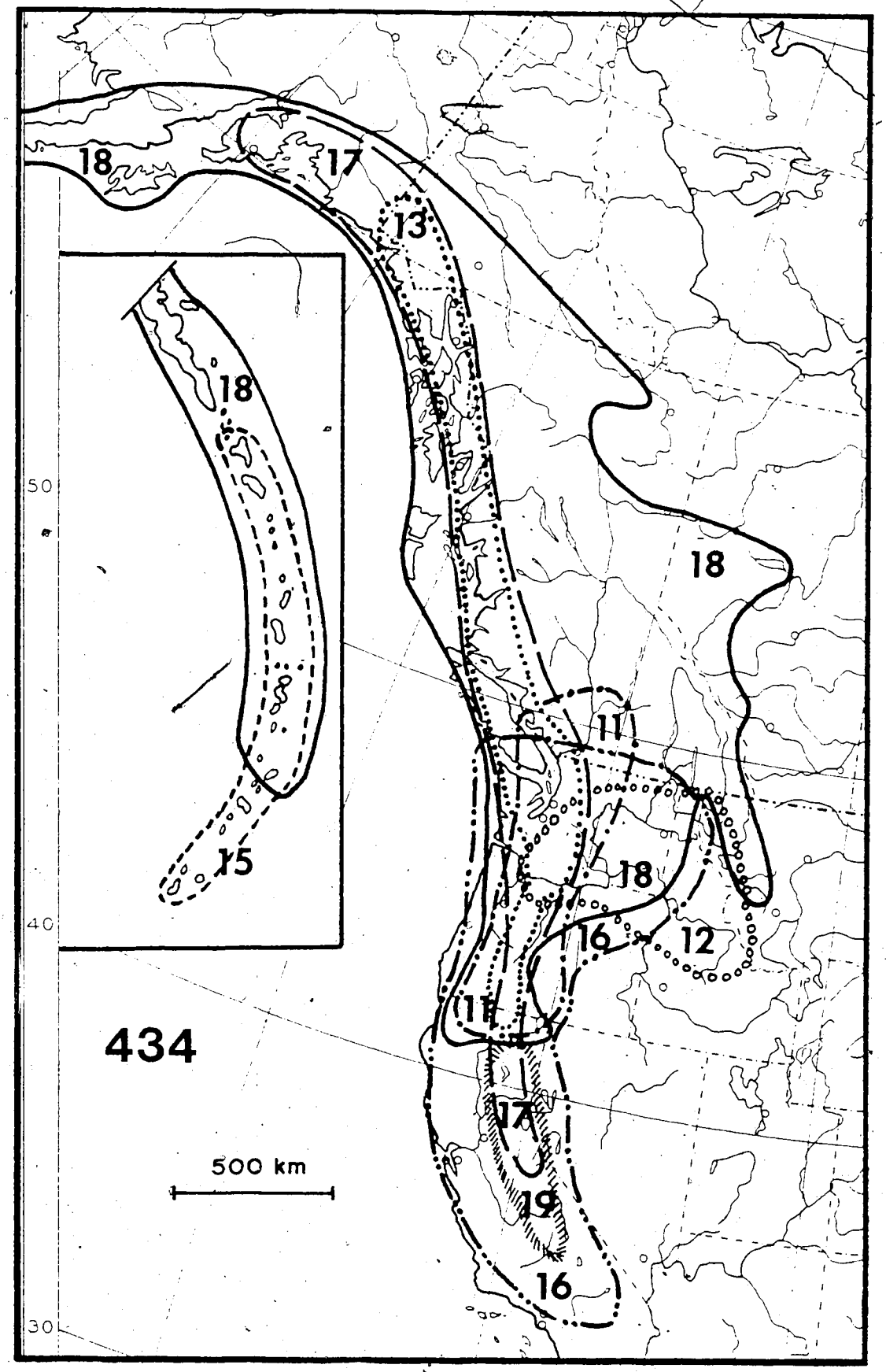

18
17
13
18
15
18
11
18
16
12
11
17
19
16
434
500 km
50
40
30

Fig. 435. Northern and transamerican geographical range patterns; pattern 20 = dotted line; pattern 21 = broken (dashed) line; pattern 22 = line of small open circles; pattern 23 = solid line.

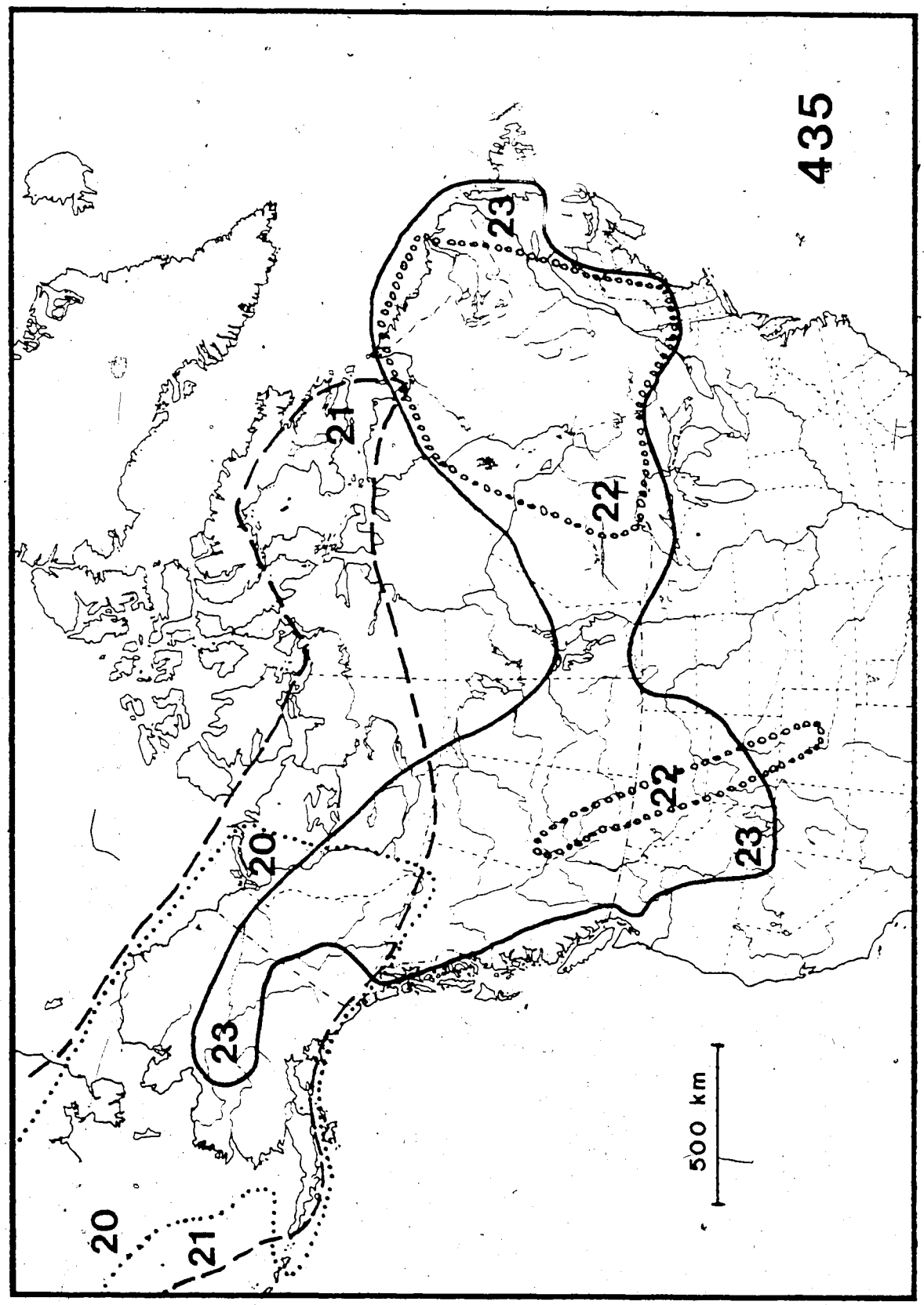
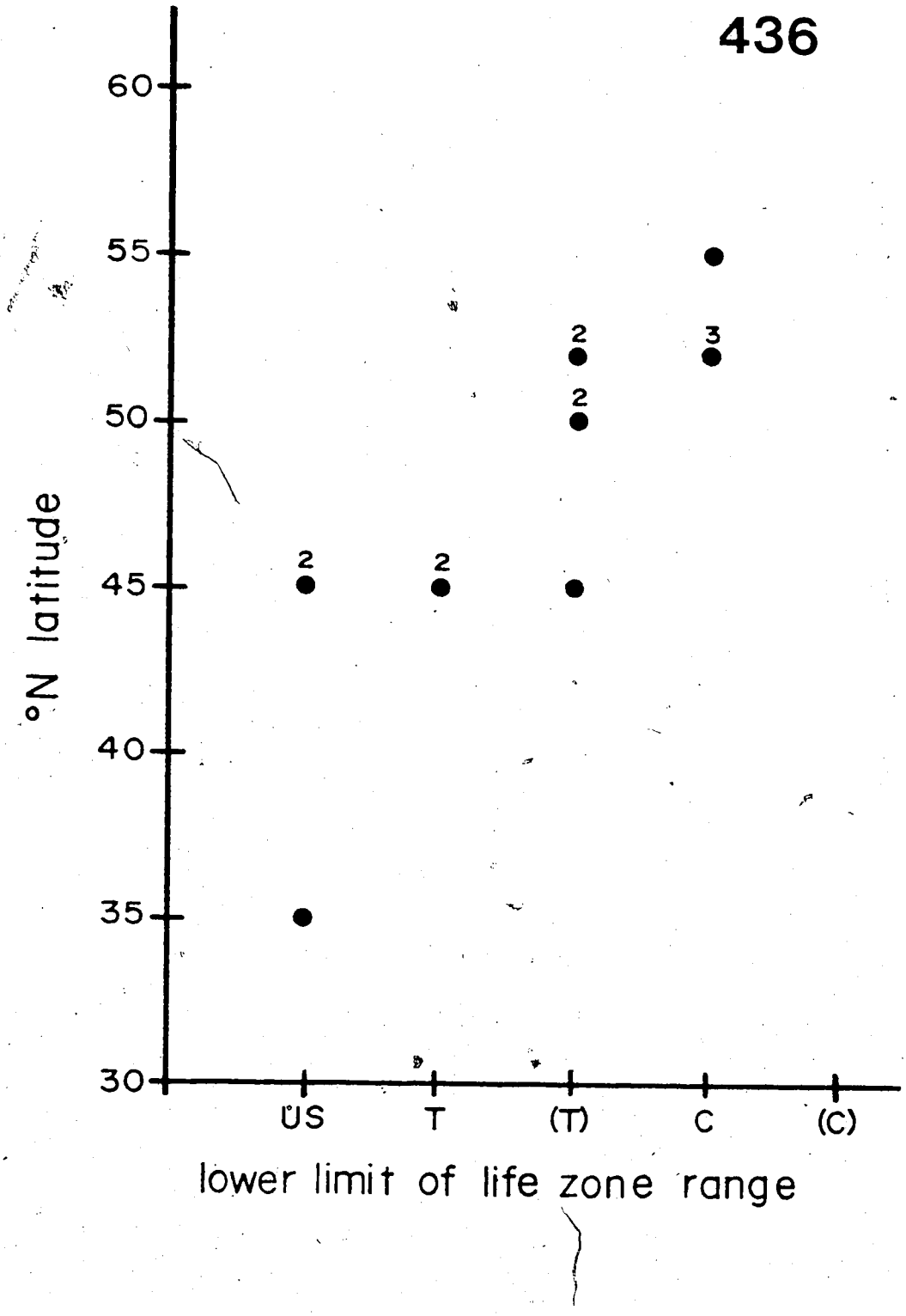
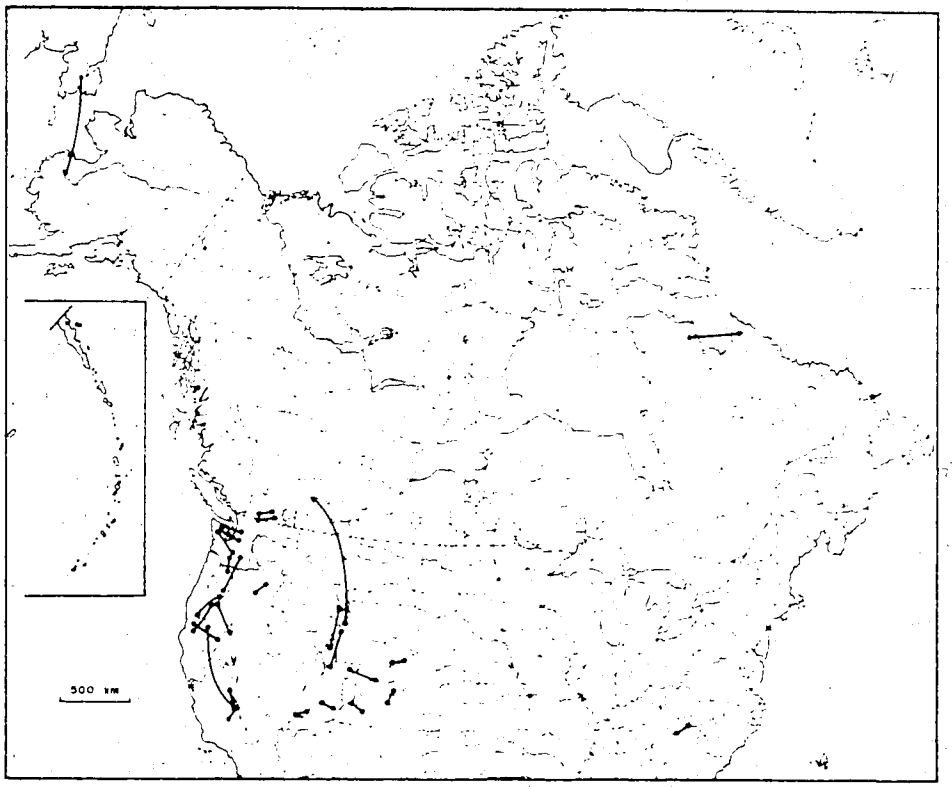

435
23
21
22
20
22
23
23
20
21
500 km

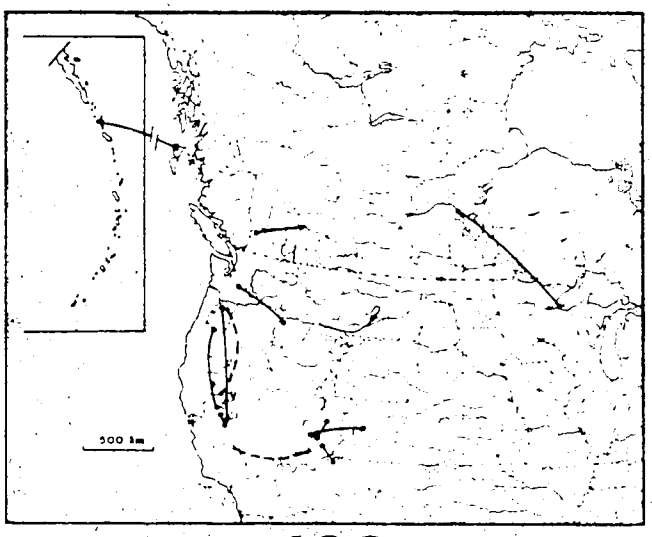
Fig. 436. Scattergram demonstrating relationship between lower limit of macrohabitat range and southern limit of geographical range continuity in taxa common to two different general Nebria faunas. Abbreviations used for life zones are as follows: A/A = Arctic/Alpine Zone; H = Hudsonian Zone; C = Canadian Zone; T = Transition Zone; US = Upper Sonoran Zone. Numbers over dots denote number of records which fall at the same point on the graph.


436
60
55
50
45
40
35
30
°N latitude
2
3
2
2
2
US
T
(T)
C
(C)
lower limit of life zone range

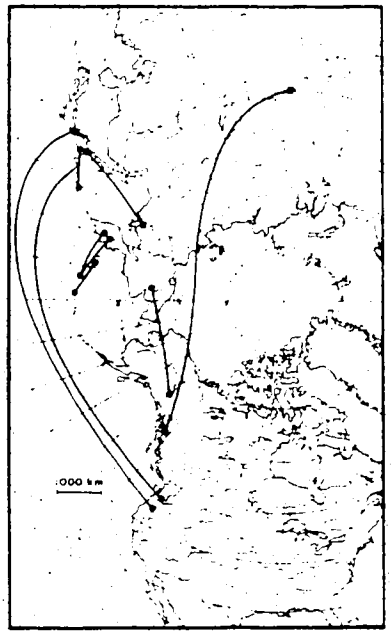
Figs. 437 - 439. Patterns of vicariance. In the following figures, lines connect points which define the shortest distance between respective ranges of vicars (i.e. sister taxa). Fig. 437. Diagrammatic representation of vicariance patterns among Nearctic Nebria subspecies. Fig. 438. Diagrammatic representation of vicariance patterns among sister species (solid lines) or closely related species (broken lines) of Nearctic Nebria. Fig. 439. Diagrammatic representation of vicariance patterns within Nearctic Nebria species groups.



437



438



439

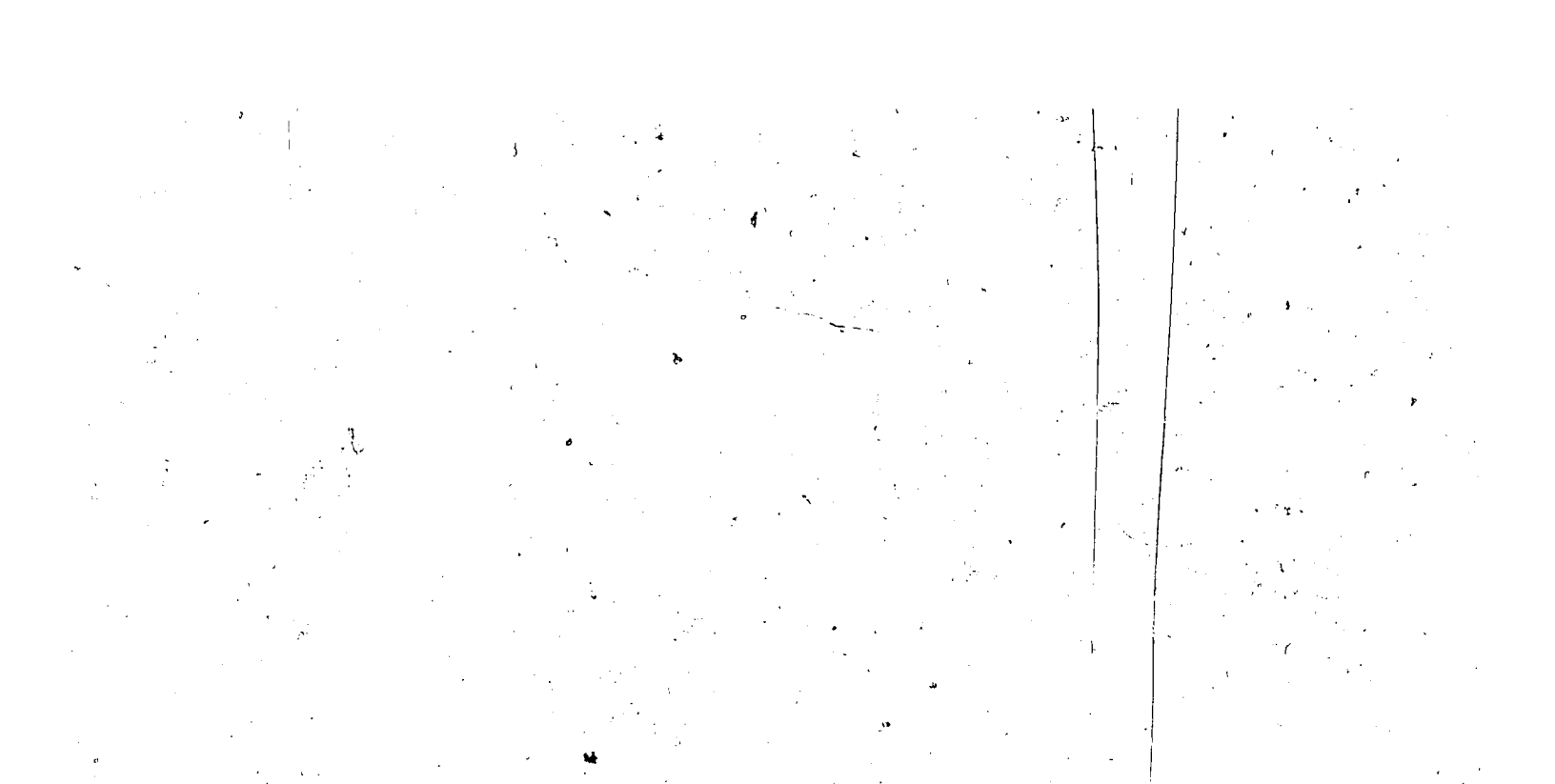


Fig. 440. Relationship between geographical range patterns and vicariance in Nebria subspecies. Range patterns are those illustrated in Figs. 432 - 435 and discussed in the text. Internal vicariance = vicariance within a single recognized range pattern; external vicariance = vicariance between two different, recognized range patterns. N/S and E/W refer to orientation of vicariance (i.e. north/south and east/west, respectively). Numbers indicate number of vicariance relationships which involve a given pattern; and lines indicate range patterns connected by vicariance relationships.

440

Range pattern no.	Internal Vicariance N/S	Internal Vicariance E/W	External Vicariance N/S	External Vicariance E/W
1	0	0	1	0
2	0	0	1	0
3	0	0	0	1
4	0	1	2	1
5	0	0	1	1
6	0	0	0	0
7	1	1	0	0
8	0	2	1	1
9	1	1	0	0
10	0	0	0	0
11	2	0	0	3
12	0	0	0	0
13	0	2	1	0
14	0	0	0	0
15	0	0	0	0
16	0	0	0	0
17	0	1	1	0
18	2	0	0	0
19	1	1	1	1
20	0	0	0	0
21	0	0	0	1
22	0	0	0	0
23	0	0	1	1

Fig. 441. Relationship between geographical range patterns and vicariance in Nebria sister species. Range patterns are those illustrated in Figs. 432 - 435 and discussed in the text. Internal vicariance = vicariance within a single recognized range pattern; external vicariance = vicariance between two different, recognized range patterns. N/S and E/W refer to orientation of vicariance (i.e. north/south and east/west, respectively). Numbers indicate number of vicariance relationships which involve a given pattern; and lines indicate range patterns connected by vicariance relationships.

441

Range pattern no.	Internal Vicariance N/S	Internal Vicariance E/W	External Vicariance N/S	External Vicariance E/W
1	0	0	0	0
2	0	0	0	1
3	0	0	0	0
4	0	0	0	1
5	0	0	0	0
6	0	0	0	1
7	2	0	0	1
8	0	0	0	1
9	0	0	0	0
10	0	0	0	0
11	0	0	1	0
12	0	0	0	1
13	0	0	0	1
14	0	0	0	1
15	0	0	0	1
16	0	0	0	0
17	0	0	1	0
18	0	0	1	1
19	0	0	3	0
20	0	0	0	0
21	0	0	0	0
22	0	0	0	0
23	0	0	0	0

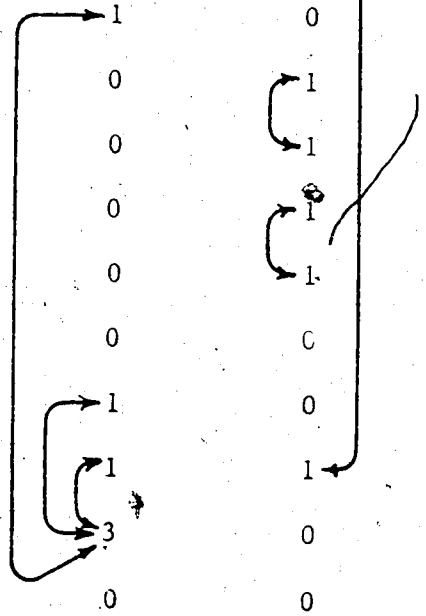


Fig. 442. Patterns of altitudinal zonation among Nebria taxa in selected mountain ranges. Upper half of figure = Cascade Range at Mountain Rainier (southern slope); lower half of figure = Sierra Nevada at Yosemite National Park (western slope). Line segments represent known altitudinal range of each taxon. Ranges of life zones in each mountain area are plotted below line segments for taxa (abbreviations: A/A = Arctic/Alpine Zone; H = Hudsonian Zone; C = Canadian Zone; T = Transition Zone; and US = Upper Sonoran Zone).

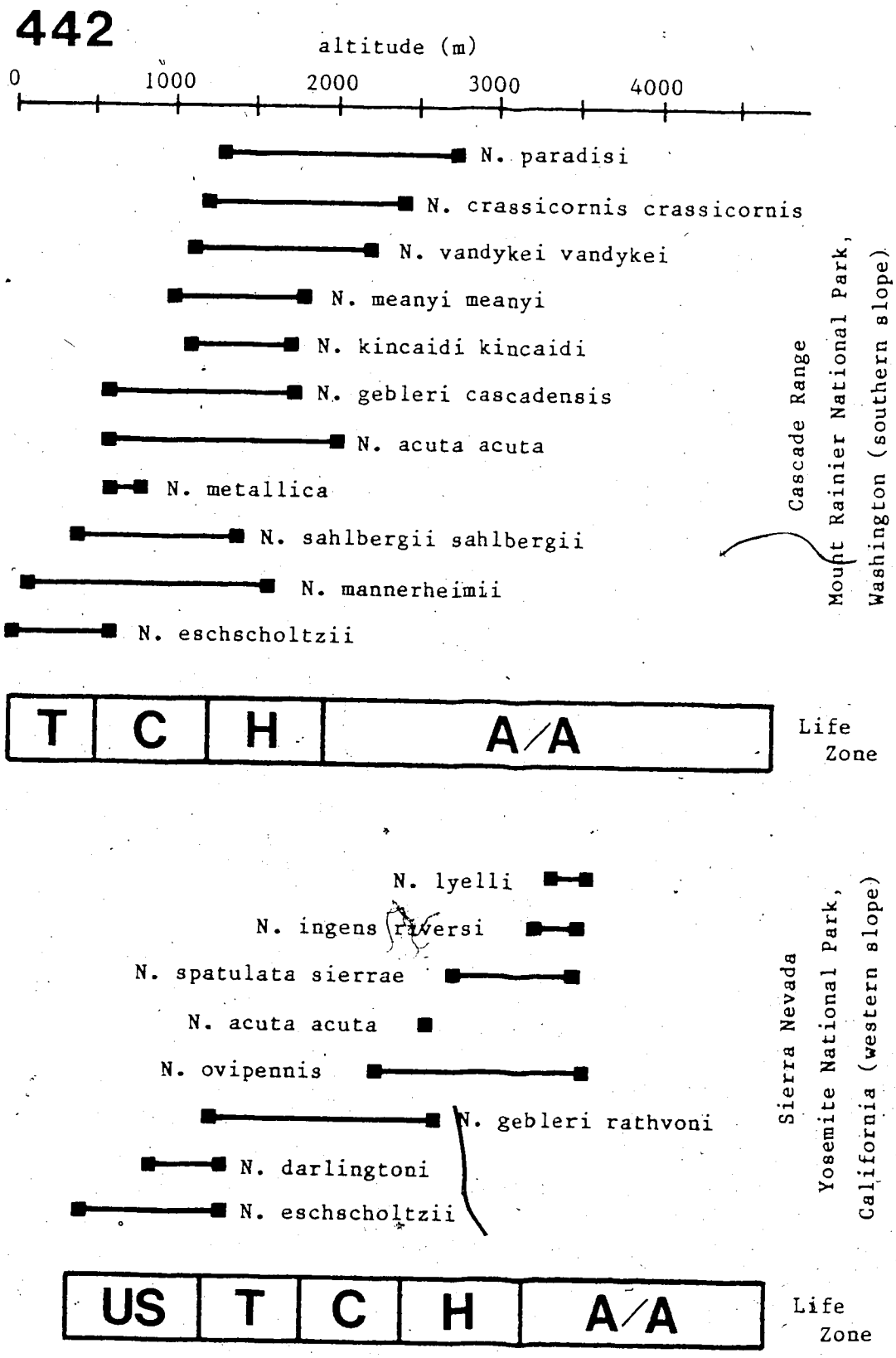

442
altitude (m)
0
1000
2000
3000
4000
N. paradisi
N. crassicornis crassicornis
N. vandykei vandykei
N. meanyi meanyi
N. kincaidi kincaidi
N. gebleri cascadensis
N. acuta acuta
N. metallica
N. sahlbergii sahlbergii
N. mannerheimii
N. eschscholtzii
Cascade Range
Mount Rainier National Park,
Washington (southern slope)
T
C
H
A/A
Life Zone
N. lyelli
N. ingens riversi
N. spatulata sierrae
N. acuta acuta
N. ovipennis
N. gebleri rathvoni
N. darlingtoni
N. eschscholtzii
Sierra Nevada
Yosemite National Park,
California (western slope)
US
T
C
H
A/A
Life Zone

Fig. 443. Patterns of altitudinal zonation among Nebria taxa in selected mountain ranges. Upper half of figure = Rocky Mountains, Front Range, Colorado (eastern slope); lower half of figure = Rocky Mountains, Sangre de Cristo Range, New Mexico (northern slope). Line segments represent known altitudinal range of each taxon. Ranges of life zones in each mountain area are plotted below line segments for taxa (abbreviations: A/A = Arctic/Alpine Zone; H = Hudsonian Zone; C = Canadian T = Transition Zone; and US = Upper Sonoran Zone).

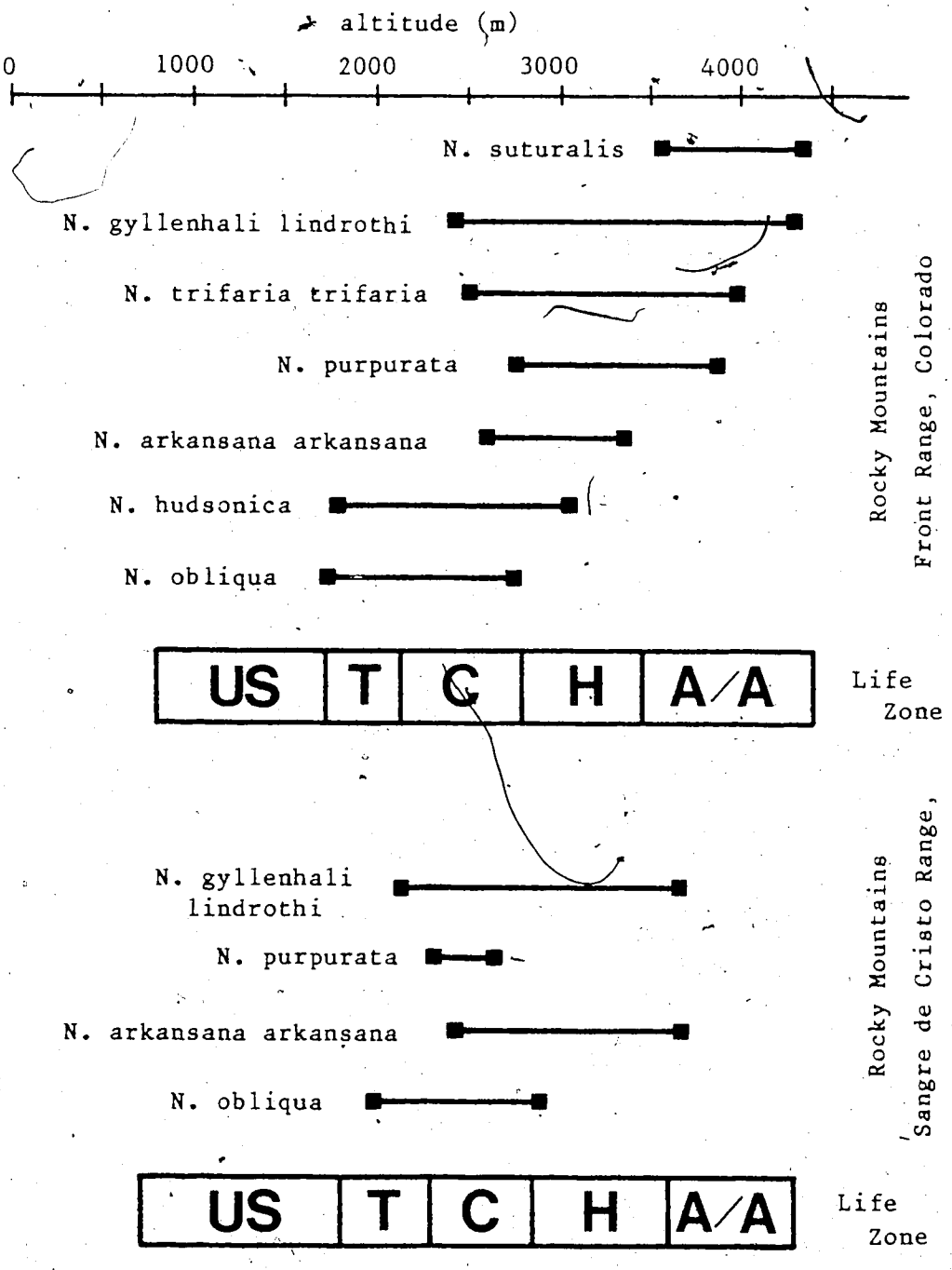
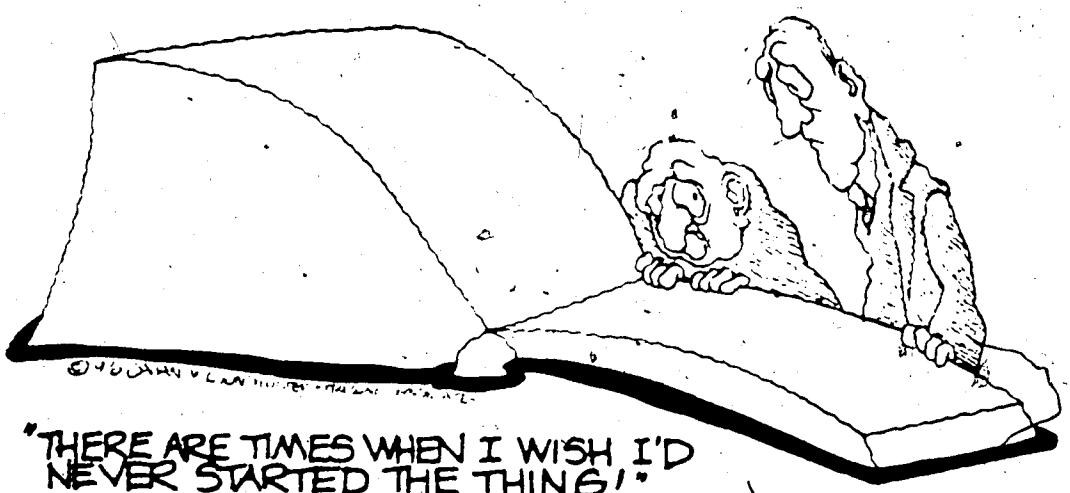

altitude (m)
0
1000
2000
3000
4000
N. suturalis
N. gyllenhali lindrothi
N. trifaria trifaria
N. purpurata
N. arkansana arkansana
N. hudsonica
N. obliqua
US
T
C
H
A/A
Life Zone
Rocky Mountains
Front Range, Colorado
(eastern slope)
N. gyllenhali lindrothi
N. purpurata
N. arkansana arkansana
N. obliqua
US
T
C
H
A/A
Life Zone
Rocky Mountains
Sangre de Cristo Range,
New Mexico (northern slope)

Fig. 444. The author conferring with his major professor on a point critical to the project.



"THERE ARE TIMES WHEN I WISH I'D NEVER STARTED THE THING!"