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THE UNIVERSITY OF ALBERTA

# Classification and evolution of the eumenine wasp genus *Symmorphus* Wesmael (Hymenoptera: Vespidae)

by

Jeffrey Malcolm Cumming

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF Doctor of Philosophy

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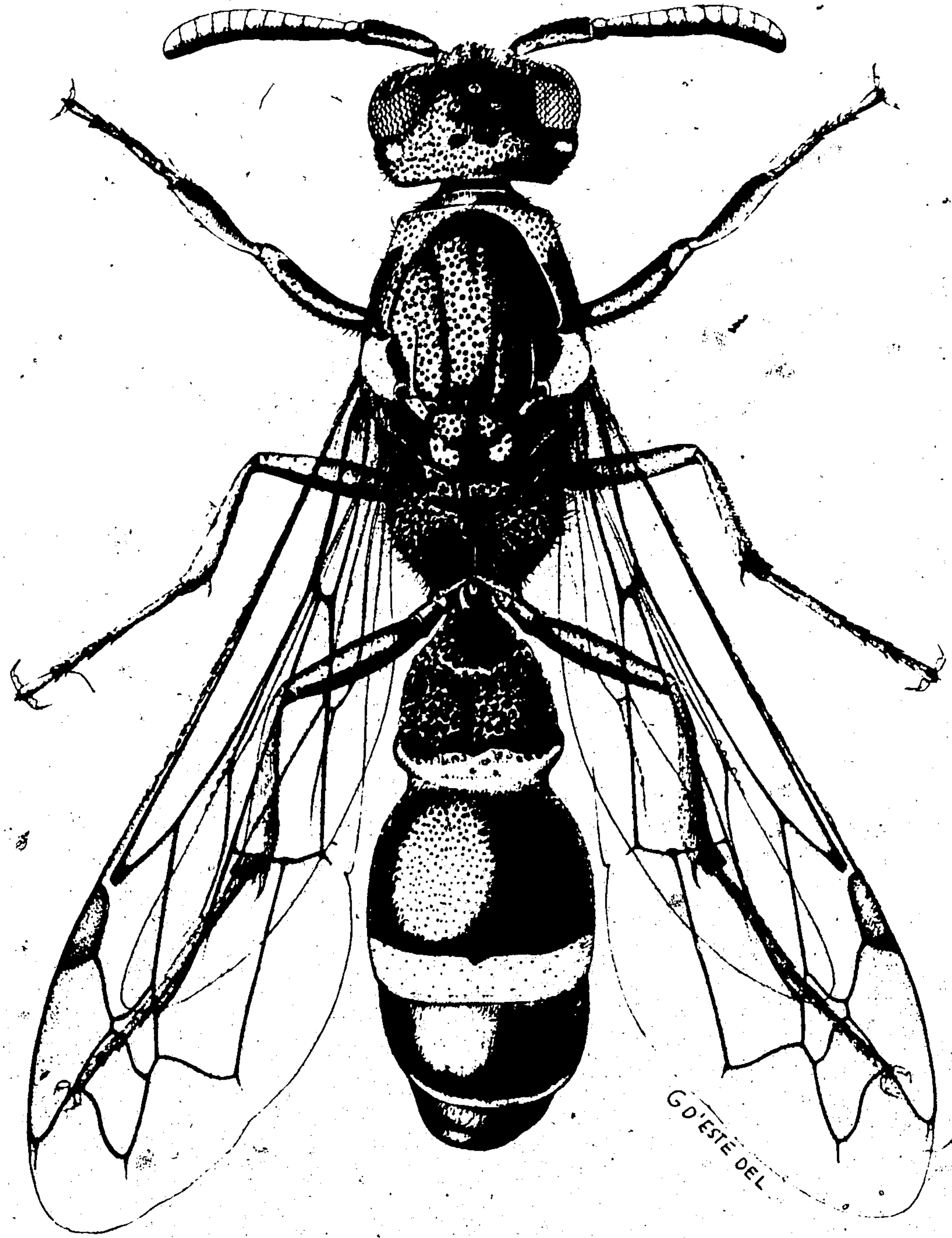
The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Classification and evolution of the eumenine wasp genus *Symmorphus* Wesmael (Hymenoptera: Vespidae) submitted by Jeffrey Malcolm Cumming in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

Supervisor

External Examiner

Date March 26, 1986



Frontispiece:

*Symmorphus glasunowi* Morawitz, female

# ABSTRACT

The genus *Symmorphus* Wesmael is distributed throughout the Oriental, Palearctic and Nearctic regions, as well as the northern most Neotropical region, and appears to occupy a relatively isolated phylogenetic position within the Eumeninae. Females of *Symmorphus* for those species in which nesting behavior is known, mass-provision cells in pre-existing cavities with chrysomelid, curculionid or microlepidopterous larvae.

Thirty-five species are recognized, including three new species and two new subspecies. Keys are provided for the identification of adult specimens, all species are described and their geographical distributions mapped.

Two subgenera, *S. (Parasymmorphus)* Cumming and Vecht and *S. (Symmorphus)* Wesmael, are recognized. *S. (Parasymmorphus)* includes *S. parvilineatus* (Cameron), *S. momunganensis* (Schulthess) and *S. negrosensis* Cumming and Vecht. Within *S. (Symmorphus)* three informal species groups are recognized, with the following included species and subspecies: (1) *S. hoozanensis* group — *S. hoozanensis* (Schulthess), *S. alkimus alkimus* Cumming and Vecht, *S. alkimus dialeukus* new subspecies (type-locality Sibolangit, N. Sumatra), *S. ambotretus* new species (type-locality Mt. Omei, Sichuan Province, China) and *S. canlaonicus* new species (type-locality Mt. Canlaon, Negros Oriental, Philippines); (2) *S. declivis* group — *S. declivis* Harttig; (3) *S. murarius* group — *S. murarius* (Linnaeus), *S. foveolatus* Gussakovskij, *S. glasunowi* Morawitz, *S. sichuanensis* Lee, *S. crassicornis* (Panzer), *S. captivus* (Smith), *S. angustatus* (Zetterstedt), *S. albomarginatus albomarginatus* (Saussure), *S. albomarginatus midas* new subspecies (type-locality Bentsen Rio Grande Valley State Park, Texas, USA), *S. decens* (Kostylev), *S. violaceipennis* Soika, *S. mizuhonis* Tsuneki, *S. bifasciatus* (Linnaeus), *S. debilitatus* (Saussure), *S. cliens* Soika, *S. connexus* (Curtis), *S. lucens* (Kostylev), *S. sublaevis* (Kostylev), *S. canadensis* (Saussure), *S. projectus* Bohart, *S. tukvarensis* (Meade-Waldo), *S. nipteroides* new species (type-locality N. Yourdou, India), *S.*

*fuscipes* (Herrich-Schaeffer), *S. apiciornatus* (Cameron), *S. allobrogus* (Saussure), *S. cristatus* (Saussure), *S. gracilis* (Brullé) and *S. paralleliventris* Soika.

A cladistic analysis of 28 characters indicates that *S. (Parasymmorphus)* is the sister group to *S. (Symmorphus)*, with *S. parvilineatus* inferred to be the sister species of *S. momunganensis* + *S. negrosensis* within *S. (Parasymmorphus)*. In the nominate subgenus, the *S. hoozanensis* group is hypothesized to be the sister group of the *S. murarius* group + the monobasic *S. declivis* group. Within the *S. hoozanensis* group, *S. hoozanensis* and *S. canlaonicus* are inferred to be sister species, with *S. ambotretus* and *S. alkimus* forming an unclarified trichotomy with this lineage. The relationships of the species included within the *S. murarius* group are mainly unresolved. *S. murarius* is hypothesized to be the sister group of the *S. sichuanensis* + *S. foveolatus* + *S. glasunowi* lineage, of which *S. sichuanensis* is considered the most primitive. *S. crassicornis, S. captivus, S. angustatus* and *S. albomarginatus* appear closely related and together may share a sister group relationship with *S. decens*. In addition, the following sister species pairs are suggested: *S. violaceipennis* + *S. mizuhonis*, *S. debilitatus* + *S. cliens*, *S. lucens* + *S. sublaevis*, *S. tukvarensis* + *S. nipteroides*, *S. allobrogus* + *S. cristatus*, and *S. gracilis* + *S. paralleliventris*. Available data are insufficient to resolve the relationships of these lineages to each other, or to the remaining species in the *S. murarius* group.

Comparison of these proposed phylogenetic relationships with the chorological patterns observed within *Symmorphus* and other Vespidae, interpreted in context of current paleogeographic and paleoclimatic reconstructions, suggests the following hypotheses about the historical zoogeography of the genus: (1) *Symmorphus* appears to have originated in the Oriental region at the end of the Mesozoic; (2) divergence of *S. (Parasymmorphus)* from *S. (Symmorphus)* probably occurred in the earliest Cenozoic of this region; (3) expansion of *S. (Symmorphus)* north into Asia during the early Paleocene, accompanied by a north-south vicariance probably resulted in production of both the more southerly *S. hoozanensis* group and

the more northerly *S. declivis* + *S. murarius* group lineages; (4) the brief partial northern withdrawal of the Turgai Sea from Eurasia in the Paleocene may have allowed westward expansion of the *S. declivis* group + *S. murarius* group clade from Asia, with re-establishment of this barrier in the early Eocene isolating the ancestral stock of these groups in Europe and Asia respectively; (5) within *S. (Parasymmorphus)*, differentiation of *S. parvilineatus* from the *S. momunganensis* + *S. negrosensis* clade appears to be due to a relatively old perhaps early mid-Tertiary vicariance, with the much more recent fluctuating sea levels of the Pleistocene presumably responsible for isolation of *S. momunganensis* and *S. negrosensis* on separate Philippine islands; (6) similarly within the *S. hoozanensis* group, fluctuating Pleistocene sea levels may have allowed for vicariances between *S. hoozanensis* and *S. canlaonicus*, as well as *S. alkimus alkimus* and *S. alkimus dialeukus*; (7) much of the evolution of the cool adapted *S. murarius* group probably occurred since the end of the Eocene, with permanent withdrawal of the Turgai Sea allowing the first westward expansion of the group into Europe, possibly at the expense of the European *S. declivis* group; (8) the *S. murarius* - *S. sichuanensis* - *S. foveolatus* - *S. glasunowi* lineage may have been one of the earliest established within the *S. murarius* group; (9) the vicariant events involved in the separation of *S. violaceipennis* and *S. mizuhonis*, as well as *S. tukvarensis* and *S. nipteroides*, are hypothesized to be correlated with the orogeny of the Himalaya during the mid-Miocene; (10) the ancestor of *S. gracilis* and *S. paralleliventris* probably reached the Atlas Mountains of northern Africa via Iberia in the late Miocene, with *S. paralleliventris* having become isolated there in the early Pliocene; (11) the four New World species appear to represent separate invasions from the Palearctic region via the Bering land bridge, beginning perhaps as early as the Oligocene or Miocene for the ancestor of *S. projectus*, but probably occurring during the Pliocene or Pleistocene for the ancestors of *S. canadensis*, *S. cristatus* and *S. albomarginatus*; (12) fragmentation of the range of *S. albomarginatus* during the late Pleistocene is hypothesized to have resulted in isolation of *S. albomarginatus midas* in Central America.

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I wish to express my appreciation to the individuals and institutions mentioned below, for without their generous assistance this work could not have been completed.

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For allowing me to examine material in their collections, or for the loan of specimens, I am grateful to the individuals listed under Section 2.1. In addition I would like to thank Dr. R. M. Bohart (UCD), M. C. Day (BMNH), Dr. A. S. Menke (USNM), Dr. A. G. Soika (MSNV) and Dr. J. van der Vecht (Putten) for being such helpful hosts while studying material at their respective institutions.

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My study of type material was assisted by a number of individuals. Dr. R. M. Bohart provided me with notes on some of the types of *Symmorphus* housed in the BMNH, prior to my visit there. Dr. J. van der Vecht help me with the location of a number of types housed in European institutions. Dr. N. V. Kurzenko supplied me with valuable information on the type material of *Symmorphus* residing in the collection of ZIL, which Dr. R. E. Roughley kindly delivered to me by hand from Leningrad. D. Hollingdale helped me verify the location of certain types in the collection of MSUM during a visit she made to Moscow.

Numerous co-workers helped me with the technical aspects of this work. I am deeply indebted to N. J. Porteous for carefully compiling much of the distributional data given under each species treatment. I. S. Askevold and F. A. H. Sperling helped translate passages from papers in German, as did Dr. R. E. Roughley for papers in Spanish and J.-F. Landry for those in French. E. Maw translated a number of Italian papers and along with K. P. Fennie helped translate passages in Russian, as well as transliterate Russian locality labels. Dr. S. Liu kindly translated the Chinese description of *S. sichuanensis* Lee. D. R. Maddison and J. E. O'Hara both assisted with the computer generated production of the manuscript, significantly contributing to quality of the final version. In addition, assistance provided G. D. Braybrook, G. W. Courtney, D. R. Maddison, J. E. O'Hara and J. S. Scott in various aspects of the preparation of the illustrations, is gratefully acknowledged. Dr. A. G. Soika generously granted permission to produced the frontispiece, which was competently illustrated by his wife.

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My wife, Susan, has continually supported my academic endeavors, directly through assistance in both field and laboratory work and indirectly through constant encouragement at home. My accomplishments as a graduate student are to a great degree due to her efforts.

Finally, financial support for this study was provided by the Natural Sciences and Engineering Research Council of Canada Grant A-1399 to Dr. G. E. Ball and through a Grant-in-Aid of Research from the Boreal Institute for Northern Studies, University of Alberta.

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# 1. INTRODUCTION

The genus *Symmorphus* Wesmael is a member of the diverse, although relatively unstudied vespid subfamily, Eumeninae. Adults of *Symmorphus* are recognized by the first metasomal tergum, which possesses both a transverse carina and median longitudinal furrow, as well as widely separated or enlarged cephalic foveae filled with setae in females and a simple antennal apex in males. As defined here, the genus contains 35 species distributed throughout the Nearctic, Palearctic and Oriental regions, with undoubtedly more undescribed species to be discovered in the latter region. Unlike females of most other eumenine taxa, which usually provision their nests exclusively with larval Lepidoptera, females of *Symmorphus* (for those species in which nesting behavior is known) mass-provision cells in pre-existing cavities, with chrysomelid, curculionid or microlepidopterous larvae.

The taxonomic history of *Symmorphus* has been primarily one of isolated species descriptions proposed under a variety of generic names, beginning with description of *Vespa muraria* by Linnaeus in 1758. This approach, in conjunction with regional revisions treating several species, the most noteworthy being those of Saussure (1875) for North America, Berland (1928) for France, Blüthgen (1961) for Middle Europe and Soika (1975) for Japan, has proceeded with little comparative basis, creating confusion over species identities and considerable potential for synonymy.

In addition, relationships of *Symmorphus* to the rest of the Eumeninae have remained unclear. Possession of a transverse carina on metasomal tergum 1 has generally been considered evidence for a relationship near *Ancistrocerus* (see for example Soika, 1941 p. 160), while the simple male antennal apex and larval curculionid provisions, features of other non-eumenine Vespidae (Carpenter and Cumming, 1985) potentially suggest a very early eumenine origin. Recently, Carpenter and Cumming (1985) tentatively placed *Symmorphus* as the sister group to a monophyletic clade containing *Odynerus*, *Pterocheilus* and related genera, on the basis of similarities in the cephalic foveae of both groups. However, subsequent detailed examination of this character system by Cumming and Leggett (1985) indicated that these similarities probably developed independently in both *Symmorphus* and the *Odynerus-Pterocheilus* lineage.

The primary purpose of this contribution is to clarify the classification of *Symmorphus* and provide workable keys for identification of adults. In addition, phylogenetic and zoogeographic aspects of the genus are considered, including discussion of the relationships of *Symmorphus* to the remainder of the Eumeninae. It is hoped that this revision will provide stimulus for further research on this interesting genus of wasps, including promotion of world-wide, rather than just regional, revisionary studies on other Vespidae.

# 2. MATERIALS AND METHODS

## 2.1 Materials

This study is based on examination of approximately 20,000 adult specimens of *Symmorphus* and other eumenines, borrowed from 73 institutions or individuals listed below. Acronyms given here, are used throughout the text, to indicate deposition of specimens.

| | |
|---|---|
| AEI | American Entomological Institute, Gainesville, Florida, USA. (H. K. Townes) |
| AMNH | American Museum of Natural History, New York, New York, USA. (M. Favreau) |
| ANSP | Academy of Natural Sciences, Philadelphia, Pennsylvania, USA. (D. Azuma and C. E. Dunn) |
| AUA | Auburn University, Auburn, Alabama, USA. (W. E. Clark) |
| BMNH | British Museum (Natural History), London, England. (M. C. Day and C. R. Vardy) |
| BPBM | Bernice P. Bishop Museum, Honolulu, Hawaii, USA. (G. M. Nishida) |
| CAS | California Academy of Sciences, San Francisco, California, USA. (P. H. Arnaud and W. J. Pulawski) |
| CDAS | California Department of Food and Agriculture, Sacramento, California, USA. (M. S. Wasbauer) |
| CMP | Carnegie Museum, Pittsburgh, Pennsylvania, USA. (G. Ekis and G. E. Wallace) |

| | |
|---|---|
| CNC | Canadian National Collection, Agriculture Canada, Ottawa, Ontario, Canada. (L. Masner) |
| CNM | Colombo National Museum, Colombo, Sri Lanka. (via K. V. Krombein, USNM) |
| CSU | Colorado State University, Fort Collins, Colorado, USA. (H. E. Evans) |
| CU | Cornell University, Ithaca, New York, USA. (J. M. Carpenter and J. A. Schafrik) |
| CUSC | Clemson University, Clemson, South Carolina, USA. (J. C. Morse) |
| DANC | H. V. Danks collection [private], Ottawa, Ontario, Canada. |
| DEI | Institute für Pflanzenschutzforschung [formerly Deutsches Entomologisches Institut], Kleinmachnow, Eberswalde, DDR. (J. Oehlke) |
| ETHZ | Eidgenössische Technische Hochschule, Zürich, Switzerland. (W. Sauter) |
| FSCA | Florida State Collection of Arthropods, Florida State Department of Agriculture and Consumer Services, Gainesville, Florida, USA. (L. A. Stange) |
| GUIC | K. Guichard collection [private], London, England. |
| GUSC | J. Gusenleitner collection [private], Linz, Austria. |
| IBPV | Institute of Biology and Pedology, Far Eastern Scientific Center, Vladivostok, USSR. (N. V. Kurzenko) |
| INHS | Illinois Natural History Survey, Urbana, Illinois, USA. (W. E. LaBerge) |
| IRSN | Institut Royal des Sciences Naturelles, Brussels, Belgium. (P. Dessart) |

| | |
|---|---|
| IZAS | Institute of Zoology, Academia Sinica, Beijing, People's Republic of China. (Lee Tie-sheng) |
| JMCU | Designates specimens in my personal collection. |
| LACM | Los Angeles County Museum of Natural History, Los Angeles, California, USA. (R. R. Snelling) |
| LARS | Lethbridge Agriculture Research Station, Agriculture Canada, Lethbridge, Alberta, Canada. (K. W. Richards) |
| LEM | Lyman Entomological Museum, McGill University, Ste. Anne de Bellevue, Quebec, Canada. (V. R. Vickery) |
| LS | Linnaean Society, London, England. (via M. C. Day, BMNH) |
| MCZ | Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA. (R. J. McGinley and M. M. Pearce) |
| MHNG | Muséum d'Histoire Naturelle, Geneva, Switzerland. (I. Löbl) |
| MIZT | Museo ed Istituto di Zoologia Sistematica, Università di Torino, Torino, Italy. (via A. Giordani Soika, MSNV) |
| MNHP | Muséum National d'Histoire Naturelle, Paris, France. (S. Kelner-Pillault) |
| MSNV | Museo Civico di Storia Naturale, Venice, Italy. (A. Giordani Soika) |
| MSUM | Moscow State University Museum, Moscow, USSR. (A. V. Antropov) |
| NAMC | T. Nambu collection [private], Yorii, Japan. |
| NCSR | North Carolina State University, Raleigh, North Carolina, USA. (C. Parron) |

| | |
|---|---|
| NHMB | Naturhistorisches Museum, Basel, Switzerland. (W. Wittmer) |
| NHMV | Naturhistorisches Museum, Vienna, Austria. (M. Fischer) |
| NMVM | National Museum of Victoria, Abbotsford [formerly Melbourne], Victoria, Australia. (A. Neboiss) |
| NRS | Naturhistoriska Riksmuseet, Stockholm, Sweden. (K.-J. Hedqvist and L.-Å. Janzon) |
| NSMT | National Science Museum, Tokyo Metropolitan University, Tokyo, Japan. (R. Ishikawa and J. Kojima) |
| ODAS | Oregon Department of Agriculture, Salem, Oregon, USA. (R. L. Westcott) |
| OSU | Ohio State University, Columbus, Ohio, USA. (C. A. Triplehorn) |
| OSUC | Oregon State University, Corvallis, Oregon, USA. (G. R. Ferguson) |
| PAGC | G. Pagliano collection [private], Torino, Italy. |
| PMV | Provincial Museum, Victoria, British Columbia, Canada. (R. A. Cannings) |
| RNHL | Rijksmuseum van Natuurlijke Histoire, Leiden, Netherlands. (C. van Achterberg and J. van der Vecht) |
| ROM | Royal Ontario Museum, Toronto, Ontario, Canada. (G. B. Wiggins) |
| SMEK | Snow Museum of Entomology, University of Kansas, Lawrence, Kansas, USA. (C. D. Michener) |
| SMF | Senckenberg Museum, Frankfurt am Main, BRD. (J.-P. Kopelke) |
| TAMU | Texas A & M University, College Station, Texas, USA. (H. R. Burke and S. J. |

Merritt)

| | |
|---|---|
| TMB | Természettudományi Múzeum, Budapest, Hungary. (J. Papp and L. Zombori) |
| UAE | University of Alberta, Edmonton, Alberta, Canada. (G. E. Ball) |
| UAF | University of Arkansas, Fayetteville, Arkansas, USA. (R. Chenowith) |
| UCB | Essig Museum of Entomology, University of California, Berkeley, California, USA. (J. A. Chemsak) |
| UCD | University of California, Davis, California, USA. (R. M. Bohart and R. O. Schuster) |
| UCR | University of California, Riverside, California, USA. (S. I. Frommer) |
| UGA | University of Georgia, Athens, Georgia, USA. (C. L. Smith and C. K. Starr) |
| UGO | University of Guelph, Guelph, Ontario, Canada. (S. A. Marshall and D. H. Pengelly) |
| UIM | University of Idaho, Moscow, Idaho, USA. (W. F. Barr) |
| UMAA | University of Michigan, Ann Arbor, Michigan, USA. (R. D. Alexander and D. P. Cowan) |
| UMSP | University of Minnesota, St. Paul, Minnesota, USA. (P. J. Clausen) |
| USNM | National Museum of Natural History [formerly United States National Museum], Smithsonian Institution, Washington, D.C., USA. (K. V. Krombein and A. S. Menke) |
| UWL | University of Wyoming, Laramie, Wyoming, USA. (R. Lavigne) |

| | |
|---|---|
| UWM | University of Wisconsin, Madison, Wisconsin, USA. (S. Krauth) |
| UZIL | Universitets Zoologiska Institut, Lund, Sweden. (R. Danielsson) |
| VPI | Virginia Polytechnic Institute and State University, Blackburg, Virginia, USA. (M. Kosztarab) |
| WSU | Washington State University, Pullman, Washington, USA. (W. J. Turner) |
| YAMC | Sk. Yamane collection [private], Kagoshima University, Kagoshima, Japan. |
| ZIL | Zoological Institute, Academy of Sciences, Leningrad, USSR. (V. I. Tobias) |
| ZMHB | Zoologisches Museum, Humboldt-Universität, East Berlin, DDR. (F. Koch) |
| ZMUC | Zoologisk Museum, Universitets Copenhagen, Copenhagen, Denmark. (B. Petersen and O. Lomholdt) |
| ZSBS | Zoologische Sammlungen des Bayerischen Staates, Munich, BRD. (F. Bachmaier and E. Diller) |

## 2.2 Methods[1]

### 2.2.1 Specimen examination

Dried adult specimens were examined with a Leitz Wetzlar stereoscopic microscope. Punctation and sculpture were more easily discerned when reflection of light off the specimen being examined was reduced. This was accomplished by mounting a piece of mylar drafting film

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[1] Methods used to infer phylogenetic relationships among species of *Symmorphus*, are discussed in chapter 6.

to the specimen holder, between the specimen and the light source. In addition, details of certain structures were examined with the aid of a Cambridge Stereoscan 250 scanning electron microscope.

### 2.2.2 Sex determination

Like most other aculeates, males of *Symmorphus* possess seven visible metasomal segments and an antenna with 13 articles, compared with the female condition of six visible metasomal segments and an antenna with 12 articles. In addition, sex can usually be determined by checking the apex of the metasoma for elongate parameral spines that protrude from the genitalia of male specimens.

### 2.2.3 Measurements

Measurements and ratios used in this study are described and discussed below. They were obtained with a Leitz Wetzlar stereoscopic microscope at magnifications of 12.5, 50 and 100 X, using an eyepiece reticle with a scale interval of 0.5 mm at 12.5 X.

Head.—Height and width of the head (fig. 1) are measured in frontal view with the head oriented so that the entire ocellar triangle is just in view. Head height is measured medially from the most apical margin of the clypeus to the dorsal margin of the head. Head width is the maximum width including the eyes. A ratio of head height to width provides a measure of degree of elongation of the head.

Clypeus.—Measurements of the clypeus (fig. 2) are taken in frontal view, with the clypeus oriented as flat in the plane of the reticle as possible. Clypeal height is measured from the most apical margin of the clypeus to the frontoclypeal suture, while clypeal width is the maximum width including the lateral lobes. Clypeal height to width ratio provides a measure of degree of elongation of the clypeus.

Vertex.—The ocular ocellar line (OOL) is the minimum distance between the inner eye margin and the outer margin of the posterior ocellus. The lateral ocellar line (LOL) is the minimum distance between the inner margins of the anterior and posterior ocelli. Both measurements are conveniently expressed as ratios of the posterior ocellar line (POL), which is the minimum distance between the inner margins of the posterior ocelli (fig. 3). Cephalic foveal diameter is the maximum diameter of a single fovea and is expressed as a ratio of trans-scutal sulcus length to compensate for foveal differences based on body size. The cephalic foveal interval is the minimum distance between the inner margins of both foveae (fig. 3). It is conveniently compared to the adjacent POL, by expressing the interval as a ratio of the POL.

Antenna.—Measurements of article 13 of the male antenna are taken in profile, with length of the article measured along the inner margin and width measured basally at 90 degrees to the length measurement. Length to width ratio for this article provides a measure of degree of elongation of article 13.

Trans-scutal sulcus.—Length of the trans-scutal sulcus (fig. 6) is the average length of the medial portion of the sulcus, measured from its posterior margin to the trans-scutal articulation, which is extended along the anterior edge of the sulcus (use of average length of the medial portion of the sulcus is necessary, because in some specimens irregularity along the posterior margin of the sulcus causes length measured at the midline alone, to be greater or less than might be expected based on specimen size). Length of the trans-scutal sulcus appears to vary proportionally with size of a specimen and unlike many other features (e.g. ocellar diameter) does not vary significantly between species of *Symmorphus*. As such, this measurement is usefully incorporated into ratios with those of other structures, to compenstate for differences correlated with body size.

Propodeal superior shelf.—Length of the propodeal superior shelf is measured medially, with the entire mesosoma (but not necessarily the shelf) oriented horizontally (fig. 5). Shelf length is expressed as a ratio of trans-scutal sulcus length, to compensate for differences based on body size.

Metasomal tergum 1.—Measurements of metasomal tergum 1 (fig. 7) are taken dorsally, with the postcarinal area oriented as flat in the plane of the reticle as possible. Apical width is equivalent to the maximum width of the tergum. Carinal width is measured along an imaginary line, drawn between the most posterior lateral points of the transverse carina as viewed dorsally, so that irregularity along the medial portion of the carina is disregarded. Postcarinal length is measured medially, from this imaginary carinal line to the apical margin of the tergum. A ratio of postcarinal length to apical width provides a measure of degree of elongation of the postcarinal area, while a ratio of carinal width to apical width measures degree of convergence of the postcarinal sides towards the base of metasomal tergum 1.

Metasomal segment 2.—Measurements of metasomal tergum 2 are taken dorsally. Width of the tergum is the maximum width, while length of the tergum is measured medially and does not include the longitudinally ridged base usually concealed under the apex of metasomal tergum 1. Tergum 2 length to width ratio provides a measure of degree of elongation of metasomal tergum 2. Length of the apical margin of metasomal segment 2 is the maximum length on either tergum or sternum. Apical margin length is expressed as a ratio of trans-scutal sulcus length, to compensate for differences based on body size.

Body length.—Length of the body is taken as the combined length of head, mesosoma, metasomal tergum 1 and metasomal tergum 2, with each region oriented horizontally and measured dorsally. This measurement eliminates differences due to flexure, or telescoping of the retractible segments of the metasoma.

### 2.2.4 Illustration

Line drawings of structural features were made with the aid of a camera lucida attached to a Wild M5 stereoscopic microscope. Drawings were altered before inking so that characteristics of each species were drawn in comparable positions. After inking, drawings were compared to the structure for accuracy.

Scanning electron micrographs were made with a Cambridge Stereoscan 250 scanning electron microscope (SEM). Specimens to be photographed were prepared by first soaking them in a 50% solution of concentrated ammonium hydroxide until they were relaxed and clean. Any remaining dirt was removed, by transferring specimens in ammonium hydroxide solution, to an ultrasonic cleaner for brief periods. Specimens were then rinsed in distilled water and dehydrated in 70% and 95% ethyl alcohol, before being air dried or critical point dried. If a specimen was to be air dried, it was soaked briefly in chloroform after dehydration, to promote rapid drying so that setae would not adhere to the cuticle. Specimens were then attached to SEM stubs using double-sided sticky tape and grounded with silver conducting paint. If sculptural details of a specimen were obscured by setae, the setae were removed with a small amount of adhesive on the end of a pin, scratched from double-sided tape, as described by Gibson (1985). After final removal of setae and any minute particles of dirt, specimens were coated with gold in a sputter coater.

### 2.2.5 Terms and word usage

Terms used for adult structure (figs. 1-60) primarily follow those in Carpenter and Cumming (1985). Description of surface sculpture and punctation follows Harris (1979), while names used for propodeal carinae are those proposed by Bohart and Stange (1965). The groove dividing the mesoscutum (excluding the axillae) from the mesoscutellum, has been generally referred to as the trans-scutal suture in aculeates (Duncan, 1939; Snodgrass, 1935). In specimens of *Symmorphus* it is formed by the trans-scutal articulation, a line of flexibility, anteriorly, as well as a prominent invaginated ridge (sulcus *sensu* Daly, 1964) posteriorly. The trans-scutal articulation occurs in most apocritans and a few symphytans (Gibson, 1985). The more posterior invaginated ridge may be homologous with the medial portion of the scuto-scutellar sulcus that primitively subdivides the entire mesoscutum from the mesoscutellum in Hymenoptera, but is variedly prominent in aculeates, including the Vespidae and is referred to here as the trans-scutal sulcus. In addition, the terms used for the carinae of metasomal sternum 1, which are not similar to the sternal carinae of other eumenines (Carpenter and Cumming, 1985), are newly proposed.

In certain instances where features of taxa are discussed, reference to membership within the taxon being referred to is omitted, if the main point is obscured by addition of such phrases as "members of", "females of", "males of species of" etc.

### 2.2.6 Species and subspecies concepts

The concept of species adopted here, is essentially that of the evolutionary species concept of Simpson (1961) and Wiley (1978, 1981), while considering interbreeding among individuals of a bisexual species an important component in species cohesion. Although not directly observed, evolutionary identity and reproductive isolation are inferred on the basis of two criteria, that of phenetic divergence and geographical distribution. Forms differing in at least two attributes that occur sympatrically are considered separate species, as are allopatric forms that exhibit a similar degree of phenetic divergence. Very similar forms that differ in only a single feature, or geographically separated forms connected by extensive clines of intermediate specimens, are both recognized as belonging to single species.

A subspecies is here considered a geographically separate portion of a species, not connected by extensive clines of intermediate specimens, that consistently differs from the remaining portion of that species by a single feature. Subspecies are recognized in only two species, *Symmorphus alkimus* and *S. albomarginatus*.

### 2.2.7 Descriptive format

For previously described species or subspecies, reference to the original publication of the valid name and each junior synonym is provided, with repositories of primary types following in parentheses. Misidentifications where determined, are also included in the synonymical list, which is presented chronologically, with questionable synonyms given last. Where applicable, alternate senses of listed nominal species are provided for cross-referencing purposes, following the synonymical list.

Label data for primary types and allotypes, of both new and described species, including subspecies, are cited in full, following the system described by O'Hara (1983). Labels are listed from the top downward, with data from each label enclosed in quotation marks and the lines of each label delimited by oblique slash marks. Data are recorded exactly as found on the labels, with additional information included in square brackets. Label data for paralectotypes and paratypes other than allotypes, are listed alphabetically and in a uniform manner, although treated less rigorously than for other types. Repositories for all types examined are given in parentheses.

Additional diagnostic information to that given in the keys, including comparison with similar taxa, is provided prior to both subgeneric and species level descriptions, under the heading "Recognition". Determinations made with the keys should be verified by consulting this section under the pertinent taxa.

Due to time constraints involved with the completion of this dissertation, complete descriptions are presented for only the first 12 included species. Remaining species are described cursorily through reference to Tables 1 through 4, which give measurements and important character states for each species. These species will be fully described in the published version of the present work. Variation is included throughout each species description, although variation observed to occur along geographic clines is additionally discussed under a separate heading.

Information concerning geographical distribution and adult seasonal occurrence is taken from label data. These data, exclusive of locality records previously given for type material, are listed for each included species and subspecies in the following manner. For Old World taxa, localities are listed alphabetically by country, with countries arranged alphabetically. Since records for many of the taxa are numerous and excessive relative to information supplied, the data are summarized for each country, if there are more than five localities recorded. In such instances only the earliest and latest seasonal records are listed, in addition to records along the periphery of the range. However, all records from USSR are given, due to the relatively small number of specimens examined for the very large area represented. New World taxa are similarly listed for each province (Canada) and state (USA), rather than for each country, with provinces arranged from east to west and states arranged alphabetically. However, again because of the relatively small number of specimens examined for the large area represented, all records for Northwest Territories, Yukon and Alaska are listed. To facilitate comparison, all collection dates are presented in a uniform manner, in the order of day, month (in Roman numerals) and year. In addition, distributional information is visually depicted and further summarized, with shade maps provided for each species and subspecies. Finally, if less than 25 non-type specimens of a particular species or subspecies were examined, repositories for each specimen are given in parentheses following the label data.

# 3. LIFE HISTORY

## 3.1 Prospectus

Due to time constraints involved with completion of this dissertation, I present here only a brief outline of what will appear in this chapter, in the published version of the present work.

Information gathered from specimen labels, trap-nesting studies, personal observations and published accounts, will form a basis for discussion of the following aspects of life history of *Symmorphus* species: habitats occupied, seasonal activity, nesting requirements, prey taken (see Tables 3 and 4, character 37[2]) and mating behavior.

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[2] Based on records in Berland, 1928; Blüthgen, 1943, 1961; Evans, 1973; Grandi, 1961; Guichard, 1972; Iwata, 1938; Jorgensen, 1942; Krombein, 1967; Lith, 1964; Malyshev, 1911; Maneval, 1932; Medler, 1966; Nielsen, 1932; Richards, 1980; Weaver and Dorsey, 1965; and Wilcke, 1952.

# 4. COMPARATIVE MORPHOLOGY

## 4.1 Prospectus

Due to time constraints involved with completion of this dissertation, I present here only a brief outline of what will appear in this chapter, in the published version of the present work.

Patterns of variation observed, speculations on functional significance (where appropriate) and usefulness in delimiting taxa, will be discussed for character systems of the following adult features of *Symmorphus* species: size, punctation, setation, coloration, head, antenna, mouthparts, prothorax, mesothorax, metathorax, legs, wings, propodeum, metasoma and genitalia. In addition, lack of useful characters on immature stages of *Symmorphus* will be noted.

# 5. CLASSIFICATION

## 5.1 Genus *Symmorphus* Wesmael

*Symmorphus* Wesmael, 1836. Subgenus of *Odynerus* Latreille. Type-species: *Odynerus elegans* Wesmael, 1833 (designated by Richards, 1935).

*Protodynerus* Saussure, 1855. New name for *Symmorphus* Wesmael, based on supposed homonymy with *Symmorpha* Klug, 1807.

*Odynerus* Latreille *sensu* Blüthgen, 1938[3]. Type-species: *Vespa muraria* Linnaeus, 1758 according to Blüthgen.

*Koptodynerus* Blüthgen, 1943. Subgenus of *Odynerus* Latreille *sensu* Blüthgen. Type-species: *Symmorphus declivis* Harttig, 1932 (monobasic).

*Parasymmorphus* Cumming and Vecht, 1986. Subgenus of *Symmorphus* Wesmael. Type-species: *Odynerus (Symmorphus) momunganensis* Schulthess, 1934.

Notes about synonymy.—Blüthgen (1938, and subsequent papers) accepts Westwood's (1840) designation of *Vespa muraria* Linnaeus as the type of *Odynerus* Latreille, although, as Richards and Vecht (1968) note, the type of *Odynerus* had been fixed by Shuckard's earlier designation of *V. spinipes* Linnaeus in 1837. In addition, Blüthgen (1938, 1961) regards Ashmead's (1902) designation of *V. sinuata* Fabricius as the valid type of *Symmorphus* Wesmael, even though Richards (1935) indicates this species was not originally included when Wesmael proposed the name in 1836. Blüthgen (1938) apparently accepts Ashmead's designation, because earlier Wesmael (1833) listed *V. sinuata* Fabricius as a junior synonym of one of the originally included species, *O. bifasciatus* (Linnaeus). However, as Vecht (1966) points out, it is uncertain whether Wesmael still regarded *V. sinuata* Fabricius a synonym of *O.*

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[3] Blüthgen refers to the genus *Symmorphus* as *Odynerus* in all his subsequent papers concerning this taxon.

*bifasciatus* (Linnaeus) when he later proposed *Symmorphus* in 1836. Therefore, Richards' (1935) designation of *O. elegans* Wesmael as the type of *Symmorphus*, must stand.

Recognition.—Adults of *Symmorphus* are distinguished from those of other eumenine genera by the first metasomal tergum which possesses a transverse carina followed by a median longitudinal furrow (figs. 11, 12), widely separated or enlarged cephalic foveae filled with setae in females (figs. 3, 14, 27) and simple antennal apex in males (fig. 28).

Description.—*Female*. Head with height including clypeus 0.91 to 1.16 as high as wide. Clypeus with height 0.58 to 0.76 maximum width; shallowly to deeply emarginate apically; in profile evenly convex throughout, or markedly convex through apical third. Interantennal carina prominent, faint or absent. Antennocular space moderately wide, less than diameter of antennal socket. Interocellar area at approximately same level as remainder of vertex, or abruptly elevated vertically directly posteriad of anterior ocellus. Ocelli with maximum diameter of median ocellus 0.75 to 1.60 trans-scutal sulcus length. OOL 0.80 to 1.37 POL; LOL 0.44 to 0.68 POL. Vertex with cephalic foveae very small to markedly enlarged maximum foveal diameter 0.25 to 5.00 trans-scutal sulcus length; approximate to widely spaced, minimum interval between foveae 0.06 to 1.10 POL; each fovea filled with setae and bordered, or not bordered, posteriorly by a sharp carina. Occipital carina without sharp angle laterally; not forked ventrally; with or without submedial incisions. Antenna with article 3 (flagellomere 1) of moderate length, approximately 1.5 to 2.0 times as long as broad. Mandible with four or five teeth. Maxillary palpus with six and labial palpus with four articles.

Pronotum with carina at crest of anterior face complete, or obsolete dorsally; humeral angle obtusely rounded to acute, not projected to greatly projected, humeral carina absent; pretegular carina present. Notaulus complete, or partially obsolete. Tegula emarginate interiorly, with posterior lobe barely extended past parategula. Axillary fossa broadly rounded, not narrow or slit-like. Mesepisternum with epicnemial carina complete and extended to posterolateral margin of pronotum, or dorsally to entirely obsolete. Pseudosternum with or without high reflexed border along anterior margin. Metanotum with dorsal surface narrow to subequal size of posterior surface. Propodeum with superior shelf present or absent; submedian carina of propodeum complete, or entirely absent to present ventrally; propodeal valvula produced posteriorly or short, fused distally to posterolateral projection of submarginal carina or free; propodeal orifice narrowly acute to broadly rounded dorsally. Mid tibia with single apical spur. Hind coxa with dorsal carina dentiform basomedially. Fore wing with second submarginal cell (1Rs) sessile anteriorly, not petiolate; basal angle of second submarginal cell (formed by Rs + M) acute, not truncate; prestigma short, less than half length of posterior border of pterostigma.

Metasomal tergum 1 broad to markedly elongate, medial postcarinal length 0.46 to 0.91 apical width; sides of postcarinal area markedly to barely convergent towards base, width at transverse carina 0.58 to 0.94 apical width; transverse carina complete or laterally obsolete; longitudinal furrow broadly or sharply impressed, very shallowly to deeply depressed, with or without deeper narrow medial sulcus; tergum with or without depressed apical margin. Metasomal sternum 1 with basal carina straight and transverse, or deeply curved, or inflated and raised posteriorly (faint or absent in some species); basal carina fused to, or well separated from, lateral oblique ridges when ridges present; median longitudinal ridge present or absent. Metasomal segment 2 in profile with base of tergum gradually rounded to obtusely angulate and sternum flat to markedly convex or abruptly truncate posteriad of basal sulcus; tergum with length 0.78 to 1.26 maximum width; sternum without basomedian longitudinal sulcus; apical margin of segment 2 depressed or not depressed, slightly to markedly developed, its maximum length 0.28 to 2.50 length of trans-scutal sulcus.

Body small to relatively large, length to apex of metasomal tergum 2, 5.0 to 15.0 mm, with anterior pronotal face obscurely imbricate to smooth, base of metasomal tergum 2 (under apex of tergum 1) longitudinally ridged and not forming acarinarium, short to moderately long pubescence with or without lengthened setae, and white to yellow to orange-red maculation with hyaline to moderately infuscate wings.

*Male*. Similar to female except as follows: mandible with four teeth; pronotum with humeral angle barely to greatly projected.

Antenna with apex simple, terminal articles not formed as coil or hook; articles 9 to 13 or 10 to 13 each with single tyloid, or tyloids absent from a few species.

Length to apex of metasomal tergum 2, 5.0 to 12.0 mm.

Included taxa and geographical distribution.—The genus contains 35 species plus two additional subspecies, classified into two subgenera. It is distributed throughout the Nearctic, Palearctic and Oriental regions.

### 5.1.1 Key to subgenera of *Symmorphus*

1. Propodeum with valvula produced posteriorly, free distally from posterolateral projection of submarginal carina (figs. 49, 50); mesepisternum with epicnemial carina complete, extended to posterolateral margin of pronotum (fig. 9); female mandible with four teeth........................................................................................................ *S. (Parasymmorphus)* Cumming and Vecht

1'. Propodeum with valvula short posteriorly, fused distally to posterolateral projection of submarginal carina (fig. 51); mesepisternum with epicnemial carina dorsally obsolete, not extended to posterolateral margin of pronotum (figs. 4, 16), or absent; female mandible with five teeth........................................................................................................ *S. (Symmorphus)* Wesmael

### 5.1.2 Subgenus *Parasymmorphus* Cumming and Vecht

*Parasymmorphus* Cumming and Vecht, 1986. Type species: *Odynerus (Symmorphus) momunganensis* Schulthess, 1934.

Recognition.—In addition to those features given in the key to subgenera, members of *S. (Parasymmorphus)* are readily distinguished from most members of the nominate subgenus by a narrowly acute propodeal orifice dorsally and depressed markedly developed apical margin on metasomal segment 2, although both features are approached in a few species of *S. (Symmorphus)* (see "Recognition" under the nominate subgenus).

Description.—*Female*. Clypeus shallowly emarginate apically (fig. 57). Interocellar area at approximately same level as remainder of vertex, or abruptly elevated vertically directly posteriad of anterior ocellus. Ocelli reduced or unreduced, maximum diameter of median ocellus 0.75 to 1.25 trans-scutal sulcus length. Vertex with cephalic foveae small, maximum foveal diameter 0.42 to 0.50 trans-scutal sulcus length; moderately to widely spaced, minimum interval between foveae 0.71 to 1.02 POL; each fovea bordered posteriorly by a sharp carina (fig. 14). Mandible with four teeth.

Pronotum with carina at crest of anterior face complete (somewhat faint dorsally in *S. negrosensis*); humeral angle obtusely rounded, not projected. Notaulus obsolete or faint medially, deep posteriorly. Mesepisternum with epicnemial carina complete dorsally, extended to posterolateral margin of pronotum (fig. 9). Pseudosternum without high reflexed border along anterior margin. Metanotum with dorsal surface narrow to about half size of posterior surface. Propodeum with submedian carina present ventrally, or absent; propodeal valvula posteriorly produced, free distally from posterolateral projection of submarginal carina; propodeal orifice narrowly acute dorsally (figs. 49, 50).

Metasomal tergum 1 with transverse carina complete; longitudinal furrow broadly impressed, very shallowly to shallowly depressed, without deeper narrow medial sulcus (fig.

11); tergum with or without depressed apical margin. Metasomal sternum 1 with basal carina straight and transverse (faint in *S. parvilineatus* and *S. momunganensis*), clearly separated from lateral oblique ridges when ridges present; median longitudinal ridge present or absent. Metasomal sternum 2 in profile, markedly convex or abruptly truncate posteriad of basal sulcus; apical margin of segment 2 depressed, markedly developed, its maximum length 2.22 to 2.50 length of trans-scutal sulcus (fig. 53).

Body relatively large, length to apex of metasomal tergum 2, 10.6 to 13.5 mm, with moderately dense foveolate to foveate major punctures on metasomal sternum 1, uniformly distributed foveolate major punctures on metasomal segment 2 (somewhat sparser medially in *S. parvilineatus*), short to moderately long pubescence without lengthened setae, and lightly to moderately infuscate wings.

*Male*. Unknown.

Included taxa and geographical distribution.—This Oriental subgenus contains *S. parvilineatus*, *S. momunganensis* and *S. negrosensis*.

### 5.1.2.1 Key to species of *S. (Parasymmorphus)*

1. Metasomal segment 2 in profile with base of tergum obtusely angulate and sternum abruptly truncate posteriad of basal sulcus (fig. 52); metasomal tergum 1 elongate, medial postcarinal length 0.73 apical width; occipital carina with two submedial incisions (fig. 13) that delimit sharp median tooth; interocellar area unraised (fig. 17). .......................................... *S. parvilineatus* (Cameron)

1'. Metasomal segment 2 in profile with base of tergum gradually rounded and sternum markedly convex posteriad of basal sulcus (fig. 53); metasomal tergum 1 slightly broad, medial postcarinal length 0.50 to 0.56 apical width; occipital carina without submedial incisions, slightly pointed medially (fig. 14); interocellar area raised, abruptly elevated vertically directly posteriad of anterior ocellus (fig. 10). .............................................................................. 2

2(1'). Metasomal tergum 2 with major punctures closely spaced and deeply impressed (see Cumming and Vecht, 1986 fig. 1f); propodeum with posterolateral projection of submarginal carina broadly attached basally and not elongate, valvula somewhat truncate apically (fig. 49); pronotal carina raised medially (fig. 55)............................................... *S. momunganensis* (Schulthess)

2'. Metasomal tergum 2 with major punctures moderately spaced and impressed (see Cumming and Vecht, 1986 fig. 2f); propodeum with posterolateral projection of submarginal carina narrow and elongate, valvula rounded apically (fig. 50); pronotal carina evenly arcuate medially. ..................................................
.................................................... *S. negrosensis* Cumming and Vecht

### 5.1.2.1.0.1 *S. (Parasymmorphus) parvilineatus* (Cameron)

*Eumenes parvilineata* Cameron, 1904 (BMNH).
*Nortonia parvilineata* (Cameron); Bequaert, 1928.
*Pseudonortonia parvilineata* (Cameron); Soika, 1941.
*Symmorphus (Parasymmorphus) parvilineatus* (Cameron); Cumming and Vecht, 1986.

Type material examined.—HOLOTYPE, female labelled: "Type [circular red bordered label]"; "Cameron Coll./ 1903-121."; "B.M. TYPE/ HYM./ 18.969."; "Pseudonortonia/ parvilineata/ (Cam.) [female symbol]" (BMNH).

Recognition.—In addition to features given in the key to species of *S. (Parasymmorphus)*, specimens of *S. parvilineatus* are distinguished from those of either *S. momunganensis* or *S. negrosensis* by presence of unreduced ocelli, medially obsolete notaulus, distinct mesoscutellar and dorsal mesepisternal sculpture, non-vertical non-crenate metanotum, propodeum with short superior shelf and ventrally produced submedian carina, metasomal tergum 1 with shallowly depressed longitudinal furrow and short depressed apical margin, metasomal sternum 1 with lateral oblique ridges and median longitudinal ridge anteriad of impunctate polished apex, slightly sparse medial foveolate punctures on metasomal segment 2, foveolate punctures on metasomal tergum 3, and black coloration (except white interantennal spot and subapical border on metasomal tergum 1).

Description.—*Female.* Head including clypeus approximately as high as wide (0.99). Clypeus with height 0.73 maximum width, evenly convex in profile without more flattened apical border. Interantennal carina moderately elevated, with median keel ventrally. Interocellar area not abruptly elevated, at approximately same level as remainder of vertex (fig. 17). Ocelli unreduced, maximum diameter of median ocellus 1.25 trans-scutal sulcus length. OOL 0.85 POL; LOL 0.46 POL. Vertex with cephalic foveae widely spaced, minimum interval between foveae 1.02 POL. Occipital carina with two submedial incisions (fig. 13) that delimit sharp median tooth.

Pronotum with carina at crest of anterior face evenly arcuate medially. Notaulus broadly obsolete medially. Metanotum not distinctly vertical, with size of dorsal surface about half size of posterior surface, not crenate. Propodeum with short nearly horizontal medially depressed superior shelf, medial length of shelf 1.67 length of trans-scutal sulcus; submedian carina of propodeum barely produced ventrally, absent dorsally; propodeal valvula slightly truncate apically, posterolateral projection of submarginal carina broadly attached basally and not elongate (fig. 49).

Metasomal tergum 1 elongate, medial postcarinal length 0.73 apical width; sides of postcarinal area barely convergent towards base, width at transverse carina 0.92 apical width; longitudinal furrow shallowly depressed; tergum with short depressed apical margin, length of margin 0.83 length of trans-scutal sulcus. Metasomal sternum 1 with two low lateral oblique ridges and short carinate median longitudinal ridge; ridges clearly separated from faint nearly obsolete basal carina. Metasomal segment 2 in profile with base of tergum obtusely angulate and sternum abruptly truncate posteriad of basal sulcus (fig. 52); tergum with length 1.04 maximum width; depressed apical margin of segment 2 translucent, its maximum length 2.33 length of trans-scutal sulcus.

Clypeus densely foveolate-punctate, punctures sparse medioapically. Frons and vertex foveolate, punctures densely spaced on frons, irregularly and more sparsely spaced on vertex. Pronotum, except anterior face, foveolate-puncticulate, more or less costate laterally; major punctures densely spaced, minor punctures obscure anterolaterally; anterior face smooth. Mesoscutum foveolate-puncticulate, major punctures moderately to densely spaced. Mesoscutellum foveolate-puncticulate, major punctures moderately to densely spaced, minor punctures obscure. Dorsal and ventral mesepisternum foveolate-puncticulate with some additional shallow rugosity, major punctures moderately to densely spaced, minor punctures obscure. Mesepimeron foveolate-puncticulate, major punctures densely spaced, minor punctures obscure. Metanotum foveate dorsally, obscurely imbricate ventrally. Propodeum shallowly rugose laterally, areolate-rugose dorsally; posterior face nearly smooth, with some shallow indistinct rugosity and obscure imbricate subsculpture. Metasomal tergum 1 and sternum 1 each with postcarinal area foveolate-puncticulate to foveate-puncticulate, major punctures moderately dense, minor punctures connected by obscure imbricate subsculpture; sternum with raised impunctate polished apex posteriad of lateral oblique ridges. Segment 2 foveolate-puncticulate; major punctures moderately spaced and impressed, sparser medially; minor punctures obscure medially on sternum 2, connected by obscure imbricate subsculpture. Tergum 3 with uniformily distributed foveolate punctures. Segments 3 to 6 with imbricate subsculpture.

Pubescence pale yellow to white.

Coloration black with small white interantennal spot, and narrow white medially interrupted subapical border on metasomal tergum 1. Tarsi dark brown. Wings moderately infuscate.

Length to apex of metasomal tergum 2, 13.5 mm.

*Male*. Unknown.

Geographical distribution and seasonal occurrence.—The holotype lacks locality labels and seasonal data, but was described from Sikkim. A second female of the same species, no longer located in the collection of the BMNH, has been reported from Shillong (Assam) by Bequaert (1928) and Soika (1941). See fig. 61.

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—This species is the most plesiotypic member of *S. (Parasymmorphus)* and is inferred to be the sister group of the *S. momunganensis-S. negrosensis* clade (fig. 82).

### 5.1.2.1.0.2 *S. (Parasymmorphus) momunganensis* (Schulthess)

*Odynerus (Symmorphus) momunganensis* Schulthess, 1934 (ETHZ).

*Symmorphus (Parasymmorphus) momunganensis* (Schulthess); Cumming and Vecht, 1986.

Type material examined.—HOLOTYPE, female labelled: "Momungan/ Mindanao"; "momunganensis/ det. Schulthess [1]933"; "[female symbol]"; "TYPE [red bordered label]" (ETHZ).

Recognition.—In addition to features given in the key to species of *S. (Parasymmorphus)*, specimens of *S. momunganensis* are distinguished from those of *S. parvilineatus* by presence of reduced ocelli, complete medially faint notaulus, indistinct mesoscutellar and dorsal mesepisternal sculpture, nearly vertical crenate metanotum, propodeum without superior shelf medially and without submedian carina, metasomal tergum 1 with very shallowly depressed longitudinal furrow and without depressed apical margin, metasomal sternum 1 without median longitudinal or lateral oblique ridges and with punctation to apex, uniform foveolate major punctation on metasomal segment 2, no foveolate punctures on metasomal tergum 3, and black coloration with yellow maculation. Similarly, *S. momunganensis* additionally differs from *S. negrosensis* in possessing widely spaced cephalic foveae relative to POL, metasomal tergum 1 with sides slightly convergent towards base, faint nearly obsolete basal carina on metasomal sternum 1, metasomal tergum 2 with length slightly less than maximum width, metasomal sternum 2 with convexity posteriad of basal sulcus evenly rounded in profile, mandible with large basal yellow mark and metanotum entirely black.

Description.—*Female.* Head including clypeus nearly as high as wide (0.92 to 0.95). Clypeus with height 0.72 to 0.73 maximum width, evenly convex in profile with more flattened apical border. Interantennal carina moderately elevated, with median keel ventrally. Interocellar area raised, abruptly elevated vertically directly posteriad of anterior ocellus (fig. 10). Ocelli reduced, maximum diameter of median ocellus 0.89 trans-scutal sulcus length. OOL 1.02 to 1.05 POL; LOL 0.50 to 0.51 POL. Vertex with cephalic foveae widely spaced, minimum interval between foveae 0.90 to 0.92 POL. Occipital carina without submedial incisions, slightly pointed medially (fig. 14).

Pronotum with carina at crest of anterior face raised medially (fig. 55). Notaulus complete, faint medially. Metanotum nearly vertical, with narrow nearly crenate dorsal surface. Propodeum without superior shelf medially; submedian carina of propodeum entirely absent; propodeal valvula somewhat truncate apically, posterolateral projection of submarginal carina broadly attached basally and not elongate (fig. 49).

Metasomal tergum 1 slightly broad, medial postcarinal length 0.50 to 0.56 apical width; sides of postcarinal area slightly convergent towards base, width at transverse carina 0.83 to

0.85 apical width; longitudinal furrow very shallowly depressed; tergum without depressed apical margin. Metasomal sternum 1 without median longitudinal or lateral oblique ridges; basal carina faint, nearly obsolete. Metasomal segment 2 in profile with base of tergum gradually rounded and sternum markedly and evenly convex posteriad of basal sulcus (fig. 53); tergum with length 0.87 to 0.93 maximum width; depressed apical margin of segment 2 translucent, its maximum length 2.42 to 2.50 length of trans-scutal sulcus.

Clypeus moderately foveolate-puncticulate, major punctures shallow, minor punctures sparse and indistinct; apical border impunctate. Frons and vertex foveolate-puncticulate; major punctures densely spaced on frons, irregularly and more sparsely spaced on vertex; minor punctures irregularly spaced, indistinct in some areas. Pronotum, except anterior face, foveolate-puncticulate, with major punctures densely spaced, more or less costate laterally; anterior face smooth. Mesoscutum foveolate-puncticulate; major punctures densely spaced anteriorly, sparse posteriorly. Mesoscutellum nearly impunctate. Dorsal mesepisternum foveolate-puncticulate; major punctures widely spaced, shallow and indistinct; minor punctures obscure. Ventral mesepisternum foveolate-puncticulate, major punctures widely to moderately spaced, minor punctures obscure. Mesepimeron foveolate-puncticulate, major punctures moderately spaced, minor punctures obscure. Metanotum foveate dorsally, obscurely imbricate ventrally. Propodeum rugose laterally, areolate-rugose dorsally; posterior face nearly smooth, with some shallow indistinct rugosity and obscure imbricate subsculpture. Metasomal tergum 1 and sternum 1 each with postcarinal area foveolate-puncticulate to foveate-puncticulate, major punctures moderately dense. Segment 2 foveolate-puncticulate; major punctures closely spaced and deeply impressed, uniformly distributed; minor punctures obscure medially on sternum 2. Segments 3 to 6 with imbricate subsculpture.

Pubescence pale yellow to white.

Coloration black with yellow as follows: clypeus with large basal band, interantennal spot, postocular spot, large basal mandibular mark, scape anteroventrally, medially interrupted dorsal pronotal band (thickened towards humerus), large dorsal mesepisternal spot, tegula, two large approximate mesoscutellar spots, apex of fore and mid femora (less on mid femur), line on outer surface of tibiae (on hind tibia not extended to apex), apical border of metasomal tergum 1, subapical border of metasomal terga 2, 3 and sternum 2 (on tergum 3 not extended to lateral margin). Tarsi pale brown. Wings lightly infuscate.

Length to apex of metasomal tergum 2, 12.0 mm.

*Male.* Unknown.

Geographical distribution and seasonal occurrence.—Known from the Philippine island of Mindanao (fig. 61). In addition to the holotype, which is without seasonal data, one female specimen has been examined. **Philippines**: Mindanao, Kolambugan [no seasonal data] (USNM).

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Inferred to be the sister species of *S. negrosensis*, from which it differs only slightly (fig. 82).

### 5.1.2.1.0.3 *S. (Parasymmorphus) negrosensis* Cumming and Vecht

*Symmorphus (Parasymmorphus) negrosensis* Cumming and Vecht, 1986 (AEI).

Type material examined.—HOLOTYPE, female labelled: "Mt. Canlaon 3600'/ Negros Or[iental]., Phil./ May 8, 1953/ H, M, & D. Townes"; "Symmorphus/ negrosensis/ v.d.V [female symbol]/ det. J.v.d. Vecht 1980"; "Holotype [red label]" (AEI).

Recognition.—In addition to features given in the key to species of *S. (Parasymmorphus)*, specimens of *S. negrosensis* are distinguished from those of *S. parvilineatus* by the same character states listed for *S. momunganensis*, under "Recognition" of that species. Similarly, *S. negrosensis* additionally differs from *S. momunganensis* in possessing moderately spaced cephalic foveae relative to POL, metasomal tergum 1 with sides moderately convergent towards base, distinct basal carina on metasomal sternum 1, metasomal tergum 2 with length about equal to maximum width, metasomal sternum 2 with convexity posteriad of basal sulcus slightly angulate in profile, mandible with small basal yellow mark and metanotum with two small yellow spots.

Description.—*Female*. Head including clypeus nearly as high as wide (0.95). Clypeus with height 0.70 maximum width, evenly convex in profile with more flattened apical border. Interantennal carina moderately elevated, with median keel ventrally. Interocellar area raised, abruptly elevated vertically directly posteriad of anterior ocellus (fig. 10). Ocelli reduced, maximum diameter of median ocellus 0.75 trans-scutal sulcus length. OOL 0.95 POL; LOL 0.50 POL. Vertex with cephalic foveae moderately spaced, minimum interval between foveae 0.71 POL. Occipital carina without submedial incisions, slightly pointed medially (fig. 14).

Pronotum with carina at crest of anterior face evenly arcuate medially, somewhat faint dorsally. Notaulus complete, faint medially. Metanotum nearly vertical, with narrow nearly crenate dorsal surface. Propodeum without superior shelf medially; submedian carina of propodeum entirely absent; propodeal valvula apically rounded, posterolateral projection of submarginal carina narrow and elongate (fig. 50).

Metasomal tergum 1 slightly broad, medial postcarinal length 0.55 apical width; sides of postcarinal area moderately convergent towards base, width at transverse carina 0.77 apical width; longitudinal furrow very shallowly depressed; tergum without depressed apical margin. Metasomal sternum 1 without median longitudinal or lateral oblique ridges; basal carina distinct. Metasomal segment 2 in profile with base of tergum gradually rounded and sternum with marked convexity slightly angulate posteriad of basal sulcus; tergum with length 0.99 maximum width; depressed apical margin of segment 2 translucent, its maximum length 2.22 length of trans-scutal sulcus.

Clypeus moderately foveolate-puncticulate, major punctures shallow, minor punctures sparse and indistinct; apical border impunctate. Frons and vertex foveolate-puncticulate; major punctures densely spaced on frons, irregularly and more sparsely spaced on vertex; minor punctures irregularly spaced, often indistinct. Pronotum, except anterior face, foveolate-puncticulate, with major punctures densely spaced, more or less costate laterally; anterior face smooth. Mesoscutum foveolate-puncticulate; major punctures moderately to densely spaced anteriorly, sparse posteriorly. Mesoscutellum nearly impunctate. Dorsal mesepisternum foveolate-puncticulate; major punctures widely spaced, shallow and indistinct; minor punctures obscure. Ventral mesepisternum foveolate-puncticulate, major punctures widely to moderately spaced, minor punctures obscure. Mesepimeron foveolate-puncticulate, major punctures moderately spaced, minor punctures obscure. Metanotum foveate dorsally, obscurely imbricate ventrally. Propodeum rugose laterally, areolate-rugose dorsally; posterior face nearly smooth, with some shallow indistinct rugosity and obscure imbricate subsculpture. Metasomal tergum 1 and sternum 1 each with postcarinal area foveolate-puncticulate to foveate-puncticulate, major punctures moderately dense. Segment 2 foveolate-puncticulate; major punctures moderately spaced and impressed, uniformly distributed; minor punctures obscure medially on sternum 2. Segments 3 to 6 with imbricate subsculpture.

Pubescence pale yellow to white.

Coloration black with yellow as follows: clypeus with large basal band, interantennal spot, postocular spot, small basal mandibular mark, scape anteroventrally, medially interrupted dorsal pronotal band (thickened towards humerus), large dorsal mesepisternal spot, tegula, two large approximate mesoscutellar spots, two small metanotal spots, apex of fore and mid femora (less on mid femur), line on outer surface of tibiae (on hind tibia not extended to apex), apical border of metasomal tergum 1, subapical border of metasomal terga 2, 3 and sternum 2 (on tergum 3 not extended to lateral margin). Tarsi pale brown. Wings lightly infuscate.

Length to apex of metasomal tergum 2, 10.5 mm.

*Male*. Unknown.

Geographical distribution and seasonal occurrence.—Known only from the holotype, collected in May on the Philippine island of Negros (fig. 61).

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Apparently the sister species of *S. momunganensis* (fig. 82).

### 5.1.3 Subgenus *Symmorphus* Wesmael

*Symmorphus* Wesmael, 1836. Subgenus of *Odynerus* Latreille. Type-species: *Odynerus elegans* Wesmael, 1833 (designated by Richards, 1935).

*Protodynerus* Saussure, 1855. New name for *Symmorphus* Wesmael, based on supposed homonymy with *Symmorpha* Klug, 1807.

*Odynerus* Latreille *sensu* Blüthgen, 1938. Type-species: *Vespa muraria* Linnaeus, 1758 according to Blüthgen.

*Koptodynerus* Blüthgen, 1943. Subgenus of *Odynerus* Latreille *sensu* Blüthgen. Type-species: *Symmorphus declivis* Harttig, 1932 (monobasic).

Notes about synonymy.—Blüthgen (1943) erected the subgenus *Koptodynerus* for *S. declivis* Harttig, primarily on the basis of the distinctive shape of the base of metasomal segment 2 in that species. Cumming and Vecht (1986) noting that this state occurs elsewhere in *Symmorphus*, in species having little in common with *S. declivis* and even within their newly described subgenus *Parasymmorphus*, synonymized *Koptodynerus* with *Symmorphus sensu stricto*.

Recognition.—In addition to those features given in the key to subgenera, most members of the nominate subgenus are distinguished from those of *S. (Parasymmorphus)* by a broadly rounded propodeal orifice dorsally (somewhat narrowed dorsally in *S. foveolatus*, *S. glasunowi* and *S. sichuanensis*) and not depressed slightly to moderately developed apical margin on metasomal segment 2 (depressed and moderately to markedly developed in members of *S. hoozanensis* group, as well as depressed on the tergum of *S. sichuanensis*).

Description.—*Female*. Clypeus shallowly to deeply emarginate apically (figs. 57-59). Interocellar area at approximately same level as remainder of vertex. Ocelli unreduced, maximum diameter of median ocellus greater than 1.15 trans-scutal sulcus length. Vertex with cephalic foveae very small to greatly enlarged; narrowly to widely spaced; in most species each fovea not bordered posteriorly by a sharp carina. Mandible with five teeth.

Pronotum with carina at crest of anterior face complete, or obsolete dorsally; humeral angle obtusely rounded to acute, not projected to greatly projected. Notaulus complete, or partially obsolete. Mesepisternum with epicnemial carina dorsally or entirely obsolete, not extended to posterolateral margin of pronotum (figs. 4, 16, 21). Pseudosternum with or without high reflexed border along anterior margin. Metanotum with dorsal surface narrow to subequal size of posterior surface. Propodeum with submedian carina complete, or present ventrally; propodeal valvula short posteriorly, fused distally to posterolateral projection of submarginal carina (fig. 51); propodeal orifice broadly rounded dorsally to somewhat narrowed dorsally (figs. 26, 36).

Metasomal tergum 1 with transverse carina complete or laterally obsolete; longitudinal furrow broadly or sharply impressed, shallowly to deeply depressed, with or without deeper narrow medial sulcus (figs. 11, 12); tergum without distinct depressed apical margin. Metasomal sternum 1 with basal carina of varied form, not straight (faint or absent in some species), fused to lateral oblique ridges; median longitudinal ridge present or absent. Metasomal sternum 2 in profile, flat to slightly convex or abruptly truncate posteriad of basal sulcus;

apical margin of segment 2 depressed in a few species (fig. 52), slightly to moderately developed and not depressed in most species with maximum length much less than twice length of trans-scutal sulcus (figs. 41, 54).

Body small to relatively large, length to apex of metasomal tergum 2, 5.0 to 15.0 mm, with punctures on metasomal sternum 1 present or absent, sparse punctate to foveolate major punctures on metasomal segment 2, short to moderately long pubescence with or without lengthened setae, and hyaline to moderately infuscate wings.

*Male.* Similar to female except as follows: mandible with four teeth; pronotum with humeral angle barely to greatly projected.

Antennal articles 9 to 13 or 10 to 13 each with single tyloid, or tyloids absent from a few species.

Length to apex of metasomal tergum 2, 5.0 to 12.0 mm.

Included taxa and geographical distribution.—This Holarctic-Oriental subgenus contains 32 species plus two additional subspecies, informally classified into three proposed species groups.

### 5.1.3.1 Key to species and subspecies of *S. (Symmorphus)*[4]

1. Metasomal segment 2 in profile with base of tergum obtusely angulate and sternum abruptly truncate posteriad of basal sulcus (fig. 52); female clypeus shallowly emarginate apically (fig. 57, *S. hoozanensis* and *S. declivis* groups)...... ........................................................................................ 2

1'. Metasomal segment 2 in profile with base of tergum gradually rounded and

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[4] For New World species begin at couplet 36

sternum flat to slightly convex posteriad of basal sulcus (fig. 54); female clypeus shallowly to deeply emarginate apically (*S. murarius* group)........................ 7

2(1). Metasomal segment 2 with apical margin depressed, moderately to markedly developed with maximum length 1.13 to 2.25 length of trans-scutal sulcus (fig. 52); metasomal sternum 1 with basal carina and carinate median longitudinal ridge (fig. 8); metasomal tergum 1 with longitudinal furrow broadly impressed, without deeper narrow medial sulcus (fig. 11, *S. hoozanensis* group)............. 3

2'. Metasomal segment 2 with apical margin not depressed, slightly developed with maximum length 0.38 to 0.75 length of trans-scutal sulcus (fig. 54); metasomal sternum 1 without basal carina and median longitudinal ridge; metasomal tergum 1 with longitudinal furrow sharply impressed, with deeper narrow medial sulcus posteriorly (fig. 12). ........................................................ *S. declivis* Harttig

3(2). Propodeum with superior shelf very short, medial length 0.78 to 1.00 length of trans-scutal sulcus; metasomal tergum 1 broad, medial postcarinal length 0.47 to 0.49 apical width. ........................................................................ 4

3'. Propodeum with superior shelf short, medial length 1.18 to 2.00 length of trans-scutal sulcus; metasomal tergum 1 slightly broad to slightly elongate, medial postcarinal length 0.52 to 0.60 apical width.......................................... 5

4(3). Maculation yellow; wings lightly infuscate; from Sri Lanka. ............................ ................................................ *S. alkimus alkimus* Cumming and Vecht

4'. Maculation ivory to white; wings hyaline, except lightly infuscate patch adjacent anterior apical margin of fore wing; from northern Sumatra.......................... ................................................ *S. alkimus dialeukus* new subspecies

5(3'). Pronotal carina prominent throughout (figs. 13, 47); occipital carina with two submedial incisions that delimit blunt median tooth (fig. 13)..........................

............................................................... *S. ambotretus* new species

5'. Pronotal carina obsolete dorsolaterally; occipital carina without submedial incisions, slightly pointed medially (fig. 14) or with short blunt median projection delimited by two shallow submedial depressions .......................... 6

6(5'). Metasomal tergum I slightly elongate, medial postcarinal length 0.59 to 0.60 apical width, postcarinal area mostly yellow except for black basomedial strip; metasomal segment 2 with maximum length of apical margin 1.88 to 2.25 length of trans-scutal sulcus .................................... *S. hoozanensis* (Schulthess)

6'. Metasomal tergum 1 slightly broad, medial postcarinal length 0.52 apical width, postcarinal area mostly black except for yellow apical border; metasomal segment 2 with maximum length of apical margin 1.13 length of trans-scutal sulcus. ....... ............................................................... *S. canlaonicus* new species

7(1'). Old World species. ................................................................ 8

7'. New World species. ................................................................ 36

8(7). Clypeus broadly and shallowly emarginate apically, with teeth very widely spaced (figs. 2, 56); mesoscutum with nearly uniform dense punctate size punctures (fig. 6); cephalic foveal carina of female prominent (fig. 14). ......................... ............................................................... *S. decens* (Kostylev)

8'. Clypeus moderately to narrowly emarginate apically, with apex shallowly to deeply indented and with teeth more closely spaced (figs. 57-59); mesoscutum primarily foveolate-puncticulate, major punctures uniformly to irregularly distributed, minor punctures obscure in some specimens (figs. 45-47); cephalic foveal carina of female varied, prominent to absent. .................................. 9

9(8'). Propodeum with submedian carina complete, sharply defined throughout (fig. 15); metasomal tergum 1 elongate to markedly elongate, sides of postcarinal area markedly convergent towards base, with width at transverse carina less than 0.67 apical width; dorsal mesepisternum foveolate-puncticulate, with major punctures sparse (particularly anteriorly) and minor punctures densely distributed (fig. 16, slightly obscured in some specimens by fine oblique striae). .......................... ............................................................*S. fuscipes* (Herrich-Schaeffer)

9'. Propodeum with submedian carina at most only sharply defined ventrally, absent or faint and irregular dorsally (figs. 33, 34, 36, 43, 44); metasomal tergum 1 short to markedly elongate, sides of postcarinal area in most specimens barely to moderately convergent towards base—if width at transverse carina less than 0.67 apical width, dorsal mesepisternum without densely distributed puncticulate minor punctures..................................................................10

10(9'). Pronotal carina obsolete along entire width of dorsum of pronotum (fig. 17); pseudosternum of mesopleuron with high reflexed border along anterior margin (fig. 18); metasomal sternum 1 without basal carina (fig. 20).....................11

10'. Pronotal carina complete (figs. 45-47) or obsolete dorsomedially, present at least laterally along dorsum of pronotum; pseudosternum of mesopleuron with low to moderately low reflexed border along anterior margin (fig. 19); metasomal sternum 1 with (figs. 8, 35) or without basal carina.......................................12

11(10). Metasomal sternum 2 in profile with base slightly convex posteriad of basal sulcus (fig. 54); from Europe, Turkey, Lebanon, Iran, western Asia and Kashmir ..........................................................................*S. gracilis* (Brullé)

11'. Metasomal sternum 2 in profile with base flat posteriad of basal sulcus; from the Atlas Mountains of northern Africa ................................ *S. paralleliventris* Soika

12(10'). Mesosoma with sparse to moderately dense lengthened setae (shortened through wear on some specimens), in addition to short pubescence (figs. 21, 22); metasomal sternum 1 without basal carina in most specimens (fig. 20)...........13

12'. Mesosoma without lengthened setae in addition to short pubescence (figs. 4, 16, 38-40); metasomal sternum 1 with basal carina (figs. 8, 35; slightly obscure in some specimens). ....................................................................21

13(12). Metasomal sternum 1 with basal carina (fig. 8, slightly obscure in some specimens); propodeal valvula pointed dorsally, extended with posterolateral projection of submarginal carina as prominent acute tooth (fig. 23); small to moderate size species. ....................................................................14

13'. Metasomal sternum 1 without basal carina (fig. 20); propodeal valvula somewhat rounded dorsally, barely extended with short posterolateral projection of submarginal carina (figs. 24, 31, 32); moderate to large size species..............15

14(13). Propodeum with superior shelf moderately long, medial length 2.50 to 3.11 length of trans-scutal sulcus; female with cephalic foveae very small, maximum diameter 0.25 to 0.33 trans-scutal sulcus length; female clypeus deeply emarginate apically, with teeth slightly reflexed anteriorly (fig. 59)................. ....................................................................*S. violaceipennis* Soika

14'. Propodeum with superior shelf short, medial length 1.38 to 1.67 length of trans-scutal sulcus; female with cephalic foveae of moderate size, maximum diameter 0.67 to 0.84 trans-scutal sulcus length; female clypeus moderately emarginate apically, without reflexed teeth (fig. 58)..................................... ....................................................................*S. mizuhonis* Tsuneki

15(13'). Metasomal tergum 1 with transverse carina obsolete laterally, faint medially (fig. 25); female with cephalic foveae very large, maximum diameter 3.45 to 5.00 trans-scutal sulcus length, and nearly contiguous, minimum interval between foveae 0.06 to 0.19 POL (fig. 27); male with antennal article 13 very long, length in profile 1.47 to 1.75 maximum width; male antenna with tyloids (fig. 28)....... ....................................................................*S. murarius* (Linnaeus)

15'. Metasomal tergum 1 with transverse carina prominent medially (fig. 26) or throughout (fig. 30); female with cephalic foveae small to large, maximum diameter 0.50 to 2.00 trans-scutal sulcus length, and narrowly to widely spaced, minimum interval between foveae 0.33 to 1.06 POL; male with antennal article 13 moderately long to long, length in profile 0.98 to 1.40 maximum width—if length greater than 1.35 maximum width, male antenna without tyloids. ................16

16(15'). Metasomal tergum 1 with transverse carina laterally faint to obsolete (fig. 26), tergum slightly elongate to markedly elongate, with medial postcarinal length 0.60 to 0.91 apical width; propodeal orifice narrowed dorsally (fig. 26); cephalic foveal carina of female indistinct. ..................................................17

16'. Metasomal tergum 1 with transverse carina prominent throughout (fig. 30), tergum broad to slightly elongate, with medial postcarinal length 0.46 to 0.62 apical width; propodeal orifice broadly rounded dorsally (figs. 33, 34, 36); cephalic foveal carina of female prominent in most specimens (fig. 14)..........19

17(16). Mesepisternum with epicnemial carina present ventrally (figs. 4, 16; somewhat faint in female specimens); metasomal tergum 2 foveolate-puncticulate, with major punctures closely spaced and deeply impressed along basal and apical borders; male antenna with tyloids (fig. 28); maculation, except male clypeus, orange-yellow. ...................................................*S. sichuanensis* Lee

17'. Mesepisternum without epicnemial carina (fig. 21); metasomal tergum 2 punctate-puncticulate to foveolate-puncticulate, with major punctures widely spaced and shallowly impressed throughout (fig. 29, major punctation larger and denser basally in some specimens); male antenna without tyloids; maculation ivory to yellow. ..................................................................18

18(17'). Mesosoma with yellow tegula, dorsal pronotal band, dorsal mesepisternal spot and mesoscutellar spots; from Pamir, Tien Shan and Himalaya mountain ranges .

.................................................................... *S. glasunowi* Morawitz

18'. Mesosoma black; from Japan, Korea and Primorskij Krai in USSR ................ .............................................................. *S. foveolatus* Gussakovskij

19(16'). Metasomal tergum 1 with sides of postcarinal area slightly convergent towards base, width at transverse carina 0.83 to 0.84 apical width; female with cephalic foveae widely spaced, minimum interval between foveae 0.93 to 1.00 POL; body of large size, length to apex of metasomal tergum 2, 11.0 to 15.0 mm; from Japan .............................................................. *S. captivus* (Smith)

19'. Metasomal tergum 1 with sides of postcarinal area more convergent towards base, width at transverse carina 0.67 to 0.79 apical width; female with cephalic foveae more narrowly spaced, minimum interval between foveae 0.33 to 0.92 POL; body of moderate to large size, length to apex of metasomal tergum 2, 6.5 to 14.0 mm; from Palearctic region exclusive of Japan..............................20

20(19'). Metasomal tergum 1 slightly broad to slightly elongate, with medial postcarinal length 0.52 to 0.62 apical width, sides of postcarinal area markedly to moderately convergent towards base, with width at transverse carina 0.67 to 0.73 apical width, postcarinal area foveolate-puncticulate, with major punctures shallowly impressed (fig. 30); propodeal lateral face with fine striate rugosity (fig. 31) and superior shelf of female with concentric carinae in medial depression of most specimens (fig. 33); female with cephalic foveae moderately to widely spaced, minimum interval between foveae 0.88 to 0.92 POL; from western and eastern Palearctic region ........................................ *S. angustatus* (Zetterstedt)

20'. Metasomal tergum 1 broad, with medial postcarinal length less than 0.52 apical width, sides of postcarinal area less convergent towards base, with width at transverse carina 0.74 to 0.79 apical width, postcarinal area foveolate-puncticulate, with major punctures moderately to deeply impressed (fig. 7, major punctation difficult to see in extensively maculated specimens); propodeal lateral face with coarse striate rugosity (fig. 32) and superior shelf of female without concentric carinae in medial depression (fig. 34); female with cephalic foveae narrowly to moderately spaced, minimum interval between foveae 0.33 to 0.86 POL; from western and central Palearctic region ................ ............................................................................ *S. crassicornis* (Panzer)

21(12'). Metasomal sternum 1 with basal carina inflated and raised posteriorly (fig. 35); mesepisternum of female without epicnemial carina (fig. 21). ......................22

21'. Metasomal sternum 1 with basal carina deeply curved posteriorly as low ridge (fig. 8, faint in some specimens); mesepisternum of female with epicnemial carina present ventrally in most specimens (figs. 4, 16)..............................23

22(21). Metasomal sternum 1 with lateral oblique ridges low and barely raised basally, median longitudinal ridge prominent; propodeum with medial length of superior shelf 2.01 to 2.63 length of trans-scutal sulcus ............................................ ..........................................................................*S. nipteroides* new species

22'. Metasomal sternum 1 with lateral oblique ridges raised basally to height of posterior margin of basal carina, median longitudinal ridge indistinct (fig. 35); propodeum with medial length of superior shelf 1.13 to 1.32 length of trans-scutal sulcus . ....................................... *S. tukvarensis* (Meade-Waldo)

23(21'). Propodeum with posterior and lateral face dull, primarily very finely striate (figs. 36, 37); male with antennal article 13 short, length in profile 0.60 to 0.67 maximum width; from eastern Palearctic region ........................................ ......................................................................... *S. apiciornatus* (Cameron)

23'. Propodeum with posterior face shiny, nearly smooth with indistinct rugosity, lateral face shallowly to striately rugose and not dull; male with antennal article 13 short to moderately long; from western and eastern Palearctic region.........24

24(23'). Dorsal mesepisternum foveolate-puncticulate, with major punctures large and densely distributed (particularly posteriorly, fig. 38); metasomal tergum 1 elongate, medial postcarinal length 0.73 to 0.77 apical width; male with antennal article 13 moderately long, length in profile 1.07 to 1.09 maximum width; female clypeus moderately emarginate apically (fig. 58)........................................ ........................................................................ *S. bifasciatus* (Linnaeus)

24'. Dorsal mesepisternum punctate-puncticulate to foveolate-puncticulate, with major punctures of small to moderate size and sparsely distributed (figs. 4, 39, 40; major punctation barely apparent in some specimens); metasomal tergum 1 slightly elongate to elongate, medial postcarinal length 0.58 to 0.71 apical width; male with antennal article 13 short to moderately long, length in profile 0.67 to 1.03 maximum width; female clypeus shallowly to moderately emarginate apically.............................................................................25

25(24'). Males.............................................................................26

25'. Females...........................................................................31

26(25). Antennal article 13 moderately long, length in profile 1.00 to 1.03 maximum width; from western and central Palearctic region........................................ ............................................................................ *S. connexus* (Curtis)

26'. Antennal article 13 shorter, length in profile 0.67 to 0.85 maximum width; from western and eastern Palearctic region.....................................................27

27(26'). Metasomal tergum 1 with postcarinal area punctate-puncticulate to foveolate-puncticulate, major punctures of small to moderate size and sparsely distributed (figs. 41, 42; major punctation slightly more dense along median longitudinal furrow in most specimens); from eastern and central Palearctic region.............................................................................28

27'. Metasomal tergum 1 with postcarinal area foveolate-puncticulate to foveate-puncticulate, major punctures of moderate to large size and densely distributed (figs. 7, 12, 30; major punctation somewhat shallow in some specimens); from western and eastern Palearctic region..........................29

28(27). Metasomal tergum 2 nearly uniformly foveolate-puncticulate, with major punctures slightly larger and more closely spaced towards base (fig. 41); mesosoma minimally with yellow dorsal pronotal spots or band; from the Soviet Tien Shan and adjacent mountain ranges....................*S. sublaevis* (Kostylev)

28'. Metasomal tergum 2 foveolate-puncticulate basally to punctate-puncticulate apically, with major punctures barely apparent on apical half (fig. 42); mesosoma black; from Japan, and Siberia south to the Altai Mountains .......... ................................................................*S. lucens* (Kostylev)

29(27'). Metasomal tergum 1 with major punctures of postcarinal area shallowly impressed (fig. 30); propodeum with submedian carina prominent ventrally, markedly produced from submarginal carina to lateral ridge (fig. 43); body of moderate size, length to apex of metasomal tergum 2, 7.0 to 9.5 mm. ............... ................................................................*S. allobrogus* (Saussure)

29". Metasomal tergum 1 with major punctures of postcarinal area moderately to deeply impressed (figs. 7, 12); propodeum with submedian carina only markedly produced adjacent to submarginal carina, attenuated towards lateral ridge (fig. 44); body of small size, length to apex of metasomal tergum 2, 6.0 to 7.5 mm..... ................................................................................30

30(29'). Pronotum with humeral angle acute, moderately projected (fig. 45); metasomal tergum 1 with sides of postcarinal area moderately convergent towards base, width at transverse carina 0.75 to 0.76 apical width; from Europe .................. ................................................................*S. debilitatus* (Saussure)

30'. Pronotum with humeral angle obtuse to nearly acute, slightly projected (figs. 46, 47); metasomal tergum 1 with sides of postcarinal area slightly convergent towards base, width at transverse carina 0.83 to 0.85 apical width; from Japan ........................................................................................*S. ctiens* Soika

31(25'). Metasomal tergum 1 with postcarinal area punctate-puncticulate to foveolate-puncticulate, major punctures of small to moderate size and sparsely distributed (figs. 41, 42; major punctation slightly more dense along median longitudinal furrow in most specimens); cephalic foveae large, maximum diameter 1.43 to 2.00 trans-scutal sulcus length; from eastern and central Palearctic region ..........................................................................32

31'. Metasomal tergum 1 with postcarinal area foveolate-puncticulate to foveate-puncticulate, major punctures of moderate to large size and densely distributed (figs. 7, 12, 30; major punctation somewhat shallow in some specimens); cephalic foveae of moderate to large size, maximum diameter 0.84 to 1.45 trans-scutal sulcus length; from western and eastern Palearctic region .....33

32(31). Metasomal tergum 2 nearly uniformly foveolate-puncticulate, with major punctures slightly larger and more closely spaced towards base (fig. 41); mesosoma minimally with yellow dorsal pronotal spots or band; from the Soviet Tien Shan and adjacent mountain ranges......................*S. sublaevis* (Kostylev)

32'. Metasomal tergum 2 foveolate-puncticulate basally to punctate-puncticulate apically, with major punctures barely apparent on apical half (fig. 42); mesosoma black; from Japan, and Siberia south to the Altai Mountains ............................................................................*S. lucens* (Kostylev)

33(31'). Clypeus moderately emarginate apically (fig. 58); metasomal tergum 1 with major punctures of postcarinal area shallowly impressed (fig. 30); propodeum with submedian carina prominent ventrally, markedly produced from submarginal carina to lateral ridge (fig. 43); mesepisternum with epicnemial carina faint ventrally or absent; moderate size species, length to apex of metasomal tergum 2, 8.5 to 10.5 mm ........................ *S. allobrogus* (Saussure)

33'. Clypeus more shallowly emarginate apically (fig. 57); metasomal tergum 1 with major punctures of postcarinal area moderately to deeply impressed (figs. 7, 12); propodeum with submedian carina only markedly produced adjacent to submarginal carina, attenuated towards lateral ridge (fig. 44); mesepisternum with epicnemial carina faint to prominent ventrally; small size species, length to apex of metasomal tergum 2, 6.0 to 8.5 mm..............................................34

34(33'). Mesoscutum foveolate-puncticulate with major punctures very sparse on posterior half, nearly absent posterolaterally and sparse to very sparse posteromedially (fig. 46); metasomal tergum 1 slightly elongate, medial postcarinal length 0.61 to 0.63 apical width; clypeus in profile markedly convex through apical third (fig. 60) .................................... *S. connexus* (Curtis)

34'. Mesoscutum foveolate-puncticulate with major punctures only slightly more sparse posterolaterally and posteromedially (fig. 45); metasomal tergum 1 moderately elongate to elongate, medial postcarinal length 0.66 to 0.71 apical width; clypeus in profile more evenly rounded, slightly to markedly convex. ....35

35(34'). Pronotum with humeral angle nearly acute to acute, slightly to moderately projected (figs. 45, 46); metasomal tergum 1 with sides of postcarinal area moderately convergent towards base, width at transverse carina 0.75 to 0.76 apical width; from Europe. .................................... *S. debilitatus* (Saussure)

35'. Pronotum with humeral angle obtuse, very slightly to slightly projected (fig. 47); metasomal tergum 1 with sides of postcarinal area slightly convergent towards base, width at transverse carina 0.83 to 0.85 apical width; from Japan ............
.................................................................................................*S. cliens* Soika

36(7'). Interantennal carina absent or very faint (fig. 48); propodeum with superior shelf very short, medial length 0.40 to 0.75 length of trans-scutal sulcus; metasomal sternum 1 with basal carina (fig. 8); metasomal tergum 1 slightly broad, medial postcarinal length 0.53 to 0.55 apical width; male with antennal article 13 moderately long, length in profile 0.91 to 0.93 maximum width; from western North America. .................................................*S. projectus* Bohart

36'. Interantennal carina prominent (fig. 2); propodeum with superior shelf longer in most specimens—if medial length less than 1.00 length of trans-scutal sulcus, metasomal sternum 1 without basal carina (fig. 20); metasomal tergum 1 broad to elongate; male with antennal article 13 short to long; transamerican. ..........37

37(36'). Metasomal tergum 1 elongate, medial postcarinal length 0.71 to 0.81 apical width (fig. 12); propodeum with medial length of superior shelf 1.75 to 1.88 length of trans-scutal sulcus; metasomal sternum 1 with basal carina prominent (fig. 8) ... ........................................................................ *S. canadensis* (Saussure)

37'. Metasomal tergum 1 broad to moderately elongate, medial postcarinal length 0.46 to 0.67 apical width; propodeum with medial length of superior shelf 0.75 to 1.50 length of trans-scutal sulcus; metasomal sternum 1 with basal carina faint or absent.............................................................................................38

38(37'). Metasomal tergum 1 slightly to moderately elongate, medial postcarinal length 0.61 to 0.67 apical width; male with antennal article 13 short, length in profile less than 0.67 maximum width ........................................ *S. cristatus* (Saussure)

38'. Metasomal tergum 1 broad, medial postcarinal length 0.46 to 0.51 apical width (fig. 7); male with antennal article 13 moderately long to long, length in profile 1.00 to 1.20 maximum width...................................................................39

39(38'). Pubescence gold colored and dense, lengthened setae sparse; wings fuliginous with slight yellow tinge; maculation yellow; from southeastern Texas, Mexico and Nicaragua ........................................*S. albomarginatus midas* new subspecies

39'. Pubescence pale yellow to white and inconspicuous, lengthened setae sparse to moderately dense; wings hyaline, fuliginous with slight yellow tinge, or infuscate; maculation white to yellow; from Canada and U.S.A., south to California, New Mexico, east-central Texas and Florida ........................................................................................ *S. albomarginatus albomarginatus* (Saussure)

### 5.1.3.1.1 S. hoozanensis group

This group is characterized by a female clypeus which is shallowly emarginate apically (fig. 57), nearly vertical metanotum, metasomal tergum 1 with longitudinal furrow broadly impressed and without deeper narrow medial sulcus (fig. 11), metasomal sternum 1 with basal carina and carinate median longitudinal ridge (fig. 8), base of metasomal segment 2 in profile with tergum obtusely angulate and sternum abruptly truncate posteriad of basal sulcus, and moderately to markedly developed depressed apical margin of metasomal segment 2 (fig. 52). The group is primarily Oriental in distribution, extending northward as far as Taiwan, Sichuan Province in China and Nepal.

#### 5.1.3.1.1.1 *S. (Symmorphus) hoozanensis* (Schulthess)

*Odynerus (Symmorphus) hoozanensis* Schulthess, 1934 (DEI).

Type material examined.—HOLOTYPE, female labelled: "Formosa/ Hoozan 10 IX/ Sauter"; "Schulthess det."; "Symmorphus/ spec."; "Symmorphus/ hoozanensis/ Schulth"; "Unicum/ f.meine/ Sammlung/ erwünscht [green label]"; "Typus [red label]" (DEI).

Recognition.—Distinguished from other members of *S. hoozanensis* group by features given in the key to species and subspecies of *S. (Symmorphus)*. Additionally recognized from *S. alkimus* and *S. ambotretus* by more extensive maculation, particularly on mesosoma and metasomal tergum 1, and from *S. canlaonicus* by larger size.

Description.—*Female.* Head including clypeus nearly as high as wide (0.95 to 0.98). Clypeus with height 0.68 to 0.73 maximum width, shallowly emarginate apically, evenly convex in profile. Interantennal carina slightly to moderately elevated, with median keel ventrally. OOL 0.98 to 1.02 POL; LOL 0.48 to 0.49 POL. Vertex with cephalic foveae of moderate size, maximum foveal diameter 1.00 trans-scutal sulcus length; moderately spaced, minimum interval between foveae 0.62 to 0.84 POL; each fovea not bordered posteriorly by carina. Occipital carina without submedial incisions, slightly pointed medially (fig. 14) or with short blunt median projection delimited by two shallow submedial depressions.

Pronotum with carina at crest of anterior face obsolete dorsolaterally, evenly arcuate medially; humeral angle obtusely rounded, barely projected. Notaulus narrowly obsolete medially. Mesepisternum with epicnemial carina obsolete dorsally, faint ventrally (entirely obsolete in specimen from Wulai). Pseudosternum without high reflexed border along anterior margin (fig. 19). Metanotum nearly vertical, with narrow irregular dorsal surface. Propodeum with short nearly horizontal medially depressed superior shelf, medial length of shelf 1.67 to 2.00 length of trans-scutal sulcus; submedian carina of propodeum barely produced ventrally, absent dorsally; propodeal valvula pointed dorsally, moderately extended with posterolateral projection of submarginal carina; propodeal orifice broadly rounded dorsally (fig. 36).

Metasomal tergum 1 slightly elongate, medial postcarinal length 0.59 to 0.60 apical width; sides of postcarinal area barely convergent towards base, width at transverse carina 0.89 to 0.91 apical width; transverse carina complete; longitudinal furrow broadly impressed, shallowly depressed, without deeper narrow medial sulcus. Metasomal sternum 1 with basal carina deeply curved posteriorly, fused posteriorly to carinate median longitudinal and lateral oblique ridges. Metasomal segment 2 in profile with base of tergum obtusely angulate and sternum abruptly truncate posteriad of basal sulcus; tergum with length 1.19 to 1.25 maximum width; apical margin of segment 2 translucent, depressed, its maximum length 1.88 to 2.25

length of trans-scutal sulcus.

Clypeus moderately punctate-puncticulate to foveolate-puncticulate, punctures sparse medioapically. Frons and vertex foveolate-puncticulate, major punctures moderately spaced. Pronotum, except anterior face, foveolate-puncticulate, with major punctures moderately spaced, more or less costate laterally; anterior face obscurely imbricate. Mesoscutum foveolate-puncticulate, major punctures moderately spaced. Mesoscutellum foveolate-puncticulate; major punctures widely spaced, shallow and indistinct; minor punctures obscure. Dorsal mesepisternum punctate-puncticulate to foveolate-puncticulate; major punctures widely spaced, indistinct; minor punctures obscure. Ventral mesepisternum foveolate-puncticulate, major punctures widely spaced, minor punctures obscure. Mesepimeron foveolate-puncticulate, major pun[illegible]s moderately spaced, minor punctures obscure. Metanotum foveolate-puncticulate dorsally, obscurely puncticulate ventrally. Propodeum striate to shallowly rugose laterally, areolate-rugose dorsally; posterior face obscurely sculptured, transversely strigate medially, shallowly rugose laterally. Metasomal tergum 1 with postcarinal area foveolate-puncticulate; sternum 1 rugose to shallowly rugose anteriorly, median longitudinal ridge flanked by carinate longitudinal rugae. Segment 2 foveolate-puncticulate, major punctures larger and more closely spaced towards apex, minor punctures connected by obscure imbricate subsculpture. Terga 3 to 5 and sternum 3 with sparse punctate or foveolate major punctures subapically. Segments 3 to 6 with imbricate subsculpture.

Pubescence pale yellow to white, without lengthened setae.

Coloration black with yellow to orange-yellow as follows: clypeus with large basal yellow band, interantennal spot, postocular dot, medially interrupted dorsal pronotal band (thickened towards humerus), large dorsal mesepisternal spot; tegula, two large approximate mesoscutellar spots, two large approximate to nearly approximate metanotal spots, apex of fore and mid femora (less on mid femur), tibiae (except outer apical surface of hind tibia), postcarinal area of metasomal tergum 1 (interrupted basomedially), subapical border of metasomal tergum 2 and sternum 2. Tarsi reddish brown basally to dark brown apically. Wings lightly infuscate.

Length to apex of metasomal tergum 2, 10.0 to 10.5 mm.

*Male*. Unknown.

Geographical distribution and seasonal occurrence.—Known from Taiwan (fig. 62). In addition to the holotype, which was collected in September, two female specimens have been examined. **Taiwan**: Taipei, Wulai, 23.IV.1956 (RNHL); Wushe, 1150 m., 15.V.1983 (AEI).

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Tentatively considered the sister species of *S. canlaonicus* (fig. 83).

### 5.1.3.1.1.2 *S. (Symmorphus) alkimus* Cumming and Vecht

#### 5.1.3.1.1.2.1 *S. (Symmorphus) alkimus alkimus* Cumming and Vecht

*Symmorphus (Symmorphus) alkimus* Cumming and Vecht, 1986 (USNM).

Type material examined.—HOLOTYPE, female labelled: "HOLOTYPE [red label]"; "SRI LANKA: Kan[dy]. Dist./ Udawattakele/ 26-30 March 1975/ S. & P. B. Karunaratne"; "Symmorphus/ alkimus/ Cumming & Vecht/ Holotype [red bordered label]" (USNM).

ALLOTYPE, male labelled: "ALLOTYPE [red label]"; "W. Haputale, 6000'/ Ceylon, 2-7-VIII-37"; "Symmorphus/ alkimus/ Cumming & Vecht/ Allotype [red bordered label]" (USNM on long term loan from CNM).

PARATYPES: Ceylon, C. P. [Central Province], Kandy, Lady Horton's, 22.XI.1953, F. Keiser-female (NHMB); Ceylon, Kandapola, Goatfell, 13-17.IV.1933-female (USNM on long term loan from CNM); Sri Lanka, Kan[dy Dist.], Kandy, Udawattakele Sanctuary, 2100 feet, 20-30.VII.1976, S. Karunaratne-female (USNM).

Recognition.—Distinguished from other members of *S. hoozanensis* group by features given in key to species and subspecies of *S. (Symmorphus)*. Additionally recognized from *S. hoozanensis* and *S. canlaonicus* by absence of yellow on mesosoma, and from *S. ambotretus* by the non-incised occipital carina and paler maculation.

Description.—*Female.* Head including clypeus nearly as high as wide (0.92 to 0.96). Clypeus with height 0.68 to 0.72 maximum width, shallowly emarginate apically, evenly convex in profile. Interantennal carina slightly to moderately elevated, with short median keel ventrally. OOL 0.80 to 0.94 POL; LOL 0.47 to 0.50 POL. Vertex with cephalic foveae of moderate size, maximum foveal diameter 0.72 to 0.88 trans-scutal sulcus length; moderately spaced, minimum interval between foveae 0.57 to 0.75 POL; each fovea not bordered posteriorly by carina. Occipital carina without submedial incisions, slightly pointed medially (fig. 14).

Pronotum with carina at crest of anterior face complete, evenly arcuate medially (fig. 13); humeral angle obtuse (fig. 47), barely projected. Notaulus very faint, broadly obsolete medially. Mesepisternum with epicnemial carina obsolete dorsally. Pseudosternum without high reflexed border along anterior margin (fig. 19). Metanotum nearly vertical, with narrow irregular dorsal surface. Propodeum with very short nearly horizontal medially depressed superior shelf, medial length of shelf 0.78 to 1.00 length of trans-scutal sulcus; submedian carina of propodeum slightly produced ventrally, absent dorsally; propodeal valvula abruptly pointed dorsally, slightly extended with posterolateral projection of submarginal carina (fig. 51); propodeal orifice broadly rounded dorsally (fig. 36).

Metasomal tergum 1 broad, medial postcarinal length 0.47 to 0.49 apical width; sides of postcarinal area barely convergent towards base, width at transverse carina 0.90 to 0.94 apical width; transverse carina complete; longitudinal furrow broadly impressed, shallowly depressed, without deeper narrow medial sulcus. Metasomal sternum 1 with basal carina deeply curved posteriorly, fused posteriorly to carinate median longitudinal and lateral oblique ridges. Metasomal segment 2 in profile with base of tergum obtusely angulate and sternum abruptly truncate posteriad of basal sulcus; tergum with length 1.07 to 1.11 maximum width; apical margin of segment 2 translucent, depressed, its maximum length 1.22 to 1.38 length of trans-scutal sulcus.

Clypeus moderately to densely puncticulate to punctate, punctures sparse medioapically. Frons and vertex foveolate-puncticulate, major punctures moderately spaced. Pronotum, except anterior face, foveolate-puncticulate, with major punctures moderately spaced, more or less costate laterally; anterior face obscurely imbricate. Mesoscutum foveolate-puncticulate; major punctures moderately spaced anteriorly, widely spaced posteriorly. Mesoscutellum foveolate-puncticulate, major punctures widely spaced. Dorsal mesepisternum foveolate-puncticulate, major punctures widely spaced, minor punctures obscure. Ventral mesepisternum foveolate-puncticulate, major punctures widely spaced, minor punctures obscure. Mesepimeron foveolate-puncticulate, major punctures moderately spaced, minor punctures obscure. Metanotum foveolate-puncticulate dorsally, obscurely puncticulate ventrally. Propodeum finely striate laterally, areolate-rugose dorsally; posterior face nearly smooth, with some shallow indistinct rugosity and obscure imbricate subsculpture. Metasomal segments with imbricate subsculpture. Tergum 1 with postcarinal area foveolate-puncticulate to foveate-puncticulate; sternum 1 rugose anteriorly, median longitudinal ridge flanked by carinate longitudinal rugae. Segment 2 foveolate-puncticulate, major punctures larger and more closely spaced towards apex. Terga 3 to 5 and sternum 3 with sparse punctate or foveolate major punctures subapically.

Pubescence pale yellow to white, without lengthened setae.

Coloration black with yellow as follows: interantennal spot, postocular dot, faint line on outer surface of tibiae (on hind tibia not extended to apical half), apical border of metasomal tergum 1, subapical border of metasomal tergum 2 and sternum 2. Tarsi pale brown basally to dark reddish brown apically. Wings lightly infuscate.

Length to apex of metasomal tergum 2, 8.0 to 8.5 mm.

*Male.* Similar to female except as follows: clypeus moderately emarginate apically; humeral angle slightly projected; metasomal tergum 1 with postcarinal area foveate-puncticulate; sternum 3 with major punctures primarily foveate subapically; mandible yellow basally; clypeus with large basal yellow spot; legs slightly lighter, reddish to dark brown, mid tibia with yellow line not extended to apex, hind tibia with basal yellow spot, tarsi pale brown to reddish brown apically, fore leg with basitarsus yellow.

Antennal articles 10 to 13 each with single tyloid, article 13 in profile with length 0.81 maximum width.

Length to apex of metasomal tergum 2, 7.5 mm.

Geographical distribution and seasonal occurrence.—Known only from the type series collected from March to November in the central highlands of Sri Lanka (fig. 62).

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Presumably the sister taxon of *S. alkimus dialeukus.* The relationships of the entire species, beyond inclusion within the *S. hoozanensis* group however, are unclear (fig. 83).

### 5.1.3.1.1.2.2 *S. (Symmorphus) alkimus dialeukus* **new subspecies**

Holotype.—Female labelled: "HOLOTYPE [red label]"; "N Sumatra/ Sibolangit, 500 m/ 1954. 19|12/ J v d Vecht"; "Museum Leiden/ ex coll. J.v.d. Vecht"; "Symmorphus/ alkimus dialeukus/ Cumming/ Holotype [red bordered label]" (RNHL).

Derivation of subspecific epithet.—Derived from the Greek word *dialeukos*, meaning marked with white, in reference to the white maculation in members of this subspecies.

Description.—*Female*. Similar to typical subspecies except maculation paler, ivory to white, with additional marks as follows: clypeus with basal band, pronotum with two dorsal spots, small dorsal mesepisternal spot and two small mesoscutellar spots. Wings hyaline with lightly infuscate patch adjacent anterior apical margin of fore wing.

*Male*. Unknown.

Geographical distribution.—Known from northern Sumatra (fig. 62).

Seasonal occurrence.—Known only from the holotype collected in December.

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Considered the sister taxon of *S. alkimus alkimus*, as indicated under that subspecies.

### 5.1.3.1.1.3 *S. (Symmorphus) ambotretus* **new species**

Holotype.—Female labelled: "HOLOTYPE [red label]"; "Mt[.]Omei [Emei Shan]/ Szechuen [Sichuan Province] China/ 4400ft"; "DCGraham/ Collector"; "Symmorphus/ bifoveolatus/ n.sp. [manuscript name]/ C. L. Lui [black bordered label]"; "S-10 [yellow label]"; "Symmorphus/ ambotretus/ Cumming/ Holotype [red bordered label]" (USNM).

Allotype.—Male labelled: "ALLOTYPE [red label]"; "NEPAL/ Kathmandu/ Valley/ B. KIAUTA &/ M. BRINK leg."; "Chaunii 1350 m./ 16-25.V.1973"; "Netherlands Centre/ for Alpine Biological/ Research"; "Symmorphus [male symbol]/ det.J.v.d.Vecht 1974"; "Symmorphus/ ambotretus/ Cumming/ Allotype [red bordered label]" (RNHL).

Derivation of specific epithet.—Derived from the Greek words, *ambon*, meaning rim, and *tretos*, meaning perforated, in reference to the incised occipital carina in members of this species.

Recognition.—Easily distinguished from all members of the *S. hoozanensis* group, except *S. hoozanensis*, by the presence of an occipital carina with two submedial incisions that delimit a blunt median tooth. Specimens of *S. hoozanensis*, which are recognized from those of *S. ambotretus* by differences in the pronotal carina and degree of maculation, may have the occipital carina depressed submedially with the concomitant development of a slight median projection similar to that seen in *S. ambotretus*.

Description.—*Female*. Head including clypeus nearly as high as wide (0.96). Clypeus with height 0.73 maximum width, shallowly emarginate apically, evenly convex in profile. Interantennal carina slightly to moderately elevated, with median keel ventrally. OOL 0.90 to 0.93 POL; LOL 0.53 POL. Vertex with cephalic foveae of moderate size, maximum foveal diameter 0.72 to 0.84 trans-scutal sulcus length; moderately spaced, minimum interval between foveae 0.67 to 0.73 POL; each fovea not bordered posteriorly by carina. Occipital carina with two submedial incisions that delimit blunt median tooth (fig. 13).

Pronotum with carina at crest of anterior face complete, evenly arcuate medially (fig. 13); humeral angle obtusely rounded, barely projected. Notaulus faint, narrowly obsolete medially. Mesepisternum with epicnemial carina obsolete dorsally. Pseudosternum without high reflexed border along anterior margin (fig. 19). Metanotum nearly vertical, with narrow irregular dorsal surface. Propodeum with short nearly horizontal medially depressed superior shelf, medial length of shelf 1.18 to 1.75 length of trans-scutal sulcus; submedian carina of propodeum slightly produced ventrally, faint and irregular dorsally; propodeal valvula pointed to abruptly pointed dorsally, moderately extended with posterolateral projection of submarginal carina; propodeal orifice broadly rounded dorsally (fig. 36).

Metasomal tergum 1 slightly broad, medial postcarinal length 0.54 to 0.57 apical width; sides of postcarinal area barely convergent towards base, width at transverse carina 0.90 apical width; transverse carina complete; longitudinal furrow broadly impressed, shallowly depressed, without deeper narrow medial sulcus. Metasomal sternum 1 with basal carina deeply curved posteriorly, fused posteriorly to carinate median longitudinal and lateral oblique ridges. Metasomal segment 2 in profile with base of tergum obtusely angulate and sternum abruptly truncate posteriad of basal sulcus; tergum with length 1.18 to 1.26 maximum width; apical margin of segment 2 translucent, depressed, its maximum length 1.29 to 1.34 length of trans-scutal sulcus.

Clypeus moderately punctate-puncticulate to foveolate-puncticulate, punctures sparse medioapically. Frons and vertex foveolate-puncticulate, major punctures moderately to densely spaced. Pronotum, except anterior face, foveolate-puncticulate, with major punctures moderately to densely spaced, more or less costate laterally; anterior face obscurely imbricate. Mesoscutum foveolate-puncticulate; major punctures moderately to densely spaced anteriorly, widely to moderately spaced posteriorly. Mesoscutellum foveolate-puncticulate, major punctures widely to moderately spaced. Dorsal mesepisternum foveolate-puncticulate, major punctures widely spaced, minor punctures obscure. Ventral mesepisternum foveolate-puncticulate, major punctures widely spaced, minor punctures obscure. Mesepimeron foveolate-puncticulate, major punctures moderately spaced, minor punctures obscure. Metanotum foveolate-puncticulate dorsally, obscurely puncticulate ventrally. Propodeum striately rugose to rugose laterally, areolate-rugose dorsally; posterior face nearly smooth, with some shallow indistinct rugosity and obscure imbricate subsculpture. Metasomal tergum 1 with postcarinal area foveolate-puncticulate to foveate-puncticulate; sternum 1 rugose anteriorly, median longitudinal ridge flanked by carinate longitudinal rugae. Segment 2 foveolate-puncticulate, major punctures larger and more closely spaced towards apex, minor punctures connected by obscure imbricate subsculpture. Terga 3 to 5 and sternum 3 with sparse punctate or foveolate major punctures subapically. Segments 3 to 6 with imbricate subsculpture.

Pubescence pale yellow to white, without lengthened setae.

Coloration black with orange-yellow to orange-red as follows: clypeus with two basal spots (absent in female paratype), interantennal spot (absent in female paratype), postocular dot, two dorsal pronotal spots (absent in holotype), apical border of metasomal tergum 1, subapical border of metasomal tergum 2 and sternum 2. Tarsi dark brown. Wings lightly infuscate.

Length to apex of metasomal tergum 2, 9.0 mm.

*Male.* Similar to female except as follows: clypeus moderately emarginate apically; humeral angle obtuse, slightly projected; metasomal sternum 3 with foveolate to foveate major punctures subapically; mandible light yellow basally; clypeus light yellow except black apical border; scape with basal yellow spot; interantennal spot and postocular dot yellow; pronotal spots distinctly thickened towards humerus; mesoscutellum with two small orange-yellow spots (absent in male paratype from Swayambhunath); fore leg with line on outer surface of tibia and basitarsus yellow.

Antennal articles 9 to 13 each with single tyloid (absent from article 9 in allotype), article 13 in profile with length 0.83 to 0.95 maximum width.

Length to apex of metasomal tergum 2, 7.0 mm.

Geographical distribution.—Known to range from the eastern border of the Sichuan highlands in China, to the southern Himalaya in central Nepal (fig. 63).

Seasonal occurrence.—Specimens of the type series from Nepal were collected from April to May. The holotype and paratype from China are without seasonal data.

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Beyond inclusion within the *S. hoozanensis* group, the relationships of this species remain unclarified (fig. 83).

Paratypes.—**China**: Szechuen [Sichuan Province], Chengtu [Chengdu], D. C. Graham-female (USNM). **Nepal**: Kathmandu Valley, Chauni, 1350 m., 16-25.V.1973, B. Kiauta & M. Brink-male; Kathmandu Valley, small stream N. of Swayambhunath, 1350 m., 18-24.IV.1973, B. Kiauta & M. Brink-male (RNHL).

### 5.1.3.1.1.4 *S. (Symmorphus) canlaonicus* new species

Holotype.—Female labelled: "HOLOTYPE [red label]"; "Mt. Canlaon 3600'/ Negros Or[iental]., Phil./ Apr. 29, 1953/ H, M, & D. Townes"; "Symmorphus/ canlaonicus/ Cumming/ Holotype [red bordered label]" (AEI).

Derivation of specific epithet.—Latin adjective, *canlaonicus*, in reference to the type locality.

Recognition.—Distinguished from other members of *S. hoozanensis* group by features given in the key to species and subspecies of *S. (Symmorphus)*. Additionally recognized from *S. alkimus* and *S. ambotretus* by more extensive maculation of head and mesosoma, and from *S. hoozanensis* by smaller size.

Description.—*Female.* Head including clypeus nearly as high as wide (0.95). Clypeus with height 0.74 maximum width, shallowly emarginate apically, evenly convex in profile. Interantennal carina slightly to moderately elevated, with median keel ventrally. OOL 0.96 POL; LOL 0.50 POL. Vertex with cephalic foveae of moderate size, maximum foveal diameter 0.67 trans-scutal sulcus length; moderately spaced, minimum interval between foveae 0.70 POL; each fovea not bordered posteriorly by carina. Occipital carina without submedial incisions, slightly pointed medially (fig. 14).

Pronotum with carina at crest of anterior face obsolete dorsolaterally, evenly arcuate medially; humeral angle obtusely rounded, barely projected. Notaulus faint, narrowly obsolete medially. Mesepisternum with epicnemial carina obsolete dorsally, faint ventrally. Pseudosternum without high reflexed border along anterior margin (fig. 19). Metanotum nearly vertical, with narrow irregular dorsal surface. Propodeum with short nearly horizontal medially depressed superior shelf, medial length of shelf 1.50 length of trans-scutal sulcus; submedian carina of propodeum slightly produced ventrally, absent dorsally; propodeal valvula pointed dorsally, slightly to moderately extended with posterolateral projection of submarginal carina; propodeal orifice broadly rounded dorsally (fig. 36).

Metasomal tergum 1 slightly broad, medial postcarinal length 0.52 apical width; sides of postcarinal area barely convergent towards base, width at transverse carina 0.88 apical width; transverse carina complete; longitudinal furrow broadly impressed, shallowly depressed, without deeper narrow medial sulcus. Metasomal sternum 1 with basal carina deeply curved posteriorly, fused posteriorly to carinate median longitudinal and lateral oblique ridges. Metasomal segment 2 in profile with base of tergum obtusely angulate and sternum abruptly truncate posteriad of basal sulcus; tergum with length 1.06 maximum width; apical margin of segment 2 translucent, depressed, its maximum length 1.13 length of trans-scutal sulcus.

Clypeus moderately foveolate-puncticulate, major punctures shallow, minor punctures sparse medioapically, apex impunctate. Frons and vertex foveolate-puncticulate, major punctures moderately spaced. Pronotum, except anterior face, foveolate-puncticulate, with major punctures moderately spaced, more or less costate laterally; anterior face obscurely imbricate. Mesoscutum foveolate-puncticulate, major punctures moderately spaced. Mesoscutellum foveolate-puncticulate; major punctures widely spaced, shallow and indistinct; minor punctures obscure. Dorsal mesepisternum foveolate-puncticulate; major punctures widely spaced, shallow and indistinct, minor punctures obscure. Ventral mesepisternum foveolate-puncticulate, major punctures widely spaced, minor punctures obscure. Mesepimeron foveolate-puncticulate, major punctures moderately spaced, minor punctures obscure. Metanotum foveolate-puncticulate dorsally, obscurely puncticulate ventrally. Propodeum striate laterally, areolate-rugose dorsally; posterior face nearly smooth, with some shallow indistinct rugosity and obscure imbricate subsculpture. Metasomal segments with imbricate subsculpture. Tergum 1 with postcarinal area foveolate-puncticulate; sternum 1 rugose anteriorly, median longitudinal ridge flanked by carinate longitudinal rugae. Segment 2 foveolate-puncticulate, major punctures nearly uniformly distributed, slightly larger and more closely spaced towards apex. Terga 3 to 5 and sternum 3 with sparse punctate or foveolate major punctures subapically.

Pubescence pale yellow to white, without lengthened setae.

Coloration black with yellow as follows: clypeus with large basal band, interantennal spot, postocular spot, large basal mandibular mark, scape anteriorly, medially interrupted dorsal pronotal band (thickened towards humerus and extended along posterior margin nearly to tegula), large dorsal mesepisternal spot, tegula, parategula, two large nearly approximate mesoscutellar spots, two metanotal spots, apex of fore and mid femora (less on mid femur), outer surface of tibiae (on hind tibia not extended to apex), apical border of metasomal tergum 1, subapical border of metasomal tergum 2 and sternum 2. Tarsi pale brown basally to reddish brown apically. Wings hyaline to very lightly infuscate.

Length to apex of metasomal tergum 2, 7.5 mm.

*Male.* Unknown.

Geographical distribution.—Known from the Philippine island of Negros (fig. 63).

Seasonal occurrence.—Known only from the holotype collected in April.

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Inferred with uncertainty, to be the sister species of *S. hoozanensis* (fig. 83).

### 5.1.3.1.2 S. declivis group

This monobasic group contains the highly distinctive Mediterranean species *S. declivis* Harttig. It is characterized at the species group level by a female clypeus which is shallowly emarginate apically (fig. 57), non-vertical metanotum, metasomal tergum 1 with longitudinal furrow sharply impressed and with deeper narrow medial sulcus posteriorly (fig. 12), metasomal sternum 1 without basal carina and median longitudinal ridge, base of metasomal segment 2 in profile with tergum obtusely angulate and sternum abruptly truncate posteriad of basal sulcus (fig. 52), and slightly developed not depressed apical margin of metasomal segment 2 (fig. 54).

#### 5.1.3.1.2.1 *S. (Symmorphus) declivis* Harttig

*Symmorphus declivis* Harttig, 1932 (coll. Harttig, ? loc.).

*Odynerus (Koptodynerus) declivis* (Harttig); Blüthgen, 1943.

Type material examined.—PARATYPES: Styria [Yugoslavian region], Podčetrtek [Windisch-Lansberg], 6.IV.1926, 19.VIII.1925 & 11.VIII.1931, Dr. Jaeger-female, 2 males (2 MSNV, 1 ZMHB).

Harttig (1932) did not explicitly state which of the nine specimens from Podčetrtek he considered as the holotype, although he did mention that he deposited it in his collection instead of in Jaeger's collection with the paratypes. Of the three specimens I have examined from the type series, the male and female from MSNV are clearly labelled as paratypes, while the male specimen from ZMHB bears a "Typus" label. I suspect that the holotype once located, will be clearly labelled as such and will probably be one of the three female specimens of the series, since Harttig described the female of *S. declivis* in much greater detail than the male.

Recognition.—Readily distinguished from species of *S. murarius* group by the basal shape of metasomal segment 2. Most easily recognized from species of *S. hoozanensis* group, which have a similarly shaped metasomal segment 2 (see also *S. parvilineatus*), by the slightly developed not depressed apical margin of metasomal segment 2 and sharply impressed longitudinal furrow of metasomal tergum 1.

Description.—*Female.* Head including clypeus slightly higher than wide (1.01 to 1.09). Clypeus with height 0.63 to 0.65 maximum width; very shallowly emarginate apically, nearly truncate; evenly convex in profile. Interantennal carina moderately elevated, with median keel ventrally. OOL 0.84 to 0.88 POL; LOL 0.50 to 0.56 POL. Vertex with cephalic foveae of moderate size, maximum foveal diameter 1.00 to 1.20 trans-scutal sulcus length; moderately spaced, minimum interval between foveae 0.68 to 0.70 POL; each fovea not bordered posteriorly by carina. Occipital carina without submedial incisions, slightly pointed medially (fig. 14).

Pronotum with carina at crest of anterior face obsolete (fig. 17); humeral angle nearly acute, slightly projected (fig. 46). Notaulus complete. Mesepisternum with epicnemial carina obsolete dorsally. Pseudosternum without high reflexed border along anterior margin (fig. 19). Metanotum not distinctly vertical, with size of dorsal surface slightly smaller to subequal size of posterior surface. Propodeum with short oblique to nearly horizontal medially depressed superior shelf, medial length of shelf 1.90 to 2.25 length of trans-scutal sulcus; submedian carina of propodeum moderately to markedly produced ventrally, absent dorsally; propodeal valvula gradually narrowed dorsally, slightly extended with posterolateral projection of submarginal carina; propodeal orifice broadly rounded dorsally (fig. 36).

Metasomal tergum 1 slightly to moderately elongate, medial postcarinal length 0.59 to 0.66 apical width; sides ~~of~~ postcarinal area moderately to slightly convergent towards base, width at transverse carina 0.77 to 0.81 apical width; transvese carina complete; longitudinal furrow sharply impressed, shallowly depressed, with deeper narrow medial sulcus posteriorly. Metasomal sternum 1 without basal carina and median longitudinal ridge; lateral oblique ridges not carinate, faint anteriorly. Metasomal segment 2 in profile with base of tergum obtusely angulate and sternum abruptly truncate posteriad of basal sulcus; tergum with length 0.94 to 1.04 maximum width; apical margin of segment 2 translucent, not depressed, its maximum length 0.38 to 0.75 length of trans-scutal sulcus.

Clypeus moderately foveolate with some additional obscure rugosity, punctures shallow. Frons and vertex foveolate-puncticulate, major punctures densely spaced. Pronotum, except anterior face, foveolate-puncticulate, with major punctures densely spaced, more or less costate laterally; anterior face smooth with sparse foveolate punctures dorsally and laterally. Mesoscutum foveolate-puncticulate, major punctures densely spaced. Mesoscutellum foveolate-puncticulate, major punctures widely spaced, minor punctures obscure. Dorsal mesepisternum foveolate-puncticulate; major punctures absent anteriorly, sparse and indistinct posteriorly; minor punctures obscure posteriorly. Ventral mesepisternum foveolate-puncticulate, major punctures widely spaced, minor punctures obscure. Mesepimeron foveolate-puncticulate, major punctures densely spaced, minor punctures obscure. Metanotum foveolate-puncticulate dorsally, obscurely puncticulate ventrally. Propodeum striately rugose laterally, areolate-rugose dorsally; posterior face transversely strigate medially, shallowly rugose laterally. Metasomal segments with imbricate subsculpture. Tergum 1 with postcarinal area foveolate-puncticulate; sternum 1 foveolate-puncticulate, apex with short shallow longitudinal rugae. Segment 2 foveolate-puncticulate, major punctures nearly uniformly distributed, slightly smaller and more widely spaced towards apex. Terga 3 to 5 and sternum 3 with sparse shallow punctate or foveolate major punctures apically.

Pubescence pale yellow to white, without lengthened setae.

Coloration black with yellow as follows: clypeus with basal band, interantennal spot, postocular spot, scape basoventrally (absent in many individuals), medially interrupted dorsal pronotal band (thickened towards humerus), large dorsal mesepisternal spot, tegula posteriorly, two large approximate mesoscutellar spots (contiguous in some individuals), apex of fore femur, outer surface of tibiae (on hind tibia not extended to apex), apical border of metasomal terga 1, 2, 4 and sternum 2 (on tergum 4 not extended to lateral margin) (terga 3 and 5 medially with apical marks in a few individuals). Tarsi pale brown to reddish brown, slightly darker apically. Wings hyaline to very lightly infuscate.

Length to apex of metasomal tergum 2, 7.0 to 8.5 mm.

*Male.* Similar to female except as follows: clypeus shallowly to moderately emarginate apically; humeral angle acute, moderately projected; mandible yellow basally; clypeus yellow; scape yellow anteriorly; mid coxa yellow anteriorly; apex of fore, mid and hind femora yellow (extensively on fore femur); tibiae nearly entirely yellow; metasomal terga 3, 5, 6 and sterna 4 and 5 medially with apical yellow marks (variously absent in some individuals); tarsi lighter, pale brown with yellow basitarsi.

Antennal articles 10 to 13 each with single tyloid (barely developed or absent on article 10), article 13 in profile with length 1.00 to 1.07 maximum width.

Length to apex of metasomal tergum 2, 6.0 to 7.0 mm.

Geographical distribution and seasonal occurrence.—Known from the northeastern Mediterranean region, north to Hungary (see Blüthgen, 1961) and Austria (fig. 64). **Austria**: Burgenland, Kulm N.E. Güssing, 16.V.1976. **Cyprus**: Kalopanayiotis, 2600ft., 28.X.1964, 28.XI.1964; Pera Pedi, 2000ft., 4.IV.1952; Potamitissa, 3000ft.; Saëttas, 6.IV.1962, 30.V.1960. **Greece**: Crete, Omalos, 3600ft., 30.IV.1974; Rhodes, Hedenb.; Rhodes, Sephyros, 10.X.1982. **Italy**: Roma [Rome], Castel Porziano, 12.V.1940. **Turkey**: Antalya [district], Finike, 50-100 m., 7.IV.1962; Antalya [district], Finike-Kas Road, 300 m., 10.IV.1962; Aydin [district], Bozdogan, 200 m., 22.IV.1962; Istanbul, Bebek, IV.1950, 27.IV.1953, 2.X.1949. **Yugoslavia** Styria, Podčetrek [Windisch-Lansberg], 18.IV.1934, 12.V.1933, 21.V.1933, 11.VIII.1934, 18.VIII.1932; Styria, Windische Bühel [Windisch-Büheln], Karnerberg, 8.VIII.1971.

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Inferred to be the sister taxon of the *S. murarius* group, primarily on the basis of the form of metasomal segments 1 and 2 (figs. 80, 81).

### 5.1.3.1.3 S. murarius group

This diverse group is characterized by a female clypeus which is shallowly to deeply emarginate apically (figs. 57-59), vertical to non-vertical metanotum; metasomal tergum 1 with longitudinal furrow sharply impressed (secondarily broadened in *S. violaceipennis*) and with deeper narrow medial sulcus posteriorly (fig. 12), metasomal sternum 1 with or without basal carina and median longitudinal ridge, base of metasomal segment 2 in profile with tergum gradually rounded and sternum flat to slightly convex posteriad of basal sulcus (fig. 54), and slightly to moderately developed not depressed apical margin of metasomal segment 2 (figs. 41, 54, slightly depressed on tergum in *S. sichuanensis*). The group is primarily Holarctic in distribution, extending southward as far as the Atlas Mountains, southern Himalaya, northern

Thailand and Taiwan in the Old World, and northern Nicaragua in the New World.

### 5.1.3.1.3.1 *S. (Symmorphus) murarius* (Linnaeus)

*Vespa muraria* Linnaeus, 1758 (LS).

*Odynerus (Protodynerus) nidulator* Saussure, 1855 (? MNHP).

*Odynerus (Symmorphus) murarius nidulator* Saussure; Berland, 1928.

Notes about synonymy.—Although the type of *S. nidulator* (Saussure) could not be located in the collection of MNHP or elsewhere, Saussure's description leaves no doubt that the female specimen (or specimens) he had before him was an extensively maculated yellow color form of *S. murarius*. Subspecific recognition of this color form as proposed by Berland (1928), is considered unwarranted, given that color pattern varies continuously over the range of *S. murarius* (see below under "Variation") and populations distinguished on this basis alone are not distinct structurally.

Type material examined.—*Vespa muraria* Linnaeus, HOLOTYPE, female labelled: "muraria" [followed by type labels] (LS).

Recognition.—Particularly distinct because of the suppressed transverse carina of metasomal tergum 1, very large cephalic foveae of females and very long antennal article 13 of males. Specimens of *S. murarius* can be confused with those of *S. foveolatus* as discussed under "Recognition" of that species.

Description.—*Female.* Head including clypeus nearly as high as wide (0.91 to 0.99). Clypeus with height 0.63 to 0.67 maximum width; shallowly to moderately emarginate apically (figs. 57, 58); evenly convex in profile. Interantennal carina moderately elevated, with median keel ventrally. OOL 1.11 to 1.21 POL; LOL 0.50 to 0.62 POL. Vertex with cephalic foveae of extremely large size, maximum foveal diameter 3.45 to 5.00 trans-scutal sulcus length;

gradually tapered and shallow anterolaterally; foveae approximate, nearly contiguous, minimum interval between foveae 0.06 to 0.19 POL; each fovea not bordered posteriorly by distinct carina (fig. 27). Occipital carina without submedial incisions, evenly arcuate medially.

Pronotum with carina at crest of anterior face obsolete medially, faint dorsolaterally; humeral angle rounded to obtusely rounded, not projected. Notaulus faint to obsolete anteriorly. Mesepisternum with epicnemial carina obsolete dorsally, very faint to obsolete ventrally. Pseudosternum without high reflexed border along anterior margin (fig. 19). Metanotum not distinctly vertical, with size of dorsal surface greater than half to subequal size of posterior surface. Propodeum with very short to short obliquely rounded to nearly horizontal medially depressed superior shelf, medial length of shelf 0.85 to 1.45 length of trans-scutal sulcus; submedian carina of propodeum slightly to moderately produced ventrally, absent dorsally; propodeal valvula gradually narrowed dorsally, barely extended with short rounded posterolateral projection of submarginal carina (fig. 24); propodeal orifice broadly rounded dorsally (fig. 36).

Metasomal tergum 1 broad to slightly elongate, medial postcarinal length 0.46 to 0.59 apical width; sides of postcarinal area moderately to slightly convergent towards base, width at transverse carina 0.70 to 0.86 apical width; transverse carina obsolete laterally, faint medially (fig. 25); longitudinal furrow sharply impressed, shallowly depressed, with deeper narrow medial sulcus posteriorly. Metasomal sternum 1 without basal carina and median longitudinal ridge; lateral oblique ridges not carinate, faint anteriorly. Metasomal segment 2 in profile with base of tergum gradually rounded and sternum slightly and evenly convex posteriad of basal sulcus; tergum with length 0.78 to 0.95 maximum width; apical margin of segment 2 translucent, not depressed, its maximum length 0.28 to 0.50 length of trans-scutal sulcus.

Clypeus moderately punctate-puncticulate to foveolate-puncticulate, punctures sparse medioapically. Frons and vertex foveolate-puncticulate, major punctures moderately spaced. Pronotum, except anterior face, foveolate-puncticulate, with major punctures widely to moderately spaced, more or less costate laterally; anterior face smooth. Mesoscutum foveolate-puncticulate, major punctures widely to moderately spaced. Mesoscutellum foveolate-puncticulate, major punctures moderately spaced, minor punctures obscure. Dorsal mesepisternum foveolate-puncticulate, major punctures widely to moderately spaced. Ventral mesepisternum foveolate-puncticulate, major punctures widely to moderately spaced, minor punctures obscure. Mesepimeron foveolate-puncticulate, major punctures moderately spaced, minor punctures obscure. Metanotum foveolate-puncticulate dorsally, obscurely puncticulate ventrally. Propodeum rugose to markedly rugose laterally, areolate-rugose dorsally; posterior face obscurely sculptured, shallowly rugose to rugose. Metasomal tergum 1 with postcarinal area foveolate-puncticulate to foveate-puncticulate; sternum 1 foveolate-puncticulate to foveate-puncticulate. Segment 2 foveolate-puncticulate basally to punctate-puncticulate apically; minor punctures connected by obscure imbricate subsculpture. Segments 3 to 6 with sparse shallow punctate or foveolate major punctures apically and imbricate subsculpture.

Pubescence pale yellow to white, with lengthened setae (figs. 21, 22, primarily on head and mesosoma).

Coloration black with yellow as follows: clypeus with large basal band (small in some individuals), interantennal spot (absent in some individuals), postocular dot, scape anteroventrally (absent in some individuals), medially interrupted dorsal pronotal band (thickened towards humerus) (reduced to two small spots in a few individuals), large dorsal mesepisternal spot (small or absent in some individuals), tegula (black in a few individuals), two large approximate mesoscutellar spots (small or absent in some individuals), apex of femora (absent in some individuals), outer surface of fore tibia, outer and inner surface of mid and hind tibiae (absent from hind tibia and inner surface of mid tibia in a few individuals), apical border of metasomal terga 1 to 6 and sterna 2 to 5 (absent from tergum 6 and sternum 5 in most individuals, additionally absent from terga 3, 5 and sterna 3, 4 in a few individuals). Tarsi pale brown to dark brown, slightly darker apically, fore leg with yellow basitarsus (without yellow in a few individuals). Wings hyaline to lightly infuscate.

Length to apex of metasomal tergum 2, 11.0 to 15.0 mm.

*Male.* Similar to female except as follows: clypeus moderately emarginate apically; humeral angle obtusely rounded; mandible yellow basally; clypeus yellow; pronotum black in a few individuals; dorsal mesepisternal spot small or absent; mid coxa yellow anteriorly (reduced to two small spots or absent in some individuals); metasomal terga 1 to 7 and sterna 2 to 6 each with yellow apical border (absent from tergum 7 in most individuals and sternum 6 in some individuals); tarsi pale brown to reddish brown.

Antennal articles 10 to 13 each with single tyloid (barely developed on article 10 in a few individuals), article 13 in profile with length 1.47 to 1.75 maximum width.

Length to apex of metasomal tergum 2, 8.0 to 12.0 mm.

Variation.—Most specimens from more northerly localities, have less of their total body area marked with yellow and tend to have paler nearly white markings, than specimens from more southerly localities.

Geographical distribution and seasonal occurrence.—Known to range from continental Europe, east through Asia, to Primorskij Krai in eastern USSR (fig. 64). **Austria:** distribution widespread, earliest seasonal record—Linz, Plesching, 18.V.1961; latest seasonal record—Brixlegg, Tirol, 2.VII.1941. **Belgium:** Namur, VI.1934. **Czechoslovakia:** distribution widespread, earliest seasonal record—Bohemia, Jirna, 14.VI.1908; latest seasonal record—Všenory, 27.VII.1912. **Denmark:** Lolland, VIII.1831; North East Zealand; Strandm. [NEZ]. **Finland:** Fennia, Kb. Joensuu, 1-9.VII.1975; Lojo [Lohja], 15.VI.1917, 28.VI.1919, 23.VII.1918, 25-27.VII.1916; Pärna. **France** distribution widespread, earliest seasonal record—Avignon, 12.V.1891; latest seasonal record—Tence, HL., 11.VII.1929. **Germany (BRD & DDR):** distribution widespread, earliest seasonal record—Roseng., 23.V.1891; latest seasonal record—Roseng., 13.VII.1891. **Hungary**: N. Bogsán; Tiszakeszi. **Iran**: 1965; Tehran, 36 km. W. Firuz-Kooh, 23-26.VI.1963. **Italy**: Bolzano Province, Dolomites, Suisialloscíliar, Seis am Schlern, 16.VI.1956; Padova, 1.VI.1938; Torino; Val Gardena, Ortisei, VI.1942. **Netherlands**: Drunen, NB., 20.VII.1956. **Poland**: Pommern [Pomerania], Gollnow [Goleniow], 26.VI.1897, 28.VI.1893; Szczawa, 49.36N 20.18E, 13-17.VII.1967; **Portugal**: Foia, 800 m., 25.VI.1978. **Spain**: Barcelone [Barcelona]; Cuenca Castilien, 1890; Cuenca Spainien; Ronda 1000 m., 1-5.VI.1974. **Sweden**: distribution widespread in south, earliest seasonal record—Sk., Vänga [Vänge], Grönhult, 24.V.1918; latest seasonal record—Öl., Löttorp, VIII-IX.1970; most northerly records—Gstr., Hille Forsby, 6.VII.1948; Vikarbyn Salarna, 1940. **Switzerland**: Bern, Bätterkdn, 9.VI.1889; Canton de Berne, Burgdorf. **Turkey**: Asia minore, Zona centrale, Ulukisla, 20.V.1961. **USSR**: Barabash-Levada, Primorskij Krai, 6.VI.1980; Dzhungar Khr. [range], n-1000, V. [E.] Kazakhstan, Topolevka, 5.VII.1957; Ferganskij Khr. [range], 1500 [m.], Kirgiziya, verch. [upland] Jassy, 17.VI.1954; Ferganskij Khr. [range], 1800 [m.], Kirgiziya, verch. [upland] Jassy, 22.VI.1954; Gosmalyan-Azerbaidnean, Talyshskie gory, Iuzh. Lerika, 27.VI.1969; Iu-v. [S.E.] Kazakhstan, 25 km. W. Alma Ata, 12.VI.1979; Kazakhstan, Khr. [range] Karatau, 10 km. Z. [W.] los. Bijlukulv, 13.V.1977; Khr. [range] Terskej, Chronkyzylsu, 20.VII.1953; Khr, [range] Zailijsk Ala-tau, environs of Alma Ata, 6.VI.1979; Khr. [range] Zailijsk Ala-tau, Ush. bol. Dalan, 3,4,10.VI.1971; Kurland, Jelowka-Lepel, 2-8.VI.1916, 23.VI.1917; Leder, Irkut, 1891; Monastero[,] Gherard [collector ?], Armenia, 13.VII.1963; Pergiuveio Lrosk. u. [? location], 6.VI.1909; Primore, environs of Anisimovki, 23.VI.1974, 4,10,17.VII.1974; Primore, environs of p. Tigrovogo, 12,16.VI.1975; Spalle, Kurland, 19.VI.1917; Stavropole Terbeda, 21.VII.1981; Turkestansk Khr.[range], 16.VI.1953; Yaresbki [Jaresvki] [? location], mirg. u. Polt. g., 25.VI.1925; Zapov. Aksu-Dzhabagly, Iu. [S.] Kazakhstan, Chimkentskaya obl., 17,19,21.VI.1966. **Yugoslavia**: Podčetrtek [Windisch-Lansberg], 18.V.1934.

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Apparently the sister group to a clade composed of *S. foveolatus*, *S. glasunowi* and *S. sichuanensis*.

### 5.1.3.1.3.2 *S. (Symmorphus) foveolatus* Gussakovskij

*Symmorphus foveolatus* Gussakovskij, 1932 (NRS).

*Odynerus captivus* Smith *sensu* Schulthess, 1934; Yasumatsu, 1938; Kostylev, 1940. **Misidentification.**

*Symmorphus captivus* (Smith) *sensu* Tsuneki, 1973. **Misidentification.**

? *Odynerus captivus* Smith *sensu* Iwata, 1938. **Misidentification.**

Notes about synonymy.—Schulthess (1934) misidentified this species as *S. captivus* (Smith), contrary to Soika (1975), and several successive authors, beginning with Yasumatsu (1938), appear to have followed this interpretation.

Type material examined.—LECTOTYPE (here designated), female labelled: "21-VI [19]30"; "Vladivostok [district]/ Sedanka/ *Malaise*"; "Symmorphus [female symbol]/ foveolatus, sp. n./ V. gussakovskij" (NRS). My lectotype label "LECTOTYPE [underlined in red]/ Symmorphus [female symbol]/ foveolatus Guss./ des. J. M. Cumming 1984 [black bordered label]" has been attached to this specimen.

Gussakovskij (1932) described *S. foveolatus* from 2 female specimens without selecting a holotype. The collection of NRS contains only one of these specimens; the one herein designated lectotype. The location of the other syntype is unknown, but it may reside in the Gussakovskij collection in ZIL.

Recognition.—Most similar to *S. glasunowi* and *S. sichuanensis* as discussed under "Recognition" of those species. Specimens of *S. foveolatus* can be confused with pale slightly marked specimens of *S. murarius*, especially given that the cephalic foveae of most female specimens of *S. foveolatus* are set in large shallow depressions that can resemble the enlarged foveae of *S. murarius* females. However, both species are readily distinguished by the form of the transverse carina of metasomal tergum 1, male antenna and shape of the propodeal orifice.

Description.—*Female*. Head including clypeus as high to slightly higher than wide (1.00 to 1.05). Clypeus with height 0.63 to 0.68 maximum width; moderately emarginate apically (fig. 58); evenly convex in profile. Interantennal carina moderately elevated, with median keel ventrally. OOL 1.01 to 1.33 POL; LOL 0.52 to 0.59 POL. Vertex with cephalic foveae of large size, maximum foveal diameter 1.25 to 2.00 trans-scutal sulcus length; set in larger anterolaterally tapered shallow depression (barely apparent in a few individuals); moderately to widely spaced, minimum interval between foveae 0.67 to 0.95 POL; each fovea not bordered posteriorly by carina. Occipital carina without submedial incisions, slightly pointed medially (fig. 14).

Pronotum with carina at crest of anterior face complete, evenly arcuate medially (fig. 13); humeral angle obtuse (fig. 47), barely to very slightly projected. Notaulus faint anteriorly. Mesepisternum with epicnemial carina entirely obsolete (fig. 21). Pseudosternum without high reflexed border along anterior margin (fig. 19). Metanotum oblique, without distinct dorsal and posterior surfaces. Propodeum without distinct superior shelf medially, slightly rounded at level of metanotum; submedian carina of propodeum slightly produced ventrally, absent dorsally; propodeal valvula gradually narrowed dorsally, slightly extended with rounded posterolateral projection of submarginal carina (fig. 31); propodeal orifice moderately narrowed dorsally (fig. 26).

Metasomal tergum 1 slightly elongate to elongate, medial postcarinal length 0.60 to 0.72 apical width; sides of postcarinal area markedly to moderately convergent towards base, width at transverse carina 0.58 to 0.75 apical width; transverse carina laterally faint or obsolete (fig. 26); longitudinal furrow sharply impressed, shallowly depressed, with deeper narrow medial sulcus posteriorly. Metasomal sternum 1 without basal carina and median longitudinal ridge;

lateral oblique ridges not carinate, faint anteriorly. Metasomal segment 2 in profile with base of tergum gradually rounded and sternum slightly and evenly convex posteriad of basal sulcus; tergum with length 0.84 to 1.00 maximum width; apical margin of segment 2 translucent, not depressed, its maximum length 0.75 to 1.00 length of trans-scutal sulcus.

Clypeus moderately punctate-puncticulate to foveolate-puncticulate, punctures sparse medioapically. Frons and vertex foveolate-puncticulate, major punctures moderately spaced. Pronotum, except anterior face, foveolate-puncticulate, with major punctures moderately spaced; anterior face smooth. Mesoscutum foveolate-puncticulate, major punctures moderately spaced. Mesoscutellum foveolate-puncticulate, major punctures moderately spaced, minor punctures obscure. Dorsal mesepisternum foveolate-puncticulate, major punctures widely to moderately spaced, minor punctures obscure. Ventral mesepisternum foveolate-puncticulate, major punctures widely to moderately spaced, minor punctures obscure. Mesepimeron foveolate-puncticulate, major punctures moderately spaced, minor punctures obscure. Metanotum foveolate-puncticulate dorsally, imbricate ventrally. Propodeum finely striate laterally, with some shallow foveolate punctures, areolate-rugose dorsally; posterior face transversely strigate medially to striately rugose laterally. Metasomal tergum 1 with postcarinal area foveolate-puncticulate to foveate-puncticulate; sternum 1 foveolate-puncticulate to foveate-puncticulate. Segment 2 punctate-puncticulate to foveolate-puncticulate, major punctures widely spaced and uniformly distributed (denser basally in some specimens). Segments 3 to 6 with sparse shallow punctate or foveolate major punctures apically and imbricate subsculpture.

Pubescence pale yellow to white, with lengthened setae (figs. 21, 22, primarily on head and mesosoma).

Coloration black with ivory to yellow as follows: interantennal spot (absent in some individuals), postocular dot, line on outer surface of fore tibia (not extended to apex in some individuals), apical border of metasomal terga 1, 2, 4 and sternum 2 (on tergum 4 not extended to lateral margin). Tarsi dark brown. Wings lightly infuscate.

Length to apex of metasomal tergum 2, 8.5 to 11.0 mm.

*Male*. Similar to female except as follows: clypeus moderately to deeply emarginate apically; humeral angle slightly projected; clypeus ivory to yellow, except margin; metasomal tergum 5 with ivory to yellow apical marks; fore leg with ivory to yellow line on outer surface of basitarsus.

Antennal articles without tyloids, article 13 in profile with length 1.14 to 1.40 maximum width.

Length to apex of metasomal tergum 2, 7.5 to 9.0 mm.

Geographical distribution and seasonal occurrence.—Known from Primorskij Krai in USSR, North Korea (see Yasumatsu, 1938), South Korea and Japan (fig. 65). **Japan**: distribution widespread, earliest seasonal record—Tokyo, 1.V.1931; latest seasonal record—Honshu, Saitama [Pref.], Otaki, 31.VII.1973; most northerly records—Hokkaido, Sapporo, 22.VII.1976; Sapporo, 6.VII.1954; most southerly record—Kiushiū [Kyushu], Bassin Superieur de la Sendaigawa [Sendai, Kagoshima Pref.], 1906. **South Korea**: Suigen [Suwon], 20.V.1927. **USSR**: Barabash-Levada, Primorskij krai, 1.VII.1978; environs of Vladivostok, Primorskij krai, 18.VI.1978; Primor. kr., siup Such[an] [Sutshan] r.n., 19.VII.1940; Primore, environs of Anisimovki, 20.VI.1974, 20.VI.1975, 1.VII.1974, 2.VII.1974, 10.VII.1974; Primore, environs of s. [N.] Brovnicha r. sica, 15.VI.1975; Primorskij krai, Ussurijskij r-n. Sumutinskij zan., 22.VII.1978.

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Inferred to be the sister species of *S. glasunowi*, from which it differs only slightly.

### 5.1.3.1.3.3 *S. (Symmorphus) glasunowi* Morawitz

*Symmorphus glasunowi* Morawitz, 1895 (ZIL).

*Odynerus (Symmorphus) calciatii* Zavattari, 1912a (MIZT). New synonymy.

Notes about synonymy.—It appears that Zavattari (1912a) was unaware of Morawitz's description of *S. glasunowi* from Turkestan in 1895, when he later described *S. calciatii* from neighboring Kashmir. I have examined the holotype of *S. calciatii* and regard it as conspecific with the lectotype of *S. glasunowi*.

Type material examined.—*Symmorphus glasunowi* Morawitz, LECTOTYPE (here designated), female labelled: "Artutsch./ VI.9.[18]92"; "K [coll.]. *F. Morawitz* [in Russian]"; "glasunowi/ F. Mor. [female symbol]"; Lectotypus Symmor-/ phus glasunowi Mor. [female symbol]/ des. Kurzenko 1976 [red label] [unpublished invalid designation]" (ZIL). My lectotype label "LECTOTYPE [underlined in red]/ Symmorphus [female symbol]/ glasunowi Mor./ des. J. M. Cumming 1985 [black-bordered label]" has been attached to this specimen.

PARALECTOTYPES: Artutsch.-male; Artutsch., 9.VI.[18]92-2 females; Artutsch., glasun.-female; Seravschan [Zeravschan Range, Tadzhik S.S.R.], Kschtut [Kshtut], Artutsch., 1892, Glasunov-female (ZIL). My paralectotype labels have additionally been attached to these specimens.

Morawitz (1895) described *S. glasunowi* from a series of female specimens and at least one male specimen from Artutsch., Tadzhik S.S.R., but did not select a holotype. Six specimens of the type series, including the lectotype designated herein, are in the collection of ZIL and probably represent all the syntypes of *S. glasunowi*.

*Odynerus (Symmorphus) calciatii* Zavattari, HOLOTYPE, female labelled: "Cashmir [Kashmir, Baltistan]/ Khapulu [Khapalu] Calciati"; "Typus"; "Odynerus/ calciatii Zav./ [female symbol] E. Zavattari, det."; "Holotype [orange label]" (MSNV on long term loan from

MIZT).

Recognition.—Very similar to *S. foveolatus*. In addition to features given in the key to species and subspecies of *S.* (*Symmorphus*), specimens of *S. glasunowi* are distinguished from those of *S. foveolatus* by the rounder less projected humeral angle of the female pronotum, shallower emargination of the male clypeal apex and generally smaller size. *S. glasunowi* is also similar to *S. sichuanensis* as discussed under "Recognition" of that species.

Description.—*Female*. Head including clypeus slightly higher than wide (1.02 to 1.06). Clypeus with height 0.65 to 0.67 maximum width; moderately emarginate apically (fig. 58); evenly convex in profile. Interantennal carina moderately elevated, with median keel ventrally. OOL 1.02 to 1.10 POL; LOL 0.52 to 0.58 POL. Vertex with cephalic foveae of large size, maximum foveal diameter 1.38 to 1.67 trans-scutal sulcus length; set in larger anterolaterally tapered shallow depression (barely apparent in some individuals); moderately spaced, minimum interval between foveae 0.79 to 0.85 POL; each fovea not bordered posteriorly by distinct carina. Occipital carina without submedial incisions, slightly pointed medially (fig. 14).

Pronotum with carina at crest of anterior face complete, evenly arcuate medially (fig. 13); humeral angle obtusely rounded, barely projected. Notaulus faint anteriorly. Mesepisternum with epicnemial carina entirely obsolete (fig. 21). Pseudosternum without high reflexed border along anterior margin (fig. 19). Metanotum oblique to nearly vertical, with narrow rounded dorsal surface. Propodeum without distinct superior shelf medially, slightly rounded at level of metanotum; submedian carina of propodeum slightly produced ventrally, absent dorsally; propodeal valvula gradually narrowed dorsally, slightly extended with rounded posterolateral projection of submarginal carina (fig. 31); propodeal orifice moderately narrowed dorsally (fig. 26).

Metasomal tergum 1 moderately elongate to elongate, medial postcarinal length 0.65 to 0.73 apical width; sides of postcarinal area markedly to moderately convergent towards base, width at transverse carina 0.64 to 0.73 apical width; transverse carina laterally faint (fig. 26); longitudinal furrow sharply impressed, shallowly depressed, with deeper narrow medial sulcus posteriorly. Metasomal sternum 1 without basal carina and median longitudinal ridge; lateral oblique ridges not carinate, faint anteriorly. Metasomal segment 2 in profile with base of tergum gradually rounded and sternum slightly and evenly convex posteriad of basal sulcus; tergum with length 0.86 to 0.95 maximum width; apical margin of segment 2 translucent, not depressed, its maximum length 0.50 to 0.67 length of trans-scutal sulcus.

Clypeus moderately punctate-puncticulate to foveolate-puncticulate, punctures sparse medioapically. Frons and vertex foveolate-puncticulate, major punctures moderately spaced. Pronotum, except anterior face, foveolate-puncticulate, with major punctures moderately spaced; anterior face smooth. Mesoscutum foveolate-puncticulate, major punctures moderately spaced. Mesoscutellum foveolate-puncticulate, major punctures moderately spaced, minor punctures obscure. Dorsal mesepisternum foveolate-puncticulate, major punctures widely to moderately spaced, minor punctures obscure. Ventral mesepisternum foveolate-puncticulate, major punctures widely to moderately spaced, minor punctures obscure. Mesepimeron foveolate-puncticulate, major punctures moderately spaced, minor punctures obscure. Metanotum foveolate-puncticulate dorsally, imbricate ventrally. Propodeum finely striate laterally, with some shallow foveolate punctures, areolate-rugose dorsally; posterior face transversely strigate medially to striately rugose laterally. Metasomal tergum 1 with postcarinal area foveolate-puncticulate to foveate-puncticulate; sternum 1 foveolate-puncticulate to foveate-puncticulate. Segment 2 punctate-puncticulate to foveolate-puncticulate, major punctures widely spaced and uniformly distributed (denser basally in some specimens). Segments 3 to 6 with sparse shallow punctate or foveolate major punctures apically and imbricate subsculpture.

Pubescence pale yellow to white, with lengthened setae (figs. 21, 22, primarily on head and mesosoma).

Coloration black with yellow as follows: clypeus with basal band (medially interrupted in some individuals), interantennal spot, postocular dot, scape anteroventrally, medially interrupted dorsal pronotal band (thickened towards humerus), large dorsal mesepisternal spot, tegula, two mesoscutellar spots, apex of fore femora, outer surface of tibiae (on hind tibia not extended to apex), apical border of metasomal terga 1 to 5 and sterna 2 to 4 (on tergum 5 and sternum 4 not extended to lateral margin in a few individuals). Tarsi pale brown to reddish brown, slightly darker apically. Wings very lightly infuscate.

Length to apex of metasomal tergum 2, 8.0 to 10.0 mm.

*Male.* Similar to female except as follows: humeral angle obtuse, slightly projected; mandible yellow basally; clypeus yellow; metasomal terga 6 and 7 and sterna 5 and 6 each with yellow apical marks (absent from tergum 7 in specimen from Ferganskij Khr.); tarsi lighter, pale brown with yellow basitarsi.

Antennal articles without tyloids, article 13 in profile with length 1.25 to 1.36 maximum width.

Length to apex of metasomal tergum 2, 7.0 to 8.0 mm.

Geographical distribution and seasonal occurrence.—Known from the Pamir and western slopes of the Tien Shan and Himalaya mountain ranges (fig. 65). In addition to the type series of *S. glasunowi*, which was collected in June and the holotype of *S. calciatii*, which is without seasonal data, one male and two female specimens have been examined. USSR: Chatkalskij Khr. [range], 30 km. N. Parkenma, Ushch. [canyon] Aksagama, 7-10.VI.1982 (IBPV); Ferganskij Khr. [range], 1800 [m.], Kirgiziya, verch. [upland] Jassy, 15.VI.1954 (MSUM).

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Apparently the sister species of *S. foveolatus.*

### 5.1.3.1.3.4 *S. (Symmorphus) sichuanensis* Lee

*Symmorphus (Symmorphus) sichuanensis* Lee, 1981 (IZAS).

Type material examined.—PARATYPE: Sichuan Province, Kuan [Guanxian] District, Blue Castle Mountain, 700-1600 m., 26.V.1963, Chang Shun Jung [in Chinese]-female (IZAS).

Recognition.—Similar to *S. foveolatus* and *S. glasunowi.* In addition to features given in the key to species and subspecies of *S. (Symmorphus)*, specimens of *S. sichuanensis* are distinguished from those of either species by larger size, presence of a distinct (although short) superior shelf, slightly depressed apical margin on metasomal tergum 2 and more elongate metasomal tergum 1 in most specimens.

Description.—*Female.* Head including clypeus nearly as high as wide (0.95 to 0.99). Clypeus with height 0.65 maximum width; moderately emarginate apically (fig. 58); evenly convex in profile. Interantennal carina moderately elevated, with median keel ventrally. OOL 1.01 to 1.12 POL; LOL 0.44 POL. Vertex with cephalic foveae of large size, maximum foveal diameter 2.00 trans-scutal sulcus length; slightly tapered anterolaterally; moderately spaced, minimum interval between foveae 0.71 POL; each fovea not bordered posteriorly by carina. Occipital carina without submedial incisions, flattened to slightly concave medially.

Pronotum with carina at crest of anterior face complete, evenly arcuate medially (fig. 13); humeral angle obtusely rounded, barely projected. Notaulus complete. Mesepisternum with epicnemial carina obsolete dorsally, faint ventrally. Pseudosternum without high reflexed border along anterior margin (fig. 19). Metanotum oblique to nearly vertical, with narrow rounded dorsal surface. Propodeum with very short to short nearly horizontal medially depressed superior shelf, medial length of shelf 0.93 to 1.22 length of trans-scutal sulcus;

submedian carina of propodeum slightly produced ventrally, absent dorsally; propodeal valvula gradually narrowed dorsally, barely extended with short rounded posterolateral projection of submarginal carina (fig. 24); propodeal orifice moderately narrowed dorsally (fig. 26).

Metasomal tergum 1 elongate to markedly elongate, medial postcarinal length 0.70 to 0.91 apical width; sides of postcarinal area moderately convergent towards base; width at transverse carina 0.71 to 0.74 apical width; transverse carina laterally faint or obsolete (fig. 26); longitudinal furrow sharply impressed, shallowly depressed, with deeper narrow medial sulcus posteriorly. Metasomal sternum 1 without basal carina and median longitudinal ridge; lateral oblique ridges not carinate, faint anteriorly. Metasomal segment 2 in profile with base of tergum gradually rounded and sternum slightly and evenly convex posteriad of basal sulcus; tergum with length 1.00 to 1.09 maximum width; apical margin of segment 2 translucent, slightly depressed on tergum, its maximum length 1.10 to 1.11 length of trans-scutal sulcus.

Clypeus moderately punctate-puncticulate to foveolate-puncticulate, punctures sparse medioapically. Frons and vertex foveolate-puncticulate, major punctures moderately spaced. Pronotum, except anterior face, foveolate-puncticulate, with major punctures moderately spaced, more or less costate laterally; anterior face obscurely imbricate. Mesoscutum foveolate-puncticulate, major punctures moderately spaced. Mesoscutellum foveolate-puncticulate, major punctures moderately to densely spaced, minor punctures obscure. Dorsal mesepisternum foveolate-puncticulate, major punctures widely to moderately spaced, minor punctures obscure. Ventral mesepisternum foveolate-puncticulate, major punctures widely to moderately spaced, minor punctures obscure. Mesepimeron punctate-puncticulate to foveolate-puncticulate, major punctures widely to moderately spaced, minor punctures obscure. Metanotum foveolate-puncticulate dorsally, imbricate ventrally. Propodeum finely striate laterally, with some shallow foveolate punctures, areolate-rugose dorsally; posterior face transversely strigate medially to striately rugose laterally. Metasomal tergum 1 with postcarinal area foveolate-puncticulate to foveate-puncticulate; sternum 1 foveolate-puncticulate to foveate-puncticulate. Segment 2 foveolate-puncticulate, major punctures larger and more closely spaced along basal and apical borders. Segments 3 to 6 with sparse shallow punctate or foveolate major punctures apically and imbricate subsculpture.

Pubescence pale yellow to white, with lengthened setae (fig. 21, 22, primarily on head and mesosoma).

Coloration black with orange-yellow as follows: interantennal spot, postocular dot, outer surface of fore tibia, apical border of metasomal terga 1, 2 and sternum 2. Tarsi dark brown. Wings moderately infuscate.

Length to apex of metasomal tergum 2, 13.5 to 15.0 mm.

*Male.* Similar to female except as follows: humeral angle obtuse, slightly projected; clypeus yellow, except basal margin; metasomal tergum 2 and sternum 2 entirely black.

Antennal articles 12 and 13 each with single tyloid, article 13 in profile with length 1.29 maximum width.

Length to apex of metasomal tergum 2, 10.0 mm.

Geographical distribution and seasonal occurrence.—Known to range from the eastern border of the Sichuan highlands in China, south to the high-country of northern Thailand (fig. 65). In addition to the paratype, which was collected in May, one male and two female specimens have been examined. **China**: Sichuan Province, Emei Shan [Mt. Omei], 550-750 m., 4.VI.1957 (MSNV); Sichuan Province, Kuan [Guanxian] District, Blue Castle Mountain, 700-1600 m., 26.V.1963 (MSNV). **Thailand**: Chieng Dao [Chiang Dao], Chieng Mai [Chiang Mai District], 6.IV.1958 (RNHL).

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Inferred to be the sister group of the *S. foveolatus*-*S. glasunowi* clade, with which it shares a somewhat narrow propodeal orifice dorsally.

### 5.1.3.1.3.5 *S. (Symmorphus) crassicornis* (Panzer)

*Vespa crassicornis* Panzer, 1798 (destroyed, neotype in USNM).

*Odynerus (Protodynerus) arcticus* Saussure, 1855 (? NRS).

*Odynerus (Protodynerus) herrichianus* Saussure, 1855 (possible type in MNHP).

*Odynerus nursei* Bingham, 1898 (BMNH). **New synonymy.**

*Odynerus hospes* Nurse, 1903. Homonym of *Odynerus hospes* Dufour and Perris, 1840 (BMNH). **New synonymy.**

*Odynerus hospitans* Dalla Torre, 1904. New name for *Odynerus hospes* Nurse, 1903. **New synonymy.**

*Odynerus (Symmorphus) crassicornis baltica* Blüthgen, 1937 (ZMHB).

*Odynerus (Symmorphus) crassicornis arcticus* Saussure; Blüthgen, 1961.

Notes about synonymy.—The type of *S. arcticus* (Saussure) could not be located in the collection of NRS, as recorded by Saussure (1855), or collections elsewhere. Blüthgen probably examined this type, as he implied in 1961, prior to his report (Blüthgen, 1937) on the type of *S. suecicus* (Saussure), which at one time also resided in the collection of NRS. Since Saussure's description of *S. arcticus* agrees completely with the current concept of *S. crassicornis* (Panzer), Blüthgen's synonymy of *S. arcticus* with the latter name (Blüthgen, 1938) is accepted.

The type of *S. herrichianus* (Saussure) was considered to have been destroyed with the remainder of the Herrich-Schaeffer collection (Blüthgen, 1961; Vecht and Fischer, 1972). However, a male specimen apparently determined by Saussure from Herrich-Schaeffer's collection (see below under "Type material examined"), was discovered in the collection of

MNHP and may possibly be the missing type or one of the syntypes. This specimen, which agrees perfectly with the original description, minimally indicates Saussure's concept of *S. herrichianus* and since I regard it as conspecific with the neotype of *S. crassicornis*, also confirms Blüthgen's (1938) synonymy of these two names.

In 1898 Bingham described *O. nursei* from at least two female specimens collected by Col. C. G. Nurse in Simla, northwestern India. Subsequently Nurse (1903) described a slightly discolored male specimen from Simla, as *O. hospes* (*nec* Dufour and Perris), apparently assuming it also was a female specimen (see below under "Type material examined"). I have examined the lectotype and holotype of these two nominal species respectively, and regard them both as conspecific with *S. crassicornis*.

In addition, I have examined the holotype of *S. crassicornis baltica* described by Blüthgen in 1937. This subspecies, whose name was latter synonymized by Blüthgen (1961) under *S. crassicornis articus*, is recognized entirely on the restricted yellow coloration of its members. As such, subspecific recognition of this form is considered unwarranted, given that color pattern varies continuously over the range of *S. crassicornis* (see below under "Variation") and populations distinguished on this basis alone are not distinct structurally.

Type material examined.—*Vespa crassicornis* Panzer, NEOTYPE (here designated), female labelled: "Austria superior/ Linz, Umg. 23.8.1966/ gründberg/ Karl Kudas"; "Symmorphus crassicornis (Pz.) [female symbol]/ J.Gusenleitner, det.1971" (USNM). My neotype label "NEOTYPE [underlined in red]/ Vespa crassicornis/ Panzer [female symbol]/ des. J.M.Cumming 1985" and determination label "Symmorphus/ crassicornis [female symbol]/ (Panzer)/ det./ J.M. Cumming 1985" have been attached to this specimen.

The type of *V. crassicornis* was not located in any of the collections listed under "Materials" and is presumed to have been destroyed with the remainder of the Panzer collection (Vecht and Fischer, 1972). Since the description by Panzer (1798) is insufficient to place this name with certainty, conforming equally well with *S. murarius* (Linnaeus) as indicated by Blüthgen (1938, 1961), a neotype is selected herein to fix the name in its traditional sense for the sake of stability. The female specimen selected as neotype is from Austria, the locality given by Panzer (1798) and agrees closely with the original description which also appears to have been of a female specimen.

*Odynerus (Protodynerus) herrichianus* Saussure, possible TYPE, male labelled: "[square metallic colored label] [damaged]"; "HSch [small square blue label]"; "Od. herrichi-/ anus Sauss/ [male symbol]/ crassicorn m. [in Saussure's handwriting]"; "2b/ 2b [pink label]" (MNHP). A label indicating the possiblity of type status and my *S. crassicornis* determination label have been attached to this specimen.

Although the type of *O. herrichianus* is reported to have been destroyed with the remainder of the Herrich-Schaeffer collection (Blüthgen, 1961; Vecht and Fischer, 1972), Saussure may not have deposited the type (or types) in the Herrich-Schaeffer collection as he stated in 1855. The specimen in the collection of MNHP appears to have been determined by Saussure, apparently from the Herrich-Schaeffer collection and agrees perfectly with the original description.

*Odynerus nursei* Bingham, LECTOTYPE (here designated), female labelled: "Simla/ 5.[18]97."; "[female symbol]"; "Col.C.G.Nurse/ Collection./ 1920-72 [label reversed on pin]"; "British Museum/ Loan No. 4251 [label reversed on pin]"; "nursei B."; "Symmorphus/ nursei (Bingh.)/ conf. Tipo e descrip./ A. G. Soika det., 1970" (MSNV on long term loan from BMNH). My lectotype label "LECTOTYPE [underlined in red]/ Odynerus [female symbol]/ nursei Bingham/ des. J.M. Cumming 1985 [black bordered label]" has been attached to this specimen.

Bingham (1898) appears to have described *O. nursei* from at least two specimens, although this is not apparent from his description. Soika (personal communication) compared the specimen herein designated lectotype, to a second syntype labelled as the type in the collection of the BMNH. This syntype can no longer be located in the BMNH.

*Odynerus hospes* Nurse, HOLOTYPE, male [not female] labelled: "Type [circular red bordered label]"; "Simla/ 5. 97."; "[female symbol, remarked as male symbol]"; "Type"; "Col. C.G. Nurse/ Collection/ 1920-72"; "Odynerus/ hospes/ (Nurse)"; "B.M. TYPE/ HYM./ 18.292" (BMNH).

The holotype of *O. hospes* in the collection of the BMNH is actually a male specimen, although the description by Nurse (1903) refers only to a female. It agrees entirely with the original description and bears a label marked with a female symbol (remarked subsequently as a male symbol).

*Odynerus (Symmorphus) crassicornis baltica* Blüthgen, HOLOTYPE female labelled: "[female symbol]"; "Launingken/ 24.6.1936. [blue label]"; "crassicornis/ (Pz.) v. baltica/ m. [female symbol]/ Blüthgen,det.1937."; "Type [pink label]"; "ex. coll./ Blüthgen"; "Zool. Mus./ Berlin [yellow label]" (ZMHB).

Recognition.—In the Old World very similar to *S. captivus* and *S. angustatus* as discussed under "Recognition" of those species. In addition, very similar to *S. albomarginatus* from the New World, being most readily distinguished by the more narrowly spaced cephalic foveae of *S. crassicornis* females.

Description.—*Female*. Measurements of largest and smallest specimens given in Table 1. Taxonomically important character states given in Table 3.

*Male*. Measurements of largest and smallest specimens given in Table 1. Taxonomically important character states given in Table 3.

Variation.—Most specimens from more northern localities, have less of their total body area marked with yellow and tend to have paler yellow markings, than those from more southerly localities. Some specimens from Kazakh S.S.R., possibly collected at high elevations, have white markings and resemble specimens collected much further north in the restricted extent of their markings.

Geographical distribution and seasonal occurrence.—Known to range from Europe, east through western Asia, to the foothills of the Altai Mountains in Kazakh S.S.R. and southern Himalaya in northwestern India (fig. 66). **Austria**: distribution widespread, earliest seasonal record—Salzburg-Bergheim-Au, 2.VII.1969; latest seasonal record—Neumarkt, Steiermark, VIII.1964. **Belgium** distribution widespread, earliest seasonal record—Bouillon, Lux., 1.V.1975; latest seasonal record—Chiny, Lux., 15.VIII.1945. **Czechoslovakia** distribution widespread, earliest seasonal record—Olomouc, Mor., CSR, 16.VI.1948; latest seasonal record—Ladiel (gorge), 10.VIII.1963. **Denmark** Falster, LFM; Lolland; North East Zealand; Strandm., NEZ. **Finland**: Fredrikeberg, VI; Karislojo; VI; Lojo [Lohja], 10-18.VII.1920, 23-24.VII.1916, 11.VIII.1915; Pa ¨rnaTva ¨rminne, 9.VIII.1937. **France** distribution widespread, earliest seasonal record—St. Gily, 22.V.1918; latest seasonal record—Brunoy, Seine & Oise, IX.1920. **Germany (BRD & DDR)**: distribution widespread, earliest seasonal record—Süd-Pfalz, Siebeldingen, 25.V.1953; latest seasonal record—Bildhausen, Krs. Kissingen [Bad Kissingen], 30.VIII.1946. **Greece**: C. [Central] Greece, Gravia-Lamia, 1.VI.1971; Thermopylae, 7.V.1977. **Hungary**: Hungrie Centrale, Kaspathen, Comit. Bereg. **Iran**: Tehran, 36 km. W. Firuz-Kooh, 23-26.VI.1963. **Italy**: distribution widespread, earliest seasonal record—Toscana Firenze, Cascine, 1.V.1946; latest seasonal record—Limone, Piemonte, 7.VII.1931; most southerly record—Sila, Calabria, Camigliatollo. **Luxembourg**: Kautenbach, 18-21.VIII.1956. **Netherlands** distribution widespread, earliest seasonal record—Heerlen, 11.IV.1952; latest seasonal record—Oisterwijk, 28.VIII.1921. **Poland** Sandomierz, 13.VI.1953, 27.VII.1954; Szklarska Porgba, pow Jel:So ´ra, 8.VIII.1958; Warsaw. **Spain**: Valle de Ordesa, 23.VII. **Sweden**: distribution widespread in south, earliest seasonal record—Vg., Landvetter, 15.VI.1932; latest seasonal record—Upl., Vallentuna, 20.VIII.1972; most northerly records—Hls., Bergvik kl, 21,25,27.VI.1947; Vrm., Säffle, VII.1936; Vstm., Ekshärad, 16.VII.1960. **Switzerland**: 31.VIII.1882; Canton de Berne, Burgdorf; Mt. Uetliberg, Zurich, 27.VII. **Turkey**: Ankara [Antalya district], Karagol Lake, 3500ft., 26.VI.1960; Asia minor, Eski-Tshehir, VII, VIII.1906; Asia minor, Kara-Tshehir, 9.VII.1906; Erzurum Kopdagi Gecidi, 5000ft., 22.VII.1960; Giresun Balaban Daglari, 5200ft., 9.VII.1960. **United Kingdom (& Ireland)**: distribution widespread in southern England and Wales, earliest seasonal record—West Parley, Dorsett, 5.VI.1952; latest seasonal record—Bovey Tracey, Devon, 17.VIII.1928; most northerly record—Brentwood, Essex (recorded as far north as Allerthorpe Common, Yorks., by Guichard, 1972). **USSR**: Alexander Mts., Turkestan; Alma Ata obl., Karoalinka, ival bya; Berdichyno, Yarosl. u., 29.VII.1909; C. Kazakhstan, 15-20 km. Iu [S.] Karaula, Khr. [range] Chingiz-Tau, 25,26.VI.1978; Caucase [Caucasus], Menesiner; Chatkalskij Khr. [range], 1200 [m.], Kirgiziya Arkut, 25.VI.1952; Dol. r. Chatkal, Tien-Shan, 30.VII.1973; Dor. Pzhingatal-Pzhekimdol. Alajsk. Khr. [range], Tadzhikistan, 18.VII.1971; environs of Ayak. Kapkana, Iu-v. [S.E.] Kazakhstan, 4.VI.1971; Ferganskij Khr. [range], Kirgiziya, 1800 [m.], verch. [upland] Jassy, 22.VI.1954; Grosse, Barsuki bei Tschelkar; Kazakhskij Melkosopochnik, 200 km. Sev. [N.] oz. [lake] Balchash, 25.V.1969; Kazakhstan, 30 km. V. [E.] Kokchetava, 16.VII.1977; Kirg. Uzgen, 27.VII.1924; Kirgiziya, dol r. Kokomeron ur. Sary-bulun, 26,27.VII.1974; Kirgiziya, r. Naryn, environs of Kazarman, Togz. moroo, 14.VIII.1978; Kyrm Chatyras Dag, S. [N.] Perevalnoe, 1.VII.1976; Le Gaure, L.-Inf. [Lithuania-Inf.], 5.VII.1943; Moskovskaya obl., Solkechkogorskij, r-n. Chashnikovo, 15,29.VI.1981, 8.VII.1981; Sary-bulun, Tien-Shan 26.VII.1974; Sev. [N.] Kazakhstan, environs of Derzhavinska, 7.VI.1976; Sev. [N.] Kazakhstan, Shijli, 70 km. Iu z [S.W.] Arkalyka, 2.VI.1976; St. Petersbourg [Leningrad]; Südi Uralgebiet, Kargala b. Orenburg, 1915, 1917; Vost. [E.] Kazakhstan, Nikolajevka, 30 km. Iu v [S.E.] Georgijevka, 23.VI.1979; Zapov. Aksu-Dzhabagly, Iu [S.] Kazakhstan, Chimkentskaya obl., 11.VI.1965, 19,21.VI.1966, 1.VII.1966; Zeravshansk. Khr. [range], oz. [lake] Islander-kul, 13.VII.1971. **Yugoslavia**: Basaka, Ins. Krk, 8-30.VI.1973; Sarajevo; Styrie [Styria], 1877; Vidrenjak, 100 m., 45.30N 16.31E, 17.VII.1963.

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—*S. crassicornis* is allied with *S. captivus*, *S. angustatus* and *S. albomarginatus*, although relationships among the four species are unclear.

### 5.1.3.1.3.6 *S. (Symmorphus) captivus* (Smith)

*Odynerus (Symmorphus) captivus* Smith, 1873 (BMNH).

(—*captivus* Smith *sensu* Schulthess, 1934; Yasumatsu, 1938; Kostylev, 1940; Tsuneki, 1973 = *S. foveolatus*. —*captivus* Smith *sensu* Iwata, 1938 = ? *S. foveolatus*.)

Type material examined.—HOLOTYPE, female labelled: "F. Sm. Coll./ 79-22"; "Japan/ Hiogo [Hyogo Pref.]"; "O. captivus/ Smith"; "B.M. TYPE/ HYM./ 18.321" (BMNH).

Recognition.—Very similar to both *S. crassicornis* and *S. angustatus* in the Old World, and *S. albomarginatus* in the New World. Specimens of *S. captivus* are distinguished from those of *S. crassicornis* by presence of concentric carinae in the medial depression of the propodeal superior shelf (Fig. 33), in addition to features given in the key to species and subspecies of *S. (Symmorphus)*, and are differentiated from those of *S. angustatus* as discussed under "Recognition" of that species. Separation of *S. captivus* and *S. albomarginatus* is difficult other than by geographical distribution, because of the considerable degree of intraspecific variation observed in the latter species. However, specimens of *S. albomarginatus* are smaller, have the sides of the postcarinal area of metasomal tergum 1 slightly more convergent towards the base and lack concentric carinae in the medial depression of the propodeal superior shelf in many specimens.

Description.—*Female*. Measurements of largest and smallest specimens given in Table 1. Taxonomically important character states given in Table 3.

*Male*. Measurements given in Table 1. Taxonomically important character states given in Table 3.

Geographical distribution and seasonal occurrence.—Known from central Japan, on the island of Honshu (fig. 66). In addition to the holotype, which is without seasonal data, one male and six female specimens have been examined. **Japan**: Mt. Mitake, Nishitama dist., Tokyo [Pref.], 22.VII.1951, 23.VII.1950 (NSMT); Osaka, 7.VII (MSNV); Senjugahama, Nikko, Tochigi [Pref.], 2.VIII.1971 (YAMC); Shinnyu-Zan, Hiroshima, Honshu, 25.VII.1979 (JMCU); Shioyama-C, Yamanashi [Pref.], IV-V.1978 (YAMC) (additional records, from Ishikawa and Iwate Prefectures, in Soika, 1975 and Tsuneki, 1977).

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Related to *S. crassicornis*, *S. angustatus* and *S. albomarginatus*.

### 5.1.3.1.3.7 *S. (Symmorphus) angustatus* (Zetterstedt)

*Odynerus angustatus* Zetterstedt, 1838. Priority established by Blüthgen, 1942a (UZIL).
*Odynerus alternans* Zetterstedt, 1838 (UZIL).
*Odynerus (Protodynerus) suecicus* Saussure, 1855 (? NRS).
*Odynerus laeviventris* Thomson, 1874 (UZIL).

(—*angustatus* Zetterstedt *sensu* Thomson, 1874; Dalla Torre, 1894; Aurivillius, 1918; Móczár, 1938; Blüthgen, 1938; Wilcke, 1952; Zanden, 1955 = *S. bifasciatus*.)

Notes about synonymy.—Although the type of *S. suecicus* (Saussure) could not be located in the collection of NRS or elsewhere, it was seen by Blüthgen (1937) who indicated it was conspecific with *S. alternans* (Zetterstedt) and probably also earlier by Gussakovskij (1932) who reported the name's synonymy with *S. laeviventris* (Thomson). In addition, Blüthgen's synonymy of *S. laeviventris* and *S. alternans* with *S. angustatus* (Zetterstedt) (Blüthgen, 1937, 1942a, 1942b) is confirmed, even though his acceptance of *S. alternans* as the valid name of this species (Blüthgen, 1961) cannot be justified (see Vecht, 1971).

Type material examined.—*Odynerus angustatus* Zetterstedt, HOLOTYPE male [not female] labelled: "O. angusta-/ tus [female symbol]. Bossek[op]."; "=Odynerus/ alternans/ Zett [male sy[illegible]/ Blüthgen,det.1941"; "O. suecicus/ [male symbol] E"; "Holotype/ Odynerus/ angustatus [male symbol]/ Zetterstedt" (UZIL).

*Odynerus alternans* Zetterstedt, HOLOTYPE female labelled: "O. alternans/ [female symbol]. Alten det"; "O. suecicus/ [female symbol] E"; "Holotype/ Odynerus/ alternans [female symbol]/ Zetterstedt" (UZIL).

*Odynerus laeviventris* Thomson, LECTOTYPE (here designated), female labelled: "K.K. [Kinnekulle, West Gotland]"; "Bhm [Boheman collection]"; "[female symbol]" (UZIL). My lectotype label "LECTOTYPE [underlined in red]/ Odynerus [female symbol]/ laeviventris Thomson/ des. J.M. Cumming 1984 [black bordered label]" has been attached to this specimen.

PARALECTOTYPE: [Öland]-male (UZIL). My paralectotype label has additionally been attached to this specimen.

Thomson (1874) described *O. laeviventris* from at least three females and two males collected in West Gotland, Öland and Jutland, without selecting a holotype. In addition to the lectotype and paralectotype designated herein, the Thomson collection of UZIL contains two specimens under the name "laeviventris". One is a female from southern Norway and is therefore not part of the original type series, while the other is a male specimen labelled only "Fag". If this locality is in one of the three provinces given by Thomson in the original description of *O. laeviventris*, this male specimen may potentially be considered an additional syntype. The location of the remaining syntypes is unknown.

Recognition.—Very similar to *S. albomarginatus* from the New World, but distinguished by the shape of metasomal tergum 1. In the Old World *S. angustatus* is most similar to *S. crassicornis* and *S. captivus*, being separable from the former by features given in the key to species and subspecies of *S. (Symmorphus)*, as well as by paler less extensive maculation (similar maculation seen in relatively few specimens of *S. crassicornis*). Besides differences in geographical distribution, specimens of *S. angustatus* can be differentiated from those of *S. captivus* by the shape of metasomal tergum 1 and by smaller size. In addition, specimens of *S. angustatus* resemble those of *S. allobrogus* as discussed under "Recognition" of that species.

Description.—*Female*. Measurements of largest and smallest specimens given in Table 1. Taxonomically important character states given in Table 3.

*Male*. Measurements of largest and smallest specimens given in Table 1. Taxonomically important character states given in Table 3.

Geographical distribution and seasonal occurrence.—Known to range from eastern Europe, east through Siberia, to Kamchatka Oblast, Magadan Oblast, Khabarovsk Krai and Primorskij Krai (fig. 67). **Austria**: Mur Au Mureck, Styria, 26.V.1979. **Denmark**: Horsens, 3.VI.1873, 6.VI.1880; Laeso, Kokvadgard S. for Byrum, 14.VII.1969; Rye [Ry]. **Finland** Pärnå. **Germany (BRD & DDR)**: Bayr., Alpen, 18.VI.1948; Berlin, Finkenkrug aus Austernhatr, 8.V.1911; Berlin, Gerstaecker S. **Greece**: Mármaros [Mármara]. **Norway**: Norv. merid. [southern Norway]. **Sweden**: distribution widespread in south, earliest seasonal record—Båstad, 10.VI.1937; latest seasonal record—Sm., Österkorsberga, 16-28.VII.1939; most northerly records—Jämtland, U-åker, 22.VII.1914; Nb., Kukkola [region], 10.VII.1956; Nb., Råneå, Högsön, 1.VII.1972. **USSR**: Dorpat [Tartu]; Elisovo, Kamchatka, 30.VI.1930, VII.1928; environs of Ust. Karska, lev. B. R. Shilka, Zabajkale [Zabajkal'sk], 4.VII.1970; environs of S. [N.] Zyulbzya, lev. b. r. Nercha, Zabajkale [Zabajkal'sk], 15.VII.1970; Kamchatka, 25.VIII.1958; Khabarovsk, Sueluk [? Suiuk] sr., 14-15.VI.1975; Kurland, Wezkukkul, 18.VI.1916; lac. [lake] Teletskoe, fi. [mouth of river] Kyga, 13,16-17.VII.1934; M. M. Ural i oz. Varua-ty, 22.VIII.1925; Magadansk obl., Sejmchan, 28.VII.1975; Moscow, 14.VI.1964; Moscow, Rublev les, 6.VII.1974; Priamure, environs of s. [N.] Natalino, r. Zeja, 12.VII.1975; Priamure, s. [N.] Semenovka, 35 km. NW Svobodnogo, 6.VII.1975; Primore, Anisimovka, 3.VI.1977; Primorskij Krai, Iu. [S.] Sergeevki, 20.VII.1979; Salechard, Nizovya r. ob., 24.VII.1955; Uesuri, Ussuri Krai, 19.VIII.1926; Ural centr., Sojmonowsk, VI.1908.

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Related to *S. crassicornis*, *S. captivus* and *S. albomarginatus*.

### 5.1.3.1.3.8 *S. (Symmorphus) albomarginatus* (Saussure)

#### 5.1.3.1.3.8.1 *S. (Symmorphus) albomarginatus albomarginatus* (Saussure)

*Odynerus (Protodynerus) albomarginatus* Saussure, 1855 (BMNH).
*Odynerus (Symmorphus) walshianus* Saussure, 1870 (MHNG). New synonymy.
*Symmorphus meridionalis* Viereck, 1903 (ANSP). New synonymy.

Notes about synonymy.—I have examined the holotypes of *S. walshianus* (Saussure) and *S. meridionalis* Viereck, and regard them as conspecific with the lectotype of *S. albomarginatus* (Saussure). Since both the structural and color differences upon which these nominal species were previously recognized, vary continuously over the range of *S. albomarginatus* (see below under "Variation"), formal subspecific recognition of any of the three forms is also considered unwarranted.

Type material examined.—*Odynerus (Protodynerus) albomarginatus* Saussure, LECTOTYPE (here designated), female [without metasoma] labelled: "Hudson's [Hudson]

Bay/ [on reverse side] 44/ 17 [acquisition 17, 1844]"; "Odynerus/ albomar/ ginatus/ [female symbol] Sauss. [blue label in Saussure's handwriting]"; "B.M. TYPE/ HYM./ 18.530" (BMNH). My lectotype label "LECTOTYPE [underlined in red]/ Odynerus [female symbol]/ albomarginatus Sauss./ des. J.M. Cumming 1984 [black bordered label]" has been attached to this specimen.

PARALECTOTYPES: Hudson's [Hudson] Bay-female [conspecific with lectotype], 3 females [=*S. cristatus* (Saussure)] (BMNH). My paralectotype labels and determination labels (one *S. albomarginatus*, three *S. cristatus*) have additionally been attached to these specimens.

Saussure (1855) based his description of *O. albomarginatus* on a series of female specimens from Hudson Bay that he examined in the collection of the BMNH, while visiting London. Five female specimens from this locality, in the BMNH under this name, appear to represent the entire type series of *O. albomarginatus*, although only one specimen bears Saussure's determination label, as well as a BMNH type label. As Saussure did not select a holotype, the specimen bearing his determination label is herein designated lectotype. Of the four remaining syntypes, one is conspecific with the lectotype, while the other three are members of *S. cristatus* (Saussure).

*Odynerus (Symmorphus) walshianus* Saussure, HOLOTYPE, female labelled: "[square metallic colored label]"; "Illinois"; "Typus [red label]"; "HOLO-/ TYPE/ [female symbol] walshianus/ Sss./ (RMB) [red label]" (MHNG).

*Symmorphus meridionalis* Viereck, HOLOTYPE, male labelled: "Beulah, N. M./ Aug. 8. 1900"; "T.D.A. and W.P./ Cockerell"; "TYPE No./ 516-"; "Symmorphus/ [male symbol] meridionalis/ Type Vier [in Bequaert's handwriting]" (ANSP).

Recognition.—Distinguished from other New World members by features given in the key to species and subspecies of *S. (Symmorphus)*. Specimens of *S. albomarginatus albomarginatus* are very similar to those of *S. angustatus*, *S. captivus* and *S. crassicornis* as discussed under "Recognition" of each of these Palearctic species.

Description.—*Female*. Measurements of largest and smallest specimens given in Table 1. Taxonomically important character states given in Table 3.

*Male*. Measurements of largest and smallest specimens given in Table 1. Taxonomically important character states given in Table 3.

Variation.—At least three forms are apparent from the considerable range of variation encountered over the geographical distribution of this subspecies (fig. 68).

Form 1. *Female*, pronotum with humeral angle obtusely rounded, not or barely projected; metasomal terga 2, 3 and 4 foveolate-puncticulate, with major punctures slightly larger and more closely spaced towards apex; lengthened setae moderately dense; coloration black with white markings, fascia present on apical border of metasomal tergum 3; wings hyaline. *Male*, similar to female except humeral angle obtusely rounded to obtuse, barely projected. This form was described as *Odynerus albomarginatus* by Saussure (1855).

Form 2. *Female*, pronotum with humeral angle rounded to obtusely rounded, not projected; metasomal terga 2, 3 and 4 foveolate-puncticulate, with major punctures slightly to moderately larger and more closely spaced towards apex; lengthened setae sparse to moderately dense; coloration black with yellow markings (white in specimens from Florida), fascia absent on apical border of metasomal tergum 3 in many specimens; wings lightly to moderately infuscate. *Male*, similar to female except humeral angle obtusely rounded, not or barely projected; fascia present on apical border of metasomal tergum 3 in many specimens. This form was described as *Odynerus walshianus* by Saussure (1870).

Form 3. *Female*, pronotum with humeral angle obtuse to nearly acute, barely to slightly projected; metasomal terga 2, 3 and 4 foveolate-puncticulate, with major punctures moderately to markedly larger and more closely spaced towards apex; lengthened setae sparse to moderately dense; coloration black with yellow markings (pale yellow to white in a few specimens), fascia present on apical border of metasomal tergum 3; wings hyaline to fuliginous with slight yellow tinge. *Male*, similar to female except humeral angle nearly acute, slightly to moderately projected. This form was described as *Symmorphus meridionalis* by Viereck (1903).

Specimens belonging to form 1 occur in the northern part of the range of this subspecies, throughout Canada, the northeastern U.S.A. east of the Great Lakes, northern Michigan to Minnesota, as well as both northwestern Montana and Wyoming plus northern Idaho in the west. Specimens belonging to form 2 occur in eastern U.S.A., from eastern Kansas and Iowa in the west, to Pennsylvania, southern New York, and New Jersey in the east, south to east-central Texas and southern Florida. Although part of a relatively homogeneous group, specimens of form 2 from Florida possess white markings, in contrast to other form 2 members, which are all marked with yellow. Specimens belonging to form 3 occur in the west, from southern British Columbia, northern Idaho and western Montana in the north, south through Washington, Oregon, southern Idaho, southern Wyoming and extreme western Nebraska, to Colorado, northern New Mexico, Utah, Nevada and central California.

Although no intermediate specimens were seen between forms 2 and 3, numerous specimens were examined that were intermediate in certain respects between forms 1 and 2, or between forms 1 and 3. Intermediate specimens between forms 1 and 2 were examined from Iowa, Minnesota, Wisconsin, Michigan, Illinois, southern Ontario, New York, Pennsylvania, Maryland, District of Columbia and New Jersey. Those between forms 1 and 3 were seen from the southern part of the provinces of British Columbia, Alberta and Saskatchewan, as well as from northwestern Wyoming, Montana, northwestern Nebraska, and the western border of both North and South Dakota.

Geographical distribution and seasonal occurrence.—Known transcontinentally in North America, from Yukon Territory, Northwest Territories and Labrador in the north, to California, New Mexico, Texas and Florida in the south (fig. 68). **Newfoundland**: distribution widespread in south, earliest seasonal record—Catamaran Cp., 20.VII.1962; latest seasonal record—Goose Bay, Labr., 11.VIII.1948; most northerly record—Goose Bay, Labr., 27.VII.1948, 11.VIII.1948. **Nova Scotia** Centre Rawdon, 13.VIII.1961. **New Brunswick** St. Andrews, 13.VII.1910; St. John, 8.VIII.1906. **Quebec** distribution widespread in south, earliest seasonal record—Ft. Coulonge, 14.VI.1918; latest seasonal record—Tadoussac, 11.VIII.1932; most northerly records—Godbout, 25,28.VII.1918; Mistassini Poste, 14.VII.1956. **Ontario**: distribution widespread in south, earliest seasonal record—Pt. Pelee, 8.VI.1925; latest seasonal record—Ottawa, 25.VIII.1954; most northerly records—Black Sturgeon Lake, 1-15.VIII.1956; Kenora, 18-27 mi. S.E., 17,19,22,25.VII.1968; North Bay, 11.VIII.1956; Rabbit Blanket Lake, 47.45N 84.50W, 8.VII.1977. **Manitoba** distribution widespread in south, earliest seasonal record—Shilo, 5 mi. S.W., 5.VI.1958; latest seasonal record—Headingly, 1500 m., nr. Winnipeg, 10.VIII.1962; most northerly records—Cedar Lake, VI,VII.1936; Wabowden, 1.VIII.1936, 10.VIII.1949. **Saskatchewan** distribution widespread in south, earliest seasonal record—Nipawin, 1.VII.1970; latest seasonal record—Waskesiu Lake, 19.VIII.1949; most northerly records—Wallwort, 17,20.VII.1942; Waskesiu Lake, 2.VIII.1939, 19.VIII.1949. **Alberta**: distribution widespread in south, earliest seasonal record—Medicine Hat, 19.V.1926; latest seasonal record—Mildred Lake, 57.03N 111.35W, 20.VIII.1973; most northerly records—Grande Prairie, 10,11.VI.1961; Mildred Lake, 57.03N 111.35W, 20.VIII.1973; Peace River, 14.VI.1961; Slave Lake, 14.VIII.1924. **Northwest Territories** Fort Simpson, 6.VIII.1950; Norman Wells, 7.VII.1949. **Yukon Territory** Canyon Creek, 60.06N 130.40W, 4.VIII.1948. **British Columbia**: distribution widespread in south, earliest seasonal record—Oliver, 21.V.1959; latest seasonal record—Agassiz, 7.X.1921; most northerly records—Bear Lake, 7000ft., 28.VII.1903; Terrace, 20,24.VII.1960. **Alabama** Houston Co.: UEA Site, 2 mi. S. of Columbia, 9.V.1975. **California**: distribution widespread in north, earliest seasonal record—Three Rivers, Tulare Co., 17.IV.1959; latest seasonal record—Modoc Co., Cedar Pass Camp, 28.VIII.1965; most southerly records—Monterey Co., 5 mi. S.E. Watsonville, 30.VI.1958; Three Rivers, Tulare Co., 7.IV.1959. **Colorado**: distribution widespread in west, earliest seasonal record—Boulder, 23.V.1908; latest seasonal record—Webster, 1.VIII.1933; most easterly records—Fort Collins, 30.VI.1931; Golden, 4 mi. W., 7400ft., 31.VII.1961; Manitou, 1877. **Connecticut**: Colebrook, VIII.1918; Riverbank, E. Hartford, 22.VI.1941. **Delaware**: Dover, 12.VII.1937. **District of Columbia**: Washington, 27.V.1946, 30.VII.1946. **Florida**: distribution widespread, earliest seasonal record—Florida City, 25.III.1936; latest seasonal record—Ft. Lauderdale, 25.V.1928; most southerly records—Florida City, 25.III.1936; Grossman Hammock, Homestead, 2.IV.1952; Paradise Key, Everglades Nat. Pk., 29.III.1952, 30.III.1953, 1.IV.1952, 6,7,12.IV.1951. **Georgia**: Atlanta, 22.VI.1946; Cassville, 9.VI.1945; Spring Creek, Decatur Co., 7-23.VI.1911; Stone Mountain, Dekalh Co., 25.IV.1953; Tallulah Gorge, 28.VII.1930. **Idaho**: distribution widespread, earliest seasonal record—Jerome Co., Twin Falls, 19 mi. N., 2.VII.1973; latest seasonal record—Priest Lake, 19.VIII.1923. **Illinois**: distribution widespread, earliest seasonal record—Dubois, 24.V.1917; latest seasonal record—Galena, 8.VII.1917. **Indiana**: [no additional locality data] 11.VI.1898. **Iowa**: Ames, 10.VI.1929, 13.VII.1946, 24.VII.1947. **Kansas**: distribution widespread in east, earliest seasonal record—Douglas Co., 10.V.1949; latest seasonal record—Marysville, 13.VI.1950; most westerly records—Marysville, 13.VI.1950; Riley Co., V.1940. **Maine**: First Roach Pond, Piscataquis Co., 4,7.VII.1976; Orono, 1.VIII.1933; Waldoboro, 24.VII.1908. **Maryland**: N.W. Branch Pk., Montgomery Co., 18.VII.1976; Plummers Id., 13.VI.1971, 21.VI.1960, 21.VII.1962. **Massachusetts**: Farm Street, Dover, 9.VII.1925. **Michigan**: distribution widespread, earliest seasonal record—Washtenaw Co., Ann Arbor, 23.V.1975; latest seasonal record—Cheboygan Co., 19.VII.1952. **Minnesota**: distribution widespread, earliest seasonal record—Houston Co., 31.V.1914; latest seasonal record—Finland, 20.VIII.1938. **Missouri**: Columbia. **Montana**: Fresno Dam, Hill Co., 19.VI.1959; Glacier Nat. Pk., 26.VII.1958; Madison River, Gallatin Nat. Forest, 12.VIII.1943. **Nebraska**: Mitchell, 6.VII.1915; War Bonnet Canyon, Sioux Co. **Nevada**: Galena Crk., Washoe Co., 29.VI.1964. **New Hampshire**: Durham; Nelson, 15.VII.1907. **New Jersey**: Great Notch, 20.VIII.1925; Princeton. **New Mexico**: Beulah, 8000ft., VIII. **New York** distribution widespread, earliest seasonal record—Postdam, V.1899; latest seasonal record—Catskill Mts., 12.VIII.1902. **North Carolina** Burlington, 23.VI.1941; Highlands, 3800ft., 16.VI.1957. **North Dakota**: Beach; Bottineau, Bottineau Co., Turtle Mts., 21.VIII.1949; Turtle Mts., 23.VI.1943. **Ohio** distribution widespread, earliest seasonal record—Columbus, 18.V.1941; latest seasonal record—Summerfield, 6.VIII.1939. **Oklahoma** Ardmore, I.T. [Indian Territory], IV.1907. **Oregon** distribution widespread, earliest seasonal record—Kane Crk., 5 mi. W. Gold Hill, 2000ft., 23.VI.1937; latest seasonal record—Lick Crk., RS Wallowa Nat. Forest, 4600ft., 16.VIII.1937. **Pennsylvania** distribution widespread, earliest seasonal record—Spring Br., 22.V.1945; latest seasonal record—Huntington, Lehigh Gap, 21.VII.1902. **South Carolina**: Greenville, 13.V.1956. **South Dakota**: Hynn Creek, 5400ft., 8 mi. N. Pringle, 7.VII.1941; Pringle, 16.VII.1924. **Tennesee** Gr. Smoky Mt. Nat. Pk., 18.V.1957. **Texas**: Austin, 12.IV.1902; Fedor, Lee Co., 17,21,27.III.1909. **Utah** distribution widespread in north, earliest seasonal record—Oak Creek Canyon, nr. Oak City, 11.VI.1937; latest seasonal record—Mt. Logan, 9000ft., 18.VIII.1955; most southerly records—Beaver Creek Hill, Beaver Co.; Beaver Canyon, 11,14.VI.1946. **Virginia**: Arlington Co., 20.VII.1929; Blacksburg, 20,23.V.1960; Falls Church, 1.VI; Glencarlyn, 11.VI. **Washington** distribution widespread, earliest seasonal record—Toppenish, 27.IV.1926; latest seasonal record—Nahcotta, 29.VIII.1952. **West Virginia** Kingwood, Preston Co., 17.VII.1940. **Wisconsin** Cloverleaf Lks., Shawano Co., 17.VI.1934; Madison, VI.1954; Milwaukee; Milwaukee Co., 11.VI.1902. **Wyoming**: distribution widespread, earliest seasonal record—Jenny Lake, Grand Teton Nat. Pk., 20.VI.1940; latest seasonal record—Jenny Lake, Teton Co., 4-15.VIII.

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Presumably the sister taxon of *S. albomarginatus midas*. The entire species is allied with *S. crassicornis*, *S. captivus* and *S. angustatus*, although the exact relationship remains unresolved.

### 5.1.3.1.3.8.2 *S. (Symmorphus) albomarginatus midas* new subspecies

Holotype.—Female labelled: "HOLOTYPE [red label]"; "Texas: Hidalgo C[oun]ty./ Bentsen Rio Grande/ Valley State Park/ 18 MZ0 [Marzo=March] 1977/ C. Porter"; "Symmorphus/ albomarginatus midas/ Cumming/ Holotype [red bordered label]" (FSCA).

Allotype.—Male labelled: "ALLOTYPE [red label]"; "Cuernavaca Mor[elos]/ 3-17'[19]59 MEX[ICO]./ 5000 ft.elv."; "H.E.Evans &/ DM Anderson/ collectors"; "Symmorphus/ albomarginatus midas/ Cumming/ Allotype [red bordered label]" (CU).

Derivation of subspecific epithet.—Named after *Midas*, the king of Greek mythology whose touch turned everything to gold, in reference to the color of the pubescence in members of this subspecies.

Description.—*Female*. Similar to typical subspecies except covered with dense short gold colored pubescence. Pronotum with humeral angle obtuse, barely projected. Metasomal terga 2, 3 and 4 foveolate-puncticulate, with major punctures moderately larger and more closely spaced towards apex. Lengthened setae sparse and only moderately long. Coloration black with yellow as follows: interantennal spot (absent in one paratype), postocular dot, scape anteroventrally, narrow medially interrupted dorsal pronotal band, very small dorsal mesepisternal spot adjacent pronotal lobe (absent in holotype and a few paratypes), tegula posteriorly (absent in paratypes from Mexico), two small mesoscutellar spots, apical border of metasomal terga 1 to 6 and sterna 2 to 5 (sternum 6 with medial mark). Tarsi dark brown. Wings fuliginous with slight yellow tinge.

*Male*. Similar to female except as follows: humeral angle slightly projected; clypeus with basal yellow spot (absent in allotype); dorsal mesepisternum entirely black; outer surface of fore and mid tibiae with yellow marks (absent in allotype); metasomal terga 1 to 7 and sterna 2 to 7 each with yellow apical border (absent from tergum 7 and sternum 7 in two paratypes).

Geographical distribution.—Known to range from southeastern Texas, south through Mexico, to northern Nicaragua (fig. 68).

Seasonal occurrence.—Specimens of the type series were collected from March to July in Texas, March to August in Mexico and July in Nicaragua.

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Considered the sister taxon of *S. albomarginatus albomarginatus*, as indicated under that subspecies.

Paratypes.—**Mexico**: Fortin-Hua[tu]sco [Road], km 16 da [from] Fortin, 1600 m., 29.VIII.[19]75, Giordani Soika-female (MSNV); Guadalajara, Crawford-female (MCZ). **Nicaragua**: 28 mi. S. Somoto, 2000 ft., 31.VII.1963, Scullen & Bollinger-2 males (UCD). **Texas**: Cameron Co[unty], Southpoint Nursery, 1.0 mi S. Southmost Ranch, 5-6.VII.[19]82, G. Gibson-female, male (JMCU); Hidalgo C[oun]ty, Bentsen Rio Grande Valley State Park, 17,18.III.1977, C. Porter-4 females (FSCA).

### 5.1.3.1.3.9 *S. (Symmorphus) decens* (Kostylev)

*Odynerus (Odynerus) decens* Kostylev, 1940 (ZIL).

*Odynerus apiciornatus* (Cameron) *sensu* Yasumatsu, 1938. **Misidentification**.

? *Odynerus apiciornatus* (Cameron) *sensu* Iwata, 1938. **Misidentification.**

Notes about synonymy.—Yasumatsu (1938) misidentified this species as *S. apiciornatus* (Cameron), as Tsuneki (1977) indicated. Although this misidentification was first reported by Soika (1975), he was somewhat uncertain that Yasumatsu's description referred to *S. decens* (Kostylev), because in his opinion the figure given by Yasumatsu of the male clypeus did not entirely correspond with that seen in males of *S. decens*. It is apparent however that Yasumatsu followed the common practice of not illustrating the lateral lobes of the clypeus and once taken into account the figure is easily seen to represent the clypeus of a male specimen of *S. decens*. The note about bionomics of *S. apiciornatus* by Iwata (1938) also probably refers to *S. decens*, as Yasumatsu is acknowledged for determination of species discussed in that paper.

Type material examined.—LECTOTYPE (here designated), female labelled: "12.-V-1929./ Mino, Osaka [Pref.]/ Japan - Leg./ N. Tozawa."; "K [coll.]. *Volbman* [in Russian]"; "O. decens n.sp. Typ. [female symbol]/ G Kostylev det. 1936"; "Lectotypus Odynerus/ decens Kostylev [female symbol]/ des. Kurzenko 1976 [red label] [unpublished invalid designation]" (ZIL). My lectotype label "LECTOTYPE [underlined in red]/ Odynerus [female symbol]/ decens Kostylev/ des. J.M. Cumming 1985 [black bordered label]" has been attached to this specimen.

Kostylev (1940) appears to have based his description of *O. decens* on two female specimens in the collection of ZIL, without clearly indicating which he considered the holotype. Both females are from Mino, Osaka Prefecture and bear identical labels, except that Kostylev labelled one as "O. decens n.sp. Typ." and the other as "O. decens n.sp. Cotyp." (Kurzenko, personal communication). The female labelled by Kostylev as "Typ." is herein designated lectotype.

Recognition.—Readily distinguished from all other species of *Symmorphus* by the broadly and shallowly emarginate clypeus (figs. 2, 56), inconjunction with the punctation of the mesoscutum (fig. 6).

Description.—*Female*. Measurements of largest and smallest specimens given in Table 1. Taxonomically important character states given in Table 3.

*Male*. Measurements of largest and smallest specimens given in Table 1. Taxonomically important character states given in Table 3.

Geographical distribution and seasonal occurrence.—Known from southern and central Japan, on the islands of Kyushu and Honshu (fig. 67). In addition to the lectotype, which was collected in May, six male and 12 female specimens, deposited in BMNH, CNC, JMCU, LACM, MCZ, MSNV, NSMT, RNHL and YAMC, have been examined. **Japan**: distribution widespread in southern and central regions, earliest seasonal record—Kyushu, Hakozaki, Fukuoka City, 9.V.1955; latest seasonal record—Sasayama, Tanba, 5.VI.1952; most northerly record—Nagano, 400 m., 20.V.1962; most southerly record—Taniyama, Kagoshima Pref., Kyushu, 24.V.1950.

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—The evidence available, although very inconclusive, suggests a sister group relationship with the *S. crassicornis-S. captivus-S. angustatus-S. albomarginatus* clade.

### 5.1.3.1.3.10 *S. (Symmorphus) violaceipennis* Soika

*Symmorphus violaceipennis* Soika, 1966 (ZMHB).

Type material examined.—HOLOTYPE, female labelled: "Schäfer-Exped."; "Sikkim/ Lachen - Chungtang/ .8.[19]38 [yellow label]"; "HOLOTYPUS/ Symmorphus/ violaceipennis/ A.G. Soika [red label]"; "Zool. Mus/ Berlin [yellow label]" (ZMHB)

PARATYPE: Sikkim, Lachen-Chungtang, VIII.[19]38, Schäfer-Exped.-female (MSNV).

Recognition.—Most similar to *S. mizuhonis*. In addition to features given in the key to species and subspecies of *S. (Symmorphus)*, specimens of *S. violaceipennis* are distinguished from those of *S. mizuhonis* by the broader deeper longitudinal furrow of metasomal tergum 1 and Himalayan distribution.

Description.—*Female*. Measurements of largest and smallest specimens given in Table 1. Taxonomically important character states given in Table 4.

*Male*. Unknown.

Geographical distribution and seasonal occurrence.—Known from eastern Nepal and Sikkim (fig. 69). In addition to the holotype and paratype, which were collected in August, two female specimens have been examined. **Nepal**: Dudh Kosi Tal, 3500 m., 22-23.VII.1962 (ZSBS); Kathmandu [Valley], Chauni, 1350 m., 27.IX-5.X.1972 (RNHL).

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Presence of lengthened setae inconjunction with phenetic similarity, suggest a sister species relationship with *S. mizuhonis*.

### 5.1.3.1.3.11 *S. (Symmorphus) mizuhonis* Tsuneki

*Symmorphus lucens* (Kostylev) *sensu* Soika, 1963, 1975 (as *lucidus* in 1975).
*Symmorphus mizuhonis* Tsuneki, 1977 (coll. Tsuneki).
*Symmorphus kurentzovi* Kurzenko, 1981 (ZIL). **New synonymy.**

Notes about synonymy.—Soika (1963, 1975) appears to have based his concept of *S. lucens* (Kostylev) entirely on two syntypes collected from Lake Teletskoye in southern Siberia, which are now located in his collection at MSNV. As stated under the discussion of type material for *S. lucens*, the type series of *S. lucens* contains specimens of two species. I regard the male and female syntype in Soika's collection as conspecific with *S. mizuhonis* described by Tsuneki (1977) from Japan (only paratypes examined), but not conspecific with the lectotype of *S. lucens*. In addition, I have examined paratypes of *S. kurentzovi* described by Kurzenko (1981) from Soviet eastern Asia and also regard this nominal species as conspecific with *S. mizuhonis*.

Type material examined.—*Symmorphus mizuhonis* Tsuneki, PARATYPES: Honshu, Tochigi [Pref.], Okunasu [Oku-Nasu], 25.VII.1970, T. Nambu-male (NAMC); Honshu, Saitama [Pref.], Karisaka Koya [Pass], 3.VIII.1974, T. Nambu-male [apparently listed as female by Tsuneki, 1977] (NAMC).

*Symmorphus kurentzovi* Kurzenko, PARATYPES: Primorskij kr. [Krai], Barabash-Levada, 1.VII.1978, Kurzenko [in Russian]-2 females (JMCU).

Recognition.—Similar to *S. violaceipennis* as discussed under "Recognition" of that species. In addition, specimens of *S. mizuhonis* can be confused with those of *S. lucens*, but possess lengthened setae (besides short pubescence, fig. 22), denser major punctation along median longitudinal furrow of metasomal tergum 1 and smaller cephalic foveae in females, as well as a dorsal mesepisternal spot and fainter notauli in most specimens.

Description.—*Female*. Measurements of largest and smallest specimens given in Table 1. Taxonomically important character states given in Table 4.

*Male*. Measurements of largest and smallest specimens given in Table 1. Taxonomically important character states given in Table 4.

Variation.—Specimens from Taiwan and China with markings orange-yellow to orange-red, those from Japan and USSR with ivory-white to light yellow markings.

Geographical distribution and seasonal occurrence.—Known to range from Taiwan and the Japanese island of Honshu, west through China and southern Siberia, to the Altai Mountains (fig. 69). In addition to the paratypes of *S. mizuhonis*, which were collected in July and August, and the paratypes of *S. kurentzovi*, which were collected in July, nine male and 14 female specimens have been examined. China: Mt. Omei [Emei Shan], Szechuen [Sichuan], VII.1936 (USNM); U Long Konon, nr. Tatsienlu [Kangding], 10-15000ft., Szechuen [Sichuan], 25-30.VII.1923 (USNM); Wei Chow, 65 mi. N.W. Chengtu [Chengdu], 5000-8000ft., Szechuen [Sichuan], 25.VII.1933 (USNM). **Japan**: Karisaka Pass, Ootaki, Saitama [Pref.], 29.VII.1983 (JMCU); Mt. Zao, Miyagi [Pref.], 25.VI.1979 (JMCU); Tsumagoimura, Gumma Pref., 30.VIII.1949 (NSMT); Yuzawa T., Niigata [Pref.], 8.VIII.1966 (YAMC) (additional records, from Nagano and Yamanashi Prefectures, in Tsuneki, 1977). **Taiwan**: Arisan [Ali Shan], 28.V.1934 (MCZ). **USSR**: Baikal Biol. Station, State Univ. Irkutsk, Siberia, VIII (USNM); Irkutsk, gub Gi Netunskaya, 1913 (ZIL); lac [lake] Teletskoe, fi. [mouth of river] Kyga, 16-17,17.VII.1934 (MSNV, MSUM); r. Botshi, Sikhota-Alin, Prim. Obl. [Krai], 30.VII.1924, 12.VIII.1924 (ZIL); Troiskossowsk [? location], Sibirien, 10.VI.1922 (ZMCU); Ust. Amba-biry, Prim. O. [Krai], 31.VIII.1914 (ZIL); Uste r. Koldor, Teletskoye oz. [lake], Altai, 5-6.VII.1912 (ZIL).

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Probably the sister species of *S. violaceipennis*.

### 5.1.3.1.3.12 *S. (Symmorphus) bifasciatus* (Linnaeus)

*Vespa bifasciata* Linnaeus, 1761. Lectotype, female, designated by Day, 1979 (LS).

*Vespa sinuata* Fabricius, 1793. Homonym of *Vespa sinuata* Geoffroy in Fourcroy, 1785 (ZMUC). **New synonymy**.

*Odynerus angustatus* Zetterstedt *sensu* Thomson, 1874; Dalla Torre, 1894; Aurivillius, 1918; Móczár, 1938; Blüthgen, 1938; Wilcke, 1952; Zanden, 1955. **Misidentification**.

*Odynerus (Protodynerus) sinuatus mutinensis* Baldini, 1894 (MSNV). **New synonymy**.

*Symmorphus sparsus* Morawitz, 1895 (ZIL). **New synonymy**.

*Symmorphus sinuatissimus* Richards, 1935. New name for *Vespa sinuata* Fabricius, 1793. **New synonymy**.

*Odynerus (Symmorphus) mutinensis* Baldini; Blüthgen, 1961.

*Odynerus (Symmorphus) mutinensis sinuatissimus* (Richards); Blüthgen, 1961.

*Symmorphus mutinensis auster* Soika, 1975 (NSMT). **New synonymy.**

*Symmorphus mutinensis yezoanus* Tsuneki, 1977 (coll. Tsuneki). **New synonymy.**

(—*bifasciatus* Linnaeus *sensu* Fabricius, 1793; Zetterstedt, 1838 ["var. a"]; Thomson, 1874; Aurivillius, 1918; Forsius and Nordström, 1923; Blüthgen, 1938, 1943, 1952, 1961, 1965, 1967; Vecht and Fischer, 1972 = *S. allobrogus*. —*bifasciatus* Linnaeus *sensu* Saussure, 1855; Schulthess, 1887 [in part], 1930; Saunders, 1902; Dalla Torre, 1904; Berland, 1928 [in part]; Richards, 1937 = *S. connexus*. —*bifasciatus* Linnaeus *sensu* Schulthess, 1887 [in part]; Berland, 1928 [in part] = *S. debilitatus*. —*sparsus* Morawitz *sensu* Soika, 1963 = *S. sublaevis*.)

Notes about synonymy.—Except for Wesmael (1833, 1836), Lepeletier (1841) and Morawitz (1895) who regarded this species in the sense it is used here, there has been much confusion about the identity of *S. bifasciatus* (Linnaeus). Although Saussure (1855) states that he examined the Linnaean collection, he confused this species with *S. connexus* (Curtis). Several successive authors, most noteably Schulthess (1887, 1930), Berland (1928) and Richards (1937), followed Saussure's interpretation, although Schulthess (1887) and Berland (1928) additionally confused *S. debilitatus* (Saussure) under the Linnaean name. The concept of *S. bifasciatus* for most authors however, beginning at least with Fabricius (1793), has been equivalent to the nominal species *S. allobrogus*, described by Saussure in 1855 (see for example Blüthgen, 1938). Examination of the pertinent types in the Linnaean collection has confirmed the presence of two specimens agreeing with the original description, as reported by Day (1979). The first specimen labelled "bifasciata" is the same female specimen examined by Saussure (1855) and Richards (1935). The second, a female lacking its metasoma and without a determination label, is reported only by Day (1979). Considering the unlabelled female (designated by Day, 1979 as paralectotype) is conspecific with *S. allobrogus*, it is unfortunate that Day (1979) selected the labelled specimen as lectotype, since I regard it as conspecific with the nominal species *S. mutinensis* (Baldini). As such, *S. bifasciatus* must replace this well known name and all its associated synonyms (listed by Blüthgen, 1961; Vecht and Fischer, 1972).

In 1975 Soika described *S. bifasciatus auster* (as a subspecies of *S. mutinensis*) for a population of this species characterized by absence of yellow pronotal and mesepisternal spots, from the Japanese island of Honshu. Subsequently Tsuneki (1977) described *S. bifasciatus yezoanus* (also as a subspecies of *S. mutinensis*) for similarly colored but more sparsely punctate individuals occurring to the north of *S. bifasciatus auster*, in both the northern most prefecture of Honshu and on the island of Hokkaido. I have examined specimens of both these taxa, including paratypes, and regard the degree of difference in color and punctation, well within the range of variation observed within Asian and European populations of *S. bifasciatus*. As such, I regard the diagnostic differences given by Soika (1975) and Tsuneki (1977) insufficient for formal recognition of these Japanese populations as distinct subspecies.

In addition to the names discussed above, I have examined the holotype of *S. sparsus* Morawitz (not *S. sparsus* Morawitz *sensu* Soika, 1963), known only from this single female described from Ashkhabad, Turkmen S.S.R. in 1895. I regard this specimen as an extensively yellow maculated individual of *S. bifasciatus*, not warranting formal taxonomic status.

Type material examined.—*Vespa bifasciata* Linnaeus, LECTOTYPE (by designation of Day, 1979), female labelled: "bifasciata" [followed by Day's lectotype labels] (LS).

PARALECTOTYPE: [unlabelled except Day's paralectotype labels] female [without metasoma] [= *S. allobrogus* (Saussure)] (LS). My *S. allobrogus* determination label has additionally been attached to this specimen.

*Vespa sinuata* Fabricius, LECTOTYPE (here designated), female labelled: "sinuatus/ [female symbol]/ [on reverse side] K. Faester det" (ZMUC). My lectotype label "LECTOTYPE [underlined in red]/ Vespa [female symbol]/ sinuata Fabricius/ des. J.M. Cumming 1984 [black bordered label]" has been attached to this specimen.

PARALECTOTYPES: [without locality labels]-2 females [one with original Fabrician drawer label "sinuata"] (ZMUC). My paralectotype labels have additionally been attached to these specimens.

Zimsen (1964) states there are six potential syntypes under the name *V. sinuata* in the Kiel collection of Fabricius in ZMCU. Examination of these specimens, which are all without locality labels, suggests that only three are part of the original type series described from "Kilae". Two of the six specimens are females of *S. bifasciatus* (Linnaeus) with labels indicating they were moved, most probably by Faester who determined them as "sinuatus", from their original placement under *V. trifasciata* Fabricius. A third specimen, a badly damaged male of *Stenodynerus* Saussure, was probably also moved under *V. sinuata* subsequent to its description, because this specimen does not agree well with Fabricius' original description. The three remaining specimens, which probably represent the entire type series of *V. sinuata*, are all females of *S. bifasciatus* (Linnaeus) that closely agree with the original description. Two of these specimens, including one bearing Fabricius' original drawer label "sinuata", are badly damaged by dermestids. The third specimen, herein designated lectotype, is in good condition.

*Odynerus (Protodynerus) sinuatus mutinensis* Baldini, LECTOTYPE (here designated), female labelled: "Dint[orni] di/ Modena/ 6 - Jugno [18]89 [superimposed over "Ist. Zoologica/ Modena"]"; "Mutinensis/ Baldini" (MSNV). My lectotype label "LECTOTYPE [underlined in red]/ Odynerus sinuatus [female symbol]/ mutinensis Baldini/ des. J.M. Cumming 1984 [black bordered label] and determination label "= Symmorphus/ bifasciatus (L.)/ det. J.M. Cumming 1984" have been attached to this specimen.

PARALECTOTYPE: Orto bot[anico]./ 12.VI.[18]92-male (MSNV). My paralectotype label and *S. bifasciatus* determination label have additionally been attached to this specimen.

Baldini (1894) described *Odynerus sinuatus mutinensis* from at least two females and two males collected from the environs of Modena, without selecting a holotype. The lectotype and paralectotype designated herein, are apparently the only syntypes which have been located in the Baldini collection (Soika, personal communication). The location of the remaining syntypes is unknown.

*Symmorphus sparsus* Morawitz, HOLOTYPE, female labelled: "Aschabad [Ashkhabad]/ [indecipherable line]"; "K [coll.]; *F. Morawitz* [in Russian]"; "Symmorphus/ sparsus [female symbol]/ F. Moraw."; "Typ./ *F. Morawitz* det."; "Holotypus Symmor-/ phus sparsus Mor./ [female symbol] [red label]" (ZIL).

*Symmorphus mutinensis auster* Soika, PARATYPES: Iwate [Pref.], Mt. Ketozan, 9.VII.1967, lg. R. Ishikawa-female (NSMT); Iwate [Pref.], Take, foot of Mt. Hayachine, 8 & 13.VII.1967, lg. R. Ishikawa-2 females (BMNH, MSNV).

*Symmorphus mutinensis yezoanus* Tsuneki, PARATYPE: Hokkaido, Sapporo, Fushimi, XI.1958, T. Nambu-male (NAMC).

Recognition.—The large dense punctation of the head and mesosoma, especially the major punctation of the dorsal mesepisternum (fig. 38), distinguishes *S. bifasciatus* from other species of *S. (Symmorphus)*. Only specimens of *S. (Parasymmorphus) parvilineatus* have similar punctation on the dorsal mesepisternum.

Description.—*Female*. Measurements of largest and smallest specimens given in Table 1. Taxonomically important character states given in Table 4.

*Male*. Measurements of largest and smallest specimens given in Table 1. Taxonomically important character states given in Table 4.

Variation.—Most specimens collected from high elevations or more northerly localities, have paler (light yellow to white) maculation and more reduced (often absent) mesosomal markings, than those collected from lower elevations or more southerly localities. In addition, specimens from Japan also have the mesosomal markings reduced or absent.

Geographical distribution and seasonal occurrence.—Known to range from Europe, east through Asia, to northeastern Siberia (see Kurzenko, 1982) and Japan (fig. 70). **Austria:** distribution widespread, earliest seasonal record—Nordtirol, Innsbruck, 24.V.1920; latest seasonal record—Fusch, 28.VIII.1960. **Belgium:** distribution widespread, earliest seasonal record—Boitsfort, 6.VI.1945; latest seasonal records—Genval, 20.VIII.1939; Tilff, 20.VIII.1943. **China:** Mandschurei [Manchuria], Erdaochajlinche, 24.VIII.1951. **Czechoslovakia:** distribution widespread, earliest seasonal record—Celakovice, 1.VI.1913; latest seasonal record—CSR, Moravia, Hranice, 24.VIII.1923. **Denmark:** distribution widespread, earliest seasonal record—Tisvilde, 24.VI.1974; latest seasonal record—Grejsdahl, 12.VIII.1928. **Finland:** distribution widespread in south, earliest seasonal record—Ta., Vääksy, 20-22.VI.1975; latest seasonal record—Heinola, Hevossaari, S. Finland, 9.VIII.1979; most northerly record—Kb., Joensuu, 1-9.VII.1975. **France:** distribution widespread, earliest seasonal record—Vendresse, 11.V.1908; latest seasonal record—Saint-Béat, 29.IX.1956. **Germany (BRD & DDR):** distribution widespread, earliest seasonal record—Birkenheide, Pfalz, 18.V.1957; latest seasonal record—Abensberg, Bay., 28.VIII.1939. **Hungary:** Német Bogsan. **Italy:** distribution widespread in north, earliest seasonal record—Cattolica, 19.V.1960; latest seasonal record—Emilia, Mte Barbiano, X.1941; most southerly records—Lazio, Campagna di Roma; Parko Nationale D'Abruzzo, 1957. **Japan:** Chichibu, Saitama [Pref.], 31.VII.1979; Hokkaido, Rebun Is., 21.VIII.1954; Karuizawa, Kitasaku-dist., Nagano Pref., 30.VIII.1949, 8.IX.1950 (additional records, from Aomori, Fukui and Tochigi Prefectures, in Tsuneki, 1977). **Netherlands:** distribution widespread, earliest seasonal record—Leiden, Hort. Bot., 20.V.1952; latest seasonal record—Mheer, 27.VIII.1948. **Norway:** Näsby Park, Opl., 9.VIII.1967; Numedal, 22.VIII.1900; Vass. [Vassa's], 31.VIII.1977. **Poland:** Carpathians, Pieniny [illegible], VIII.1960; Nowy Sacz, 49.39N 20.40E, 30.VIII.1967; Stolac, pow Zabkowice Sl., 16.VII.1954; Wroclaw, 22.VI.1965. **Romania:** Carpathes, Azuga. **Spain:** Barcelona, 1901; Huesca, Jaca, 27.VI-6.VII.1975; Lerida, Artesa de Segre, 41.54N 1.03E, 30.VII.1969. **Sweden:** distribution widespread in south, earliest seasonal record—Sk., Kullaberg, 6.VI.1963; latest seasonal record—Upl., Österåker Täljö, 5.IX.1948; most northerly records—Nb., Kukkola [region], 10.VII.1956; Nb., Råneå, Nieniholm, 29.VI.1963. **Switzerland**: distribution widespread, earliest seasonal record—Vaud, St. Sulpice, 8.VII.1934; latest seasonal records—Chur, Luillere, VIII.1936; Jura, VIII.1934. **Turkey**: Ankara, 3000ft., 9.VII.1959; Ankara [Antalya district], Karagol Lake, 3500ft., 26.VI.1960; Bolu, Lake Abant, 1000 m., 13.VII.1962; Kovacik, 3000ft., 8.VII.1959; Trabzon, Zigana Dagi, 4200ft., 13.VIII.1960. **United Kingdom (& Ireland)**: distribution widespread in Ireland, England and Wales, north to central Scotland, earliest seasonal record—Whitchurch, Oxon, 1.V.1977; latest seasonal record—Woodwalton, Hunts., 29.IX.1922; most northerly record—Kincraig, Scotland, 14.VIII.1948. **USSR**: Alma Ata, VII.1973; Barabash-Levada, Primorskij Krai, 1.VII.1978; Chatkalskij Khr. [range], S.Z. [N.W.] Kirgiziya, 1200 [m.], verch. [upland] Jassy, 1.VI.1952; Daghestan, Kraynovka region (Dried up Lake), 11.VI.1956; Daghestan, Novobiryuzyak, 30.VI.1957; Daghestan, Trozpyepskeya foothills, 3.VI.1956; Daghestan, Tupsozsk, 25.VI.1961, 14.VII.1962; Dorpat [Tartu]; Dzhungarskij Khr. [range], h-1000, V. [E.] Kazakhstan, Topolevka, 9.VIII.1957; environs of Kiev, Darnitsa, 7.VI.1979; environs of Kiev, Feofaniya, 16.VI.1979; environs of Moscow, 22.VI.1926, 18.VII.1928; Ferganskij Khr. [range], 1700-1800 [m.], Kirgiziya verch. [upland] Jassy, 13,22.VI.1954; Iu. [S.] Primore, Ussurijskij z-k., S. [N.] Kamenushka, 30.VIII.1982; Karachand Obl., iz. Koll., Neish r., 24.VI.1929; Kazakh S.S.R., Alma Ata (Medeo), 11.VII.1976; Khabarovskij Krai, 15 km., Iu.Z. [S.W.] Elabush, 2,4.VIII.1975; Kirovskaya Obl., g. Khalturin, 6.VIII.1981; Kongaus, Siberia, VIII.1923; Kostroma, Mittel Russland, 24.VIII.24; Moskovskaya Obl., Akulovo, 24.VII.1962, 3.VIII.1962; Moskovskaya Obl., Fokodedovskij r-n. Velbe Mikovo, 5.VIII.1981; Moskovskaya Obl., Odinchovskij r-n. ZBS MGU, 20.VI.1979, 5.VII.1979; Nizhniyaya Kuriya, 15 km. W. Perm, 7,9,18-19.VIII.1967; Pavlovsk, 30 km. S. Leningrad, 27.VI.1978; Priamure, environs of s. [N.] Natalino, r. Zeja, 8.VII.1975; Priamure, S. [N.] Gribovka, r. Archara, 20,22.VII.1975; Primore, environs of Anisimovki, 10.VII.1977; Primore, Ussurijskij zapov., 16,17.VIII.1974; Pyandzhikent; Semipalatinskaya Obl., 23 km. Iu.V. [S.E.] Semenovki, 6.VII.1978;

Stavropolvskij Krai, Karachay-Cherkesskaya A.O., r. Teberdy, 11.VII.1961; Ukrainia, Shitomn Korez, 10.VIII.1942; Zapov. Asku-Dzhabagly, Iu. [S.] Kazakhstan, Chimkentskaya Obl., 15.VI.1966 (additional records, from USSR, in Kurzenko, 1982). **Yugoslavia**: Croatie [Croatia], 1914; Slovenia, Hudajuzna, 390 m., 31.VII-4.VIII.1973.

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Beyond inclusion within the *S. murarius* group, the relationships of this species are unclarified.

### 5.1.3.1.3.13 *S. (Symmorphus) debilitatus* (Saussure)

*Odynerus (Protodynerus) debilitatus* Saussure, 1855 (MHNG).

*Odynerus bifasciatus* (Linnaeus) *sensu* Schulthess, 1887 (in part); Berland, 1928 (in part).

**Misidentification.**

Notes about synonymy.—As Blüthgen (1938, 1961) indicated, both Schulthess (1887) and Berland (1928) misidentified this species, uniting it with *S. connexus* (Curtis), under the nominal species *S. bifasciatus* (Linnaeus).

Type material examined.—LECTOTYPE (here designated), female labelled: "[square metallic colored label]"; "var."; "debilitatus/ Sss. Genève [in Saussure's handwriting]"; "LECTO/ TYPE/ 1962/ des./ v.d./ Vecht [orange label] [unpublished invalid designation]" (MHNG). My lectotype label "LECTOTYPE [underlined in red]/ Odynerus [female symbol]/ debilitatus Sauss./ des. J.M. Cumming 1984 [black bordered label]" has been attached to this specimen.

Saussure (1855) described *O. debilitatus* from at least one male and female specimen from the environs of Geneva in his collection in MHNG, but did not select a holotype. Only a single Saussure specimen collected from Geneva, a female herein designated lectotype, resides under this name in the collection of MHNG. The location of the remaining syntype or syntypes is unknown.

Recognition.—Commonly confused with *S. connexus*, which is sympatric with *S. debilitatus* throughout most of Europe. Males of each species are easily distinguished by the length of antennal article 13. Females are best recognized by differences in mesoscutal punctation, length of metasomal tergum 1, clypeal convexity and prominence of the pronotal humeral angle. In addition, the more angulate transverse carina of metasomal tergum 1 seen in most specimens of *S. debilitatus*, is helpful in separating both species (compare figs. 58 and 59 in Blüthgen, 1961). *S. debilitatus* is also similar to *S. cliens*, *S. canadensis* and *S. allobrogus* as discussed under "Recognition" of those species.

Description.—*Female*. Measurements of largest and smallest specimens given in Table 1. Taxonomically important character states given in Table 4.

*Male*. Measurements of largest and smallest specimens given in Table 1. Taxonomically important character states given in Table 4.

Geographical distribution and seasonal occurrence.—Known from northern and central continental Europe, east to northern Turkey and the Caspian Sea (fig. 71). **Austria**: distribution widespread, earliest seasonal record—Austria superior, Linz, Umg., Postlingberg, 3.VI.1971; latest seasonal record—Austria superior, Linz, Umg., 27.VII.1966. **Belgium** distribution widespread, earliest seasonal record—Boitsf., 26.IV.1946; latest seasonal record—Auderghem,2.IX.1941. **Czechoslovakia**: Bohemia, Pelhřimov, 24.VII.1907; CSR Slovakia, Parkaň; Ň.c Jičn, 29.VII.1934; Smichov, 9.VI.1892; Vsˇenory, 27.VII.1912. **France**: distribution widespread in north, earliest seasonal record—Brionne, VI.1891; latest seasonal record—Vendresse, 8.VIII.1909; most southerly records—Brionne, VI.1891; Cormeille[s], Seine et Oise, 1900; Le Criou, Environs of Samoëns, 1500 m., Hte. Savoie, VII; Paris; Pont pre`s Semur, Côte d'Or, 18.VII.1946; Vall de Charmy, 950-1200 m., Hte. Savoie, VII.1938.

**Germany (BRD & DDR)**: distribution widespread, earliest seasonal record—Aschaffenburg, 25.V.1947; latest seasonal record—Umg. Starnberg, 20.VIII.1939. **Hungary**: Félegyháza [Kiskunfélegyháza]. **Italy**: Bozen [Bolzano]. **Netherlands**: Breda O., 30.VI.1953; Crits. Ginneken, 10.VI.1978; r. Roll Haag; Ulvenhout, 2.VII.1953, 1954; Ulvenhout, N.B., Rakens, 21,22,24,25.VI.1953, 4,25.VII.1954. **Poland** Geller., Stettin, 30.VI.1955; Warsay [Warsaw], 19.VI.1944; Wroclaw, 3.VI.1956. **Sweden**: distribution widespread in south, earliest seasonal record—Upl., Eldgarn, 22.IV.1972; latest seasonal record—Upl., Ekerö, 4.IX.1973; most northerly records—Gstr., Hedesunda, 23,26.VI.1977; Dlr., Täktbo, 25,28.VII.1976, 1979. **Switzerland**: distribution widespread, earliest seasonal record—Genève, Cologny, 8.VI.1933; latest seasonal record—Euseigne, Wallis., 25,26.VII.1939. **Turkey**: Zigana Dagi, 5-6000ft., 10-14.VII.1959. **USSR**: Borisowka, Ukraine, 28.VIII.1928; Daghestan, Trozpeyepskaya foothills, 3.VI.1956; Kurland, 18.VI.1916; Moskovskaya obl., Michurineu, 25.VI.1961; Ukraina, g. Cherkassy, Zerelr. Dielr, 16.VII.1981. **Yugoslavia**: Styr[ia], Lete [Leto]; Styria, Windische Bühel [Windisch-Büheln], Karnerberg, 30.VII.1972.

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Phenetic similarity suggests a sister group relationship with *S. cliens*, although no synapotypies are known that substantiate this.

### 5.1.3.1.3.14 *S. (Symmorphus) cliens* Soika

*Symmorphus cliens* Soika, 1975 (NSMT).

Type material examined.—PARATYPES: Iwate [Pref.], Mt. Ketozan, 9.VII.1967, lg. R. Ishikawa-female (NSMT); Iwate [Pref.], Take, foot of Mt. Hayachine, 8-12.VII.1967, lg. R. Ishikawa-7 females (2 BMNH, 2 MSNV, 2 NSMT and 1 RNHL); Tokyo [Pref.], Ogochi & Mt. Mito, Okutama, 5.VI.1952, R. Ishikawa-female (BMNH).

Recognition.—Most similar to the allopatric *S. debilitatus*, from which it is distinguished by the form of the pronotal humeral angle and shape of metasomal tergum 1. Also similar to *S. connexus*, *S. lucens* and *S. canadensis* as discussed under "Recognition" of those species.

Description.—*Female*. Measurements of largest and smallest specimens given in Table 1. Taxonomically important character states given in Table 4.

*Male*. Measurements of largest and smallest specimens given in Table 1. Taxonomically important character states given in Table 4.

Geographical distribution and seasonal occurrence.—Known from northern and central Japan, on the islands of Hokkaido and Honshu (fig. 71). In addition to the paratypes, which were collected in June and July, four male and four female specimens have been examined. **Japan**: Chichibu, Saitama [Pref.], 1.VIII.1979 (JMCU); Karuizawa, Nagano [Pref.], 7,8.VII.1959 (NSMT); Take, foot of Mt. Hayachine, Iwate [Pref.], 8,12.VII.1967 (BMNH, MSNV, NSMT); Shikotsu-Ko, Hokkaido, 17.VII.1977 (YAMC); Taiyoji, Saitama [Pref.], Honshu, 8.VI.1969 (JMCU) (additional records, from Akita, Aomori, Fukui, Fukushima, Gumma, Ishikawa, Miyagi, Tochigi, Toyama and Yamagata Prefectures, in Soika, 1975 and Tsuneki, 1977).

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Possibly the sister species of *S. debilitatus*, as mentioned under that species.

### 5.1.3.1.3.15 *S. (Symmorphus) connexus* (Curtis)

*Odynerus connexus* Curtis, 1826. Lectotype, male, designated by Blüthgen, 1938 (NMVM).

*Odynerus bifasciatus* (Linnaeus) *sensu* Saussure, 1855; Schulthess, 1887 (in part), 1930; Saunders, 1902; Dalla Torre, 1904; Berland, 1928 (in part). **Misidentification.**

*Symmorphus bifasciatus* (Linnaeus) *sensu* Richards, 1937. **Misidentification.**

Notes about synonymy.—Saussure (1855) misidentified this species as *S. bifasciatus* (Linnaeus), as Blüthgen (1938, 1961) indicated. Several successive authors beginning with Schulthess (1887) appear to have followed Saussure's interpretation, although Schulthess (1887) and Berland (1928) also confused *S. debilitatus* (Saussure) under the Linnaean name.

Type material examined.—LECTOTYPE (by designation of Blüthgen, 1938), male labelled: "30 June/ Hampst."; "connexus"; "TYPE [circular red bordered label]"; "Odynerus/ connexus (Curt.)/ [indecipherable signature] 10|11|48" (NMVM).

PARALECTOTYPE: [without locality labels]-male [= *S. bifasciatus* (Linnaeus)] (NMVM).

Recognition.—Compared with *S. debilitatus* and *S. allobrogus* under "Recognition" of those species. Specimens of *S. connexus* are also similar to those of *S. cliens* from Japan, but are distinguished by a longer antennal article 13 in the male, sparse major punctation on the mesoscutum (fig. 46) and a slightly shorter metasomal tergum 1.

Description.—*Female*. Measurements of largest and smallest specimens given in Table 1. Taxonomically important character states given in Table 4.

*Male*. Measurements of largest and smallest specimens given in Table 1. Taxonomically important character states given in Table 4.

Geographical distribution and seasonal occurrence.—Known to range from northern and central Europe, east through Kazakhstan, to the foothills of the Tien Shan and Altai Mountains (fig. 72). **Austria**: Linz, Plesching, 5,9.VII.1977. **Belgium**: distribution widespread, earliest seasonal record—Schaerbeek, 10.VI; latest seasonal record—Maastricht, 7.VIII.1954. **Czechoslovakia**: Bohemia, Chodau, 19.VII.1978. **Denmark**: distribution widespread, earliest seasonal record—Roden Skov, Lolland, 4.VII.1945; latest seasonal record—Pilehuset, 15.VIII.1942. **Finland**: Hanko, Tvarminne, 2-6.VIII.1979. **France**: distribution widespread in north, earliest seasonal record—Ft. de Marly, 29.VI.1913; latest seasonal record—Saintes, VIII.1926; most southerly records—Allier, VII.1915; Saintes, VIII.1926. **Germany (BRD & DDR)**: distribution widespread, earliest seasonal record—Erlangen, 29.VI.1946; latest seasonal record—Kyffh., Habichtstal, 1-12.VIII.1958. **Poland**: Haynau i. Schl., 7.VIII.1940; Krakau. **Sweden**: distribution widespread in south, earliest seasonal record—Håbo Tibble, 19,27.VI.1940; latest seasonal record—Upl., Bogesund, 27.IX.1977; most northerly records—Dlr., Täktbo, 6.VIII.1978; Upl., Bogesund, 27.IX.1977; Upl., Fiby Urskog, Va¨nge, 25.VII.1948; Upl., Finota [Finata], 18.VII.1947; Upl., Na¨sby, 28.VII.1912; Upl., Rimbo, 23.VII.1978; Upl., Ró Agnmora [Agpmora], 14.VIII.1977. **United Kingdom (& Ireland)**: distribution restricted to southeastern England, earliest seasonal record—Bricket Wood, Ht., 5.V.1950; latest seasonal record—Wood Eaton, Oxford, VIII.1897; most northerly records—Bricket Wood, Ht., 5.V.1950, 8.VII.1937, 16.VII.1938; Colchester, 1903; Stanway, 3.VII.1920; most westerly record—Crichel, Dorset, 14.VII.1940. **USSR** g. Serebransk, vost. [E.] Kazakhstan, 17.VII.1963; Kasakhstan, 25 km sv [N.E.] Ust'-Kamenogorska, 25.VII.1979; Ukraina, Kanevskij zap-k, 9.VI.1979; Zailijsk[ij] Ala-tau, verch [upland] rM [small river], Almaatin[ka], 6.VII.1938.

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—The relationships of this species remain unresolved, beyond inclusion within the *S. murarius* group.

### 5.1.3.1.3.16 *S. (Symmorphus) lucens* (Kostylev)

*Symmorphus lucens* Kostylev; Gussakovskij, 1932. **Nomen nudum**.

*Odynerus lucens* Kostylev, 1938 (ZIL).

*Symmorphus ishikawai* Soika, 1975 (NSMT). **New synonymy**.

(—*lucens* Kostylev *sensu* Soika, 1963, 1975 [as *lucidus* in 1975] = *S. mizuhonis*.)

Notes about synonymy.—Gussakovskij (1932) recorded "*S. lucens* Kostylev" from Ussuri, six years prior to its description from Soviet Asia, by Kostylev (1938). I have examined the holotype of *S. ishikawai* described by Soika (1975) from Japan and regard it as conspecific with the lectotype of *S. lucens*.

Type material examined.—*Odynerus lucens* Kostylev, LECTOTYPE (here designated), female labelled: "[female symbol]"; "[circular gold label]"; "Jakovlevka Spas[sk]. u. [district]/ Ussur[i]. kr. [Krai] 8.IX.[1]926/ Djakonov [&] Filip[j]ev [in Russian]"; "Les po raslivu [forest on flood plain]/ r. [river] Daubikhé [in Russian]"; "Symmorphus [female symbol]/ lucens n.sp. Typus/ G.Kostylev det.1928"; "Paralectotypus Odyne-/ rus lucens Kost. [female symbol]/ des. Kurzenko 1976 [red label] [unpublished invalid designation]" (ZIL). My lectotype label "LECTOTYPE [underlined in red]/ Odynerus [female symbol]/ lucens Kost./ des. J.M. Cumming 1985 [black bordered label]" has been attached to this specimen.

PARALECTOTYPES, conspecific with lectotype: Altai, s. ber. [N. bank] Teletskoye oz. [lake], 1-4.VII.[1]912, Sushkin Redikortsev [in Russian]-female (ZIL); Ilinsk., pr. na [on] r. [rivers] Kyzas s [and] Abakan, 19.VI.[18]97, IU. Vagner [in Russian]-male (ZIL); Kurgan, 11.VII.1897, IU. Vagner [in Russian]-male (ZIL); lac. [lake] Teletskoe, fl. [mouth of river] Kyga, 16-17.VII.[19]34, W. Heptner-2 males (MSUM); Prim[orskij]. O. [Krai], Slavjanka, 2.VII.[1]914, Rimsk[y].-Kors[akov]. [in Russian]-male (ZIL); st. Sedan[illegible], 15 v ot [15 E. from] Vladivostok, 30.VI.[1]915, N. Dolle [in Russian]-female (ZIL); Ussurijsk, Okeanskaja, zh. d. bl. [near] Vlad[ivostok], 29.VII.[19]14, Cherskij [in Russian]-female (ZIL); Vladivostok [district], Suchan [Sutshan], 20.VII.[1]930, Malaise-female (ZIL); zh. d. Ussur[i]. kr. [Krai], Suchanskoj, st. Tigrovaja, 8.VIII.[1]926, N. N. Kuznetsov [in Russian]-2 females (ZIL). Seven females, three males of *S. mizuhonis* Tsuneki (MSNV, MSUM and ZIL). My paralectotype labels and determination labels (11 *S. lucens*, 10 *S. mizuhonis*) have additionally been attached to these specimens.

Kostylev (1938) based his description of *O. lucens* on numerous specimens from Soviet Asia without selecting a holotype, although he only mentioned specifically specimens collected from Lake Teletskoye, Jakovleka and Slavjanka. The specimens considered here to belong to the type series, were all determined by Kostylev as *O. lucens* prior to 1938 and were collected from the three previously mentioned localities, or from those which do not oppose his statement "after this [*O. lucens*] was found in the southern parts of Siberia west as far as Kurgan". The type series consists of specimens belonging to two species, those conspecific with the lectotype designated herein, as well as a number of specimens of *S. mizuhonis* Tsuneki.

*Symmorphus ishikawai* Soika, HOLOTYPE, female labelled: "Yokoo, 1600 m./ nr Kamikochi/ Nagano Pref./ VII. 30. 1957/ R. Ishikawa"; "HOLOTYPUS/ Symmorphus/ ishikawae GS. [red label]" (NSMT).

ALLOTYPE, male labelled: "Yokoo, 1600 m./ nr Kamikochi/ Nagano Pref./ VII. 30. 1957/ R. Ishikawa"; "ALLOTYPUS/ Symmorphus/ ishikawae [red label]" (NSMT).

PARATYPES: Nagano Pref., Yokoo, 1600 m., nr Kamikochi, 30.VII.1957-3 females, male (BMNH, MSNV, NSMT).

Recognition.—Very similar to *S. sublaevis* as discussed under "Recognition" of that species. Certain males of *S. cliens* with rather sparse punctation, may potentially run to *S. lucens* in the key to species and subspecies of *S. (Symmorphus)*. These rarely encountered specimens are distinguished from *S. lucens* by denser major punctation on the mesoscutum and posterodorsal region of the pronotum (fig. 45). In addition, *S. lucens* can also be confused with *S. mizuhonis* as discussed under "Recognition" of that species.

Description.—*Female*. Measurements of largest and smallest specimens given in Table 1. Taxonomically important character states given in Table 4.

*Male*. Measurements of largest and smallest specimens given in Table 1. Taxonomically important character states given in Table 4.

Geographical distribution and seasonal occurrence.—Known to range from the Japanese island of Honshu and Sakhalin in eastern USSR, west through southern Siberia, to Kurgan (fig. 72). **Japan**: Kamikochi [Nagano Pref.], 22.V.1954; Yokoo, 1600 m., nr. Kamikochi, Nagano Pref., 30.VII.1957. **USSR**: Artybash [Lk. Teletskoye], 27.VI.1931; Buryatkaya A.S.S.R., environs of Kyakhty, 30.VII.1977; Iu. [S.] Primore, Ussurijskij zap-k., S. [N.] Kamenushka, 23,26,28.VII.1982; Ongudai, Altai, 19.VI.1909; Primore, Anisimovki, 29.VI.1975; Primore, environs of Anisimovki, 19,21.VI.1975; Primore, Ussurijskij zapov., 27.VII.1974, 14,15.VIII.1974; Primorskij Krai, Ussurijskij r-n. Sumutinskij zan. 20.VII.1973; Saghalin [Sakhalin], Adachi, 16.VIII.1914; Sichote-Alin mer, pr. Sutshan [Suchan], 5.IX.1936; Sichote-Alin mer, Promyslovka, 7.IX.1936; Ussuri, Kasakewitsch, 1907; Z. [W.] Birsherta, r. Zeja, 50 [km.] V. [E.] Blagoveshch, 5-6.VI.1914.

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Probably the sister species of *S. sublaevis*, from which it differs only slightly.

### 5.1.3.1.3.17 *S. (Symmorphus) sublaevis* (Kostylev)

*Odynerus (Odynerus) sublaevis* Kostylev, 1940 (MSUM).

*Symmorphus sparsus* Morawitz *sensu* Soika, 1963. **Misidentification**.

Type material examined.—LECTOTYPE (here designated), female labelled: "Zailijsk[ij]. Ala-tau/ verch [upland] rM [small river], Almaatin[ka]/ G. Kostylev 26.VI.[19]38 [in Russian]"; "Odynerus Typus/ sublaevis, n.sp. [female symbol]/ g. Kostylev det.1939"; "Lectotypus Odynerus/ sublaevis Kost. [female symbol]/ des. Kurzenko 1976. [red label] [unpublished invalid designation]" (MSUM). My lectotype label "LECTOTYPE [underlined in red]/ Odynerus [female symbol]/ sublaevis Kost./ des. J.M. Cumming 1985 [black bordered label]" has been attached to this specimen.

PARALECTOTYPES: Zailijsk[ij] Ala-tau, verch [upland] rM [small river], Almaatin[ka], 28.VI.-6.VII.[19]38, G. Kostylev [in Russian]-5 females, male (1 MSNV, 5 MSUM). My paralectotype labels have additionally been attached to these specimens.

Kostylev (1940) based his description of *O. sublaevis* on a series of specimens from Zailijskij Alatau in southeastern Kazakh S.S.R., without selecting a holotype. Six specimens in the collection of MSUM, including the lectotype designated herein, in addition to a single female in the collection of MSNV, probably represent the entire type series of *S. sublaevis*.

Recognition.—Most similar to *S. lucens*. In addition to features given in the key to species and subspecies of *S. (Symmorphus)*, most specimens of *S. sublaevis* are recognized from those of *S. lucens* by their more extensively maculated metasoma.

Description.—*Female*. Measurements of largest and smallest specimens given in Table 2. Taxonomically important character states given in Table 4.

*Male*. Measurements of largest and smallest specimens given in Table 2. Taxonomically important character states given in Table 4.

Geographical distribution and seasonal occurrence.—Known from the Soviet Tien Shan and adjacent mountain ranges (fig. 72). USSR: Alma Ata, VI.1973; Chatkalskij Khr. [range], S.-Z. [N.W.] Kirgiziya, Arkut, 1200-1500 [m.], 12,25.VI.1952; Chatkalskij Khr. [range], 30 km. N. Parkenma, Ushch [canyon] Aksagama, 7-10.VI.1982; Dzhungarskij Khr. [range], V. [E.] Kazakhstan, Topolevka, h-1000, 9.VIII.1957; environs of Ayak-Kalkana, Iu.-V. [S.E] Kazakhstan, 4.VI.1971; g. Alma Ata, 23.VI.1970; g. Panfilov, Iu.-V. [S.E.] Kazakhstan, 1.IX.1970; Gouldscha, Ferghana [Fergana], 1905; Kazakh S.S.R., Alma Ata, Medeo, 7.VII.1976; Turkestan, Djarkent [Jarkent = Panfilov]; Ushch [canyon] Turgen, Zailijsk[ij] Alatau, 24.VII.1971; Vost. [E.] Kazakhstan, Khr. [range] Saul., 35 km. O. [E.] Zajoqana, 11.VII.1980.

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Probably most closely related to *S. lucens.*

### 5.1.3.1.3.18 *S. (Symmorphus) canadensis* (Saussure)

*Odynerus (Protodynerus) canadensis* Saussure, 1855 (BMNH).
*Odynerus (Symmorphus) debilis* Saussure, 1870 (MHNG).
*Symmorphus cognitans* Cameron, 1906 (BMNH).

Type material examined.—*Odynerus (Protodynerus) canadensis* Saussure, HOLOTYPE, female labelled: "Canada"; "Odynerus/ canadensis/ Saus./ [female symbol] [blue label in Saussure's handwriting]"; "B.M. TYPE/ HYM./ 18.532" (BMNH).

*Odynerus (Symmorphus) debilis* Saussure, LECTOTYPE (here designated), female labelled: "[square metallic colored label]"; "Connecticut"; "LECTO-/ TYPE/ [female symbol] debilis/ Sss./ (RMB) [red label] [unpublished invalid designation]" (MHNG). My lectotype label "LECTOTYPE [underlined in red]/ Odynerus [female symbol]/ debilis Sauss./ des. J.M.

Cumming 1984 [black bordered label]" has been attached to this specimen.

PARALECTOTYPES: Illinois-2 females; Viscontin [Wisconsin]-female (MHNG). My paralectotype labels have additionally been attached to these specimens.

Although Saussure (1870) appears to have based his description of *O. debilis* on an undetermined number of female specimens collected from "America borealis", his subsequent redescription of the same material in 1875, indicates that he initially described a series of female syntypes from Connecticut, Wisconsin and Illinois. Four females collected from these three localities, including the lectotype designated herein, reside under this name in Saussure's collection in MHNG.

*Symmorphus cognitans* Cameron, HOLOTYPE, female labelled: "Cana"; "5366"; "P.Cameron Coll/ 1914-110"; "Symmorphus/ cognitans/ Cam. Type/ Canada"; "B.M. TYPE/ HYM./ 18.533" (BMNH).

Recognition.—Distinguished from other New World members by features given in the key to species and subspecies of *S. (Symmorphus)*. Specimens of *S. canadensis* are very similar to those of *S. debilitatus* and *S. cliens*, although they are differentiated from both Palearctic species by the shape of metasomal tergum 1.

Description.—*Female*. Measurements of largest and smallest specimens given in Table 2. Taxonomically important character states given in Table 4.

*Male*. Measurements of largest and smallest specimens given in Table 2. Taxonomically important character states given in Table 4.

Variation.—Most specimens collected from high elevations or more northerly localities, have paler (white) markings, than specimens collected from lower elevations or more southerly localities.

Geographical distribution and seasonal occurrence.—Known transcontinentally in North America, from Northwest Territories in the north, to California, Texas and Georgia in the south (fig. 73). **Prince Edward Island**: Brackley Beach Can. Nat. Pk., 25,30.VII.1940. **Nova Scotia**: Kentville, 28.VII.1924, 13.VIII.1915; Sydney, VII.1967; Victoria Co., Baddeck, VII.1972. **New Brunswick**: Shediac, 4.IX.1926; St. Andrews, 5.VIII.1957. **Quebec** distribution widespread in south, earliest seasonal record—Montreal, 16.V.1901; latest seasonal record—Old Chelsea, 30.VIII.1961; most northerly records—Ancienne-Lorette, 7.VI.1923; Cap Rouge, 3.VII.1966, 7,10.VII.1953; Shawbridge, 21.VIII.1929; St. Anne de la Porcatiere, 7.VIII.1914. **Ontario**: distribution widespread, earliest seasonal record—Kingsville, 23.V.1962; latest seasonal record—Eden Mills, 7.X.1975; most northerly records—Dryden, 4.VII.1955; Finland, 29.VI.1960; Harris Hill, 4.VIII.1960; Hurkett, 15.VIII.1960; Kenora, 15 mi. S.E., Rush Biv. Prov. Pk., 27.VII.1976, 4.VIII.1971, 8.VIII.1970; Kenora, 17 mi. S.E., 22.VII.1977, 27.VII.1976; One Sided Lake, 2,9,12,16,28.VII.1960, 4,5.VIII.1960. **Manitoba** distribution widespread in south, earliest seasonal record—Baldur, 13.VI.1925; latest seasonal record—Ninette, 5.VIII.1958; most northerly records—Cedar Lake, VII.1936; Dauphin; Winnipeg Beach, 16.VII.1916. **Saskatchewan**: distribution widespread in south, earliest seasonal record—Regina, 1.VII.1906; latest seasonal record—Wallwort, 20.VII.1942; most northerly records—Christopher Lake, 11.VII.1959; Somme, 7.VII.1954; Wallwort, 17,20.VII.1942; Waskesiu Lake, 14.VII.1938; White Fox, 11.VII.1944. **Alberta** distribution widespread, earliest seasonal record—Bilby, 9.VI.1924; latest seasonal record—Delburne, 23.VIII.1973; most northerly records—George Lake, 53.57N 114.06W, 1.VII.1981; Grande Prairie, 26.VII.1961; Peace River, 18.VI.1961. **Northwest Territories** Norman Wells, 23.VII.1949. **British Columbia**: distribution widespread in south, earliest seasonal record—Oliver, 8.VI.1923; latest seasonal record—Robson, 12.VIII.1950; most northerly records—Moberly, 2.VII.1977; Salmon Arm, 31.VII.1925; Strathcona Prov. Pk., VI; Vernon, 23.VII.1923, 24.VII.1917. **Arkansas** Marion Co., 1897; Washington Co., 6.V.1965. **California**: distribution widespread in north, earliest seasonal record—Three Rivers, Tulare

Co., 17.IV.1959; latest seasonal record—Mono Co., Sweetwater Mts., .5 mi. E. Lava Springs, S. Fork Cotton Wood Crk., 8300ft., 8.VIII.1979; most southerly records—Ben Lomond, IV.1931; Bridgeport, Mono Co., 18.VIII.1952; Oakhurst, Madera Co., 8.VI.1942; Three Rivers, Tulare Co., 17.IV.1959. **Colorado**: distribution widespread, earliest seasonal record—Boulder, 5.VI.1983; latest seasonal record—Hewlett Gulch, Larimer Co., 6000ft., VIII,IX.1978. **Connecticut** distribution widespread, earliest seasonal record—Storrs, 30.V.1955; latest seasonal record—Litchfield Co., 30.VIII.1952. **District of Columbia** distribution widespread, earliest seasonal record—Washington, 15.V.1944; latest seasonal record—Rock Crk., 19.IX.1948. **Georgia**: distribution widespread, earliest seasonal record—Stone Mountain, Dekalb Co., 25.IV.1953; latest seasonal record—Blood Mt., 17.IX.1939; most southerly records—Atlanta, 21.V,1940, 24.V.1947, 2.VI.1946, 10,28.VII.1942, 31.VII.1941; Oconee Co., Watkinsville vic., 12.VI. 1976; Thomasville, 28.IV.1915. **Idaho**: Dubuque, 14.VII.1941; Slate Crk. R.S., Idaho Co., 27.VI.1963. **Illinois** distribution widespread, earliest seasonal record—Dubois, 24.V.1917; latest seasonal record—Carbondale, Jackson Co., 5.X.1956. **Indiana**: Owen Co., Camp Area, McCormick's Cr. St. Pk., 25,26.VI.1950. **Iowa**: Pilot Knob, nr. Forest City, Hancook Co., 16.VI.1961. **Kansas**: Douglas Co., VI; Douglas Co., Lawrence vic., 21.V.1962; Lawrence, 17.VI.1900; Riley Co., 20.VI. **Kentucky**: [no additional data]. **Louisiana**: Shrevport, 27.III.1907. **Maine** distribution widespread, earliest seasonal record—Mt. Katahdin, 5000ft., 29.VI.1901; latest seasonal record—Lincoln Co., 26.VIII.1939. **Maryland** distribution widespread, earliest seasonal record—Colesville, Montg. Co., 9.V.1976; latest seasonal record—Thomas Rd., nr. Cumberland, 29.X.1957. **Massachusetts**: distribution widespread, earliest seasonal record—Holliston, 1.V.1911; latest seasonal record—Dorchester, 15.IX.1901. **Michigan**: distribution widespread, earliest seasonal record—Iron Co., 18.V.1976; latest seasonal record—Ann Arbor, 14.X.1975. **Minnesota**: distribution widespread, earliest seasonal record—Houston Co., 20.V.1938; latest seasonal record—Mille Lac Co., 9.X.1938. **Mississippi**: Holly Springs, Dallas Co., 29.VI.1969. **Missouri**: St. Louis, VI.1899. **Montana**: Ennis, Madison Co., 18.VII.1971; Glendive, 10.VI.1929; Lake Ronan, Lake Co., 6.VII.1932. **Nebraska**: War Bonnet Canyon. **Nevada**: Elko Co., 2 mi. N. Lamoille, 14.VI.1960; Elko Co., Deeth, Mt. View Ranch, Starr Valley, 6000ft., 19.VI.1969; Patrick, Washoe Co., 30.VI.1964; Verdi, Washoe Co., 18.VI.1964. **New Hampshire**: distribution widespread, earliest seasonal record—Nelson, 15.VI.1907; latest seasonal record—Nelson, 1.IX.1907. **New Jersey**: distribution widespread, earliest seasonal record—Westfield, 31.V.1954; latest seasonal record—Englewood, Bergen Co., 20.VIII.1960. **New Mexico** Chiconico Can˜on, nr. Raton, 25.VIII.1973; Hyde St. Pk., 8 mi. N.E. Santa Fe, Santa Fe Co., 8700ft., 2.VIII.1964; Little Tesuque Cañon, vic. Santa Fe, 9200ft., 27.VII-10.VIII.1932; Otero Co., 15 mi. E. Cloudcroft, Camp Marx White, Staris Spr., Bear Canyon, 17.VIII.1934; Ute Park, Cimmaron Canyon, 1-4.VII.1960. **New York**: distribution widespread, earliest seasonal record—Orient, L.I., 12.IV.1939; latest seasonal record—Lewisboro, Westchester Co., 16.X.1966. **North Carolina**: distribution widespread, earliest seasonal record—Raleigh, 13.V.1940; latest seasonal record—Crabtree Md., Yancey Co., 3600ft., 21.VIII.1950. **North Dakota**: Bismarck, 28.V.1939; Fargo, 19.VI.1921, 25.VII.1951; Turtle Mts., 4.VIII.1920. **Ohio** distribution widespread, earliest seasonal record—Cedar Bog, Urbana, 10.V.1930; latest seasonal record—Fairfield Co., 13.IX. **Oklahoma**: Cherokee Co., 1 mi, N.E. Scraper, 7.V.1974. **Oregon**: distribution widespread, earliest seasonal record—Corvallis, 2.V.1926; latest seasonal record—Hood River, 4.VIII.1908. **Pennsylvania** distribution widespread, earliest seasonal record—York Co., 5 mi. N.W. Davidsburg, 8-11.V.1970; latest seasonal record—All'y Co., North Park, 5.X.1973. **Rhode Island**: Westerly, 20.VI.1936. **South Carolina**: Anderson, 21.VII.1957; Blackville, 29.X.1964; Greenville, 18,24.III.1913; 24.VIII.1952; nr. Tigerville, 8.V.1944. **South Dakota**: Spring Creek Camp, 11 mi. N.E. Hill City, Pennington Co., 4300ft., 29.VI.1962. **Tennessee**: distribution widespread, earliest seasonal record—The Chimneys, Great Smokey Mts. Nat. Pk., 11.VI.1946; latest seasonal record—Ramsay Cascades Tr., Great Smokey Mts. Nat. Pk., 14.VIII.1947. **Texas** distribution widespread in east, earliest seasonal record—Dallas, 15.III.1907; latest seasonal record—Hunt Co., 22.IV.1939; most southerly records—Fedor, Lee Co., 17.III.1909; Gonzales Co., Palmetto St. Pk., 5,6.IV.1954; Hidalgo Co., Bentsen, Rio Grande Valley St. Pk., 20,22-24.III.1978; Lexington, 24.III.1951; Navasota, 7.IV.1959; Thomaston, 25.III.1951. **Utah** Allen Canyon, 20.VII.1949; Box Elder Co., Mantua - Devil's Gate, 4,31.VII.1969; Cache Co., Green Canyon, 4,9.VII.1969; Cache Co., W. Hodges Canyon, 20-23.IX.1976; Logan, 12.VI.1955; Logan Canyon, 22.VII.1940; Mirror Lake, Summit Co., 15.VII.1960; Smithfield Co., 5.VII.1958. **Vermont** distribution widespread, earliest seasonal record—Newport, 12.VII.1891; latest seasonal record—Laurel Lake, Jacksonville, 20.VIII.1939. **Virginia** distribution widespread, earliest seasonal record—E. Falls Church, 30.III.1933; latest seasonal record—Glencarlyn, 4.X. **Washington** Mill Creek, Walla Walla, 4.VII.1922; Stevens Co., 4 mi. S. Colville, Rt. 395, Colville R., 6.VII.1972. **West Virginia**: distribution widespread, earliest seasonal record—Cranberry Gls., 4.VI.1955; latest seasonal record—Lost River St. Pk., Hardy Co., 22-31.VIII.1956. **Wisconsin** distribution widespread, earliest seasonal record—Shawanoco Co., 31.V.1955; latest seasonal record—Clintonville, 7.IX.1934. **Wyoming**: Grand Teton Nat. Pk., VII.1937; Jackson Hole Res. Sta., 6700ft., 21.VII.1967; Jackson Hole Bio. Sta., Moran, 19.VII.1964; Lake Creek Camp, Park Co., 13 mi. S.E. Cooke City, Mont., 7200ft., 24.VII.1962; Jenny Lake, Teton Co., 4-15.VIII.

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Phenetically most similar to *S. debilitatus* and *S. cliens*, which together may be the sister group of this species.

### 5.1.3.1.3.19 *S. (Symmorphus) projectus* Bohart

*Symmorphus projectus* Bohart, 1950 (CAS).

Type material examined.—HOLOTYPE, male labelled: "Fallen Leaf Lk./ ElDorado Co/ Cal. VII-1931"; "Pres[ented] by/ O H Swezey/ Collector"; "Cal. Acad. Sci. Type No.

6145" (CAS).

PARATYPES, Arizona: Oak Cr[eek]. Canyon, 4-5000 ft., 10-11.VI.1940, G. E. & R. M. Bohart-2 females, 2 males; Oak Cr[eek] Can[yon], 13-21.V.1947, H. & M. Townes-2 females, 2 males; Sierra Ancha [Mts.], Workman Cr[eek], 28.IV-8.V.1947, H. & M. Townes-6 males. California: Alta, 25.VI.1933, G. E. & R. M. Bohart-female; Angora Peak, 8625 ft., 19.VII.1931, E. O. Essig-male; Berkeley, V.1934, G. E. & R. M. Bohart-male; Calaveras Co., Jenny Lind, 21.X.1917, J. C. Bradley-female; Carl Inn, 2.VII.1933, G. E. & R. M. Bohart-female; Danville, 29.IV.1939-female; Davis, 6.IV.1936 & 21.VII.1936, R. M. Bohart-2 males; Eldorado Co., Fallen Leaf L[a]k[e], VII.1931, O. H. Swezey-4 females, 4 males; Eldorado Co., Snowline Camp, 19.VI.1948, P. D. Hurd-female; Eldorado Co., Tahoe, 6200 ft, 9.VI., W. M. Giffard-male; Fort Seward, 16.VI.1935, E. W. Baker-female; Giant Forest, 28.VII.1929, R. H. Beamer-female, male; Martinez, 2.IX.1946, H. E. Cott-female; Mendocino Co., [indecipherable locality], 21.IX.1919, J. Mailliard-female; Mineral King, 8.VIII.1935, G. E. Bohart-female; Mt. Diablo, .VI.1924-female; Santa Cruz Mts, Felton, 300-500 ft., 15-19.V.1907, [J. C.] Bradley-female; S[an]ta Monica, F. C. Clark-female. Seq[uoia]. Nat[ional]. Park, Giant Forest, 6-7000 ft, 21-26.VII.1907, J. C. Bradley-female, male; Sequoia Nat[ional]. P[ar]k, Tokopah Valley, 21-25.VII.1933, C. D. Michener-2 males; Sierra Co., Gold Lake, 19-30.VII.1921, C. L. Fox-8 females, 12 males; Tahoe, G[len] Alpine Cr[eek], 7-16.VII.65, E. P. Van Duzee-female, male; Trinity Co., Coffee Creek, Big Flat, 20.VI.1934, G. E. Bohart-male. Oregon: Forest Grove, 14.IV.31, J. Schuh-female; Klamath Lake, Eagle Ridge, 29.V.1924, C. L. Fox-male; Wallowa Nat[iona]l Forest, Lick Cr[eek], 4600 ft, 16.VIII.1937, Bolinger & Jewett-male. (71 specimens deposited in CAS, CU, JMCU, MCZ, UCD and USNM.)

Recognition.—Distinguished from other New World members by features given in the key to species and subspecies of *S. (Symmorphus)*. Specimens of *S. projectus* are differentiated from those of all Old World species of *Symmorphus* by the suppressed interantennal carina (fig. 48), in combination with the very short propodeal superior shelf.

Description.—*Female*. Measurements of largest and smallest specimens given in Table 2. Taxonomically important character states given in Table 4.

*Male*. Measurements of largest and smallest specimens given in Table 2. Taxonomically important character states given in Table 4.

Geographical distribution and seasonal occurrence.—Known in North America west of the Rocky Mountains, from British Columbia in the north, to California, Arizona and New Mexico in the south (fig. 73). **British Columbia**: distribution widespread in south, earliest seasonal record—Robson, 26.V.1947; latest seasonal record—Robson, 12.IX.1955; most northerly records—Courtenay, Vancouver Island, VII.1965; Vernon, 6.VII.1932, 23.VIII.1947. **Arizona**: Oak Crk. Can., 13,16,21.V.1947, 10,11.VI.1940, 28.VI.1936; Workman Crk., Sierra Ancha, 28.IV,8.V.1947. **California**: distribution widespread, earliest seasonal record—Santa Clara Co., Stanford University, 20.II.1956; latest seasonal record—Davis, 5.XI.1955; most southerly records—Julian, 12,25.V.1974; Lake Wohlford, 21.IV,1.V.1974; Temecula, 25.IV.1974. **Idaho**: distribution widespread, earliest seasonal record—Webb, Nez Perce Co., 29.III.1951; latest seasonal record—Moscow Mt., Latah Co., 16.VIII.1964. **Montana** Ennis, Madison Co., 18.VII.1971; Lake Ronan, Lake Co., 6,26.VII.1932; Yellow Bay, Lake Co., 23.VII.1967. **Nevada**: Elko, 2.VIII.1964; Galena Crk., Washoe Co., 29.VI.1964, 18.VII.1961; Incline Village, Washoe Co., 9.VII.1964; Verdi, Washoe Co., 10.VI.1960, 18.VI.1964, 25.VI.1961. **New Mexico**: Bursum Camp, 18 mi. E. Alma, Catron Co., 9000ft., 9.VII.1961. **Oregon**: distribution widespread, earliest seasonal record—Forest Grove, 14.IV.1931; latest seasonal record—Medford, Jackson Co., 28.IX.1956. **Utah**: Cache Co., W. Hodges Can., 3-9,14-16.IX.1976; Logan Canyon, Cache Co., 6700ft., 18,19.VIII.1961. **Washington** distribution widespread, earliest seasonal record—Seattle, 21.V.1925; latest seasonal record—Fort Lewis, Pierce Co., 20.VIII.1963. **Wyoming** Grand Teton Nat. Pk., VII.1947.

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Although relationships are unclear beyond inclusion within the *S. murarius* group, phenetic comparison suggests that *S. projectus* is somewhat distantly related to other New World species.

### 5.1.3.1.3.20 *S. (Symmorphus) tukvarensis* (Meade-Waldo)

*Odynerus (Symmorphus) tukvarensis* Meade-Waldo, 1910 (BMNH).

Type material examined.—HOLOTYPE, female labelled: "Type [circular red bordered label]"; "Sikkim/ Tukvar/ 4000 ft - 4-94/ Bingham Coll."; "Col. C.T. Bingham/ 96-30."; "Odynerus (Symmorphus)/ tukvarensis/ Meade Waldo/ [female symbol]. type"; "B.M. TYPE/ HYM./ 18.307" (BMNH).

Recognition.—Readily distinguished from all other species of *Symmorphus*, except *S. nipteroides*, by the inflated posteriorly raised basal carina of metasomal sternum 1 (fig. 35). Besides the features given in the key to species and subspecies of *S. (Symmorphus)*, specimens of *S. tukvarensis* are additionally differentiated from those of *S. nipteroides* by the shorter metasomal tergum 1 with widely spaced foveolate (rather than very sparse punctate) major punctation.

Description.—*Female*. Measurements of largest and smallest specimens given in Table 2. Taxonomically important character states given in Table 4.

*Male*. Unknown.

Geographical distribution and seasonal occurrence.—Known to range along the Himalaya, from Simla in northwestern India, east to Sikkim (fig. 74). In addition to the holotype, which was collected in April, 11 female specimens have been examined. **India**: Simla,

V.1897, VIII.1898, IX.1898 (BMNH, MSNV).

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Inferred to be the sister species of *S. nipteroides*, on the basis of the shared autapotypic basal carina of metasomal sternum 1.

### 5.1.3.1.3.21 *S. (Symmorphus) nipteroides* new species

Holotype.—Female labelled: "HOLOTYPE [red label]"; "INDIEN [India]/ N Yourdou [ca. 33.30N 75.18E], 2200m/ 16.7.1980/ H., U., C.Aspöck, H.Rausch"; "Symmorphus/ nipteroides/ Cumming/ Holotype [red bordered label]" (GUSC).

Allotype.—Male labelled: "ALLOTYPE [red label]"; "INDIEN [India]/ Palmar [ca. 33.30N 75.18E] 1700-1800m/ 7.7.1980/ H., U., C.Aspöck, H.Rausch"; "Symmorphus/ nipteroides/ Cumming/ Allotype [red bordered label]" (GUSC).

Derivation of specific epithet.—*Nipter* is Greek for basin and the suffix *oides* means like, in reference to the structure on the first metasomal sternum, formed by the inflated basal carina in members of this species.

Recognition.—Shares an inflated posteriorly raised basal carina on metasomal sternum 1 only with *S. tukvarensis* and is compared with the former under "Recognition" of that species.

Description.—*Female*. Measurements of the holotype given in Table 2. Taxonomically important character states given in Table 4.

*Male*. Measurements of the allotype given in Table 2. Taxonomically important character states given in Table 4.

Geographical distribution.—Known from Yourdou and Palmar, near Kishtwar (Jammu), in northwestern India (fig. 74).

Seasonal occurrence.—The holotype and allotype were collected in July.

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Apparently most closely related to *S. tukvarensis*.

### 5.1.3.1.3.22 *S. (Symmorphus) fuscipes* (Herrich-Schaeffer)

*Odynerus fuscipes* Herrich-Schaeffer, 1838 (destroyed, neotype in SMF).
*Symmorphus karelicus* Morawitz, 1895 (ZIL).

Notes about synonymy.—Blüthgen (1938, 1961) synonymized *S. karelicus* Morawitz with *S. fuscipes* (Herrich-Schaeffer) apparently on the basis of comparison of the original descriptions of these two nominal species and information about the Morawitz type supplied to him by V. Popov of Leningrad. I have examined the holotype of *S. karelicus* described from Karelia in 1895 and regard it as conspecific with the neotype of *S. fuscipes*.

Type material examined.—*Odynerus fuscipes* Herrich-Schaeffer, NEOTYPE (here designated), female labelled: "leg. K. Vegter/ Emmen/ 6-7-[19]59"; "Symmorphus/ fuscipes H.-Sch./ [female symbol]"; "Senckenberg-/ Museum/ Frankfurt/ Main" (SMF). My neotype label "NEOTYPE [underlined in red]/ Odynerus [female symbol]/ fuscipes H.-Sch./ des. J.M. Cumming 1985" and my determination label "Symmorphus/ fuscipes [female symbol]/ (H.-Sch.)/ det./ J.M. Cumming 1985" have been attached to this specimen.

The syntypes of *O. fuscipes* were not located in any of the collections listed under "Materials" and are presumed to have been destroyed with the remainder of the Herrich-Schaeffer collection (Blüthgen, 1961; Vecht and Fischer, 1972). Since the description by Herrich-Schaeffer (1838) is insufficient to place this name with certainty, a neotype is selected herein to fix the name in its traditional sense for the sake of stability. The female specimen selected as neotype agrees closely with the original description and is from the southwestern portion of the range of *S. fuscipes*, as were the male and female specimens described by Herrich-Schaeffer.

*Symmorphus karelicus* Morawitz, HOLOTYPE, male labelled: "Terijoki"; "K [coll.] *F. Morawitz* [in Russian]"; "Symmorphus/ carelicus [male symbol]/ F. Morawitz"; "Typ/ *F. Morawitz* det."; "Holotypus Symmor-/ phus carelicus/ F. Morawitz [male symbol] [red label]" (ZIL).

Recognition.—Readily distinguished from all other species of *Symmorphus* by the complete submedian propodeal carina (fig. 15), in combination with the shape of metasomal tergum 1 and punctation of the dorsal mesepisternum (fig. 16). In addition, most specimens of *S. fuscipes* are differentiated from those of all other *S. (Symmorphus)*, except a few specimens of *S. bifasciatus*, by a nearly complete epicnemial carina that extends partially on to the dorsal mesepisternum.

Description.—*Female*. Measurements of largest and smallest specimens given in Table 2. Taxonomically important character states given in Table 4.

*Male*. Measurements of largest and smallest specimens given in Table 2. Taxonomically important character states given in Table 4.

Geographical distribution and seasonal occurrence.—Known to range from northern and central continental Europe (for additional European records see Blüthgen, 1961), east through Siberia, to Magadan Oblast and Primorskij Krai (fig. 75). **Finland**: Fennia, Ta., Vanaja, 1951. **Netherlands**: Emmen, 28.V.1960, 10.VI.1960, 17.VII.1968, 22.VII.1967. **Norway**: Norv. merid. [southern Norway], Aadalen, VIII.1845. **Sweden** distribution widespread in south, earliest seasonal record—Grisslehamn, Uppl., 28.VI.1924; latest seasonal record—Upl., Ljustero, 22.VIII.1964; most northerly record—Gstr., Hille, Forsby, 1,7.VII.1948. USSR: Barabash-Levada, Primorskij Krai, 4.VI.1980, 29.VI.1978; Distr. Moskva, Mytistshi [Mytishchi], 18.VI.1928; Dorpat [Tartu]; Ekaterinburg [Sverdlovsk], 2.VI.1924; environs of Jakutska, 26.VI.1962, 7,9,10,18.VII.1962; Gorki [Belorussian S.S.R.]; Iu.V. [S.E.] Otst. Makkavsevo, Zabajk, 12.V.1913; Kujbyshev Obl., Mirnyi, 13.VI.1964; Magadansk Obl., Tolon, 7.VII.1975; Priamure, environs of S. [N.] Natalino, r. Zeja, 12.VII.1975; S.W. Siberia, Kolpashevo, 20.VII.1924; Vost. [E.] Kazakhstan, Nikolajevka, 30 km. Iu.V. [S.E.] Georgijevka, 23.VI.1979; Zabajkale, Bayan, 15.VII.1961.

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—The relationships of this species are unresolved, beyond inclusion within the *S. murarius* group.

### 5.1.3.1.3.23 *S. (Symmorphus) apiciornatus* (Cameron)

*Ancistrocerus apiciornatus* Cameron, 1911 (BMNH).

*Odynerus (Ancistrocerus) apiciornatus* (Cameron); Schulthess, 1934.

(—*apiciornatus* Cameron *sensu* Yasumatsu, 1938 = *S. decens*. —*apiciornatus* Cameron *sensu* Iwata, 1938 = ? *S. decens.*)

Type material examined.—LECTOTYPE (here designated), female labelled: "Type [circular red bordered label]"; "P. Cameron Coll./ 1914-110"; "Ancistrocerus/ apiciornatus/ Cam. Type/ Japan"; "B.M. TYPE/ HYM./ 18.322a" (BMNH). My lectotype label "LECTOTYPE [underlined in red]/ Ancistrocerus [female symbol]/ apiciornatus Cameron/ des. J.M. Cumming 1985 [black bordered label]" has been attached to this specimen.

PARALECTOTYPES: Japan-female, male [Nos. 18.322b & 18.322c] (BMNH). My paralectotype labels have additionally been attached to these specimens.

Reference by Soika (1975) to the lectotype in his redescription of the female of *S. apiciornatus* cannot be considered a valid designation, because Soika did not indicate to which of the two female syntypes he was referring. In addition no lectotype or paralectotype labels written by Soika were found on any of the three syntypes.

Recognition.—Particularly distinct because of the very finely striate posterior and lateral face of the propodeum (figs. 36, 37). Specimens of *S. decens* possess a similarly sculptured propodeum, but are easily differentiated by their clypeal apex. The lateral face of the propodeum of specimens of *S. alkimus* is also finely striate, however this species is readily distinguished from *S. apiciornatus* by the form of metasomal segment 2, which is typical for a member of the *S. hoozanensis* group.

Description.—*Female.* Measurements of largest and smallest specimens given in Table 2. Taxonomically important character states given in Table 4.

*Male.* Measurements of largest and smallest specimens given in Table 2. Taxonomically important character states given in Table 4.

Variation.—Specimens from Foochow and Sichuan Province in China, the most western known localities for *S. apiciornatus*, are larger and have much denser major punctation on the head, pronotum, mesoscutum and apex of metasomal tergum 2, than specimens found further east. Specimens from Korea however, are intermediate in both size and punctation, between more typical specimens and those from central China.

Geographical distribution and seasonal occurrence.—Known from central and eastern China, Primorskij Krai in USSR, South Korea and Japan (fig. 75). China: Foochow [Fuzhou], 16.V.1963; Kiangsu [Jiangsu Province], Chenu [Chenyu], 8.V.1935; Shanghai, V.1917; Szechwan [Sichuan Province], Behluhdin, 6000ft., 25.VII-1.IX.1937. Japan distribution widespread on the island of Honshu, earliest seasonal records—Kamakura, Kanagawa Pref., 29.IV.1955; Kobotoke, Minamitama dist., Tokyo [Pref.], 29.IV.1950; latest seasonal record—Juso, Osaka [Pref.]; 29.X.1929; most northerly records—Nama, Sekikawa V., Niigata [Pref.], 1.VI.1968; Yunohana, Aizu, Fukushima [Pref.], 9.VI.1978; most southerly record—Juso, Osaka [Pref.], 29.X.1929 (additional records, from Fukui and Hokkaido Prefectures, in Tsuneki, 1977). **South Korea**: Suigen [Suwon], 20.V.1927. **USSR**: Prim. Krai, Khr. [range] Sinij, Evseevka, Dolinnyj les, 21.VI.1978; Primore, environs of Anisimovki, 27.V.1974, 13.VI.1974; Zabajkale, Bayan Goz, 15.VII.1961.

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Beyond inclusion within the *S. murarius* group, resolution of the relationships of this species is unclear.

### 5.1.3.1.3.24 *S. (Symmorphus) allobrogus* (Saussure)

*Vespa bifasciata* Linnaeus *sensu* Fabricius, 1793. **Misidentification.**

*Odynerus bifasciatus* (Linnaeus) *sensu* Zetterstedt, 1838 ("var. a"); Thomson, 1874; Aurivillius, 1918; Blüthgen, 1938, 1943, 1952, 1961, 1965, 1967. **Misidentification.**

*Odynerus (Protodynerus) allobrogus* Saussure, 1855. Synonym of *Symmorphus bifasciatus* (Linnaeus) according to Blüthgen, 1938 (coll. Sichel, ? loc.). **Removed from synonymy.**

*Symmorphus bifasciatus* (Linnaeus) *sensu* Forsius and Nordström, 1923; Vecht and Fischer, 1972. **Misidentification.**

(—*allobrogus* Saussure *sensu* Dusmet, 1928 = ? *S. paralleliventris*.)

Notes about synonymy.—Numerous authors beginning at least with Fabricius (1793) have referred to this species as *S. bifasciatus* (Linnaeus), with Blüthgen synonymizing *S. allobrogus* (Saussure) under the Linnaean name in 1938. Although the type of *S. allobrogus* could not be located in the Saussure collection of MHNG, or the collection of MNHP (where some Sichel material resides), the original description leaves little doubt as to the identity of this species. Therefore, even if the type cannot be found, designation of a neotype should not be required. Since I do not regard the lectotype of *S. bifasciatus* (by designation of Day, 1979) as conspecific with *S. allobrogus*, as discussed under *S. bifasciatus*, I hereby remove these nominal species from synonymy.

Recognition.—Very similar to the Nearctic *S. cristatus* as discussed under "Recognition" of that species. In the Palearctic region, *S. allobrogus* is most likely to be confused with *S. connexus* and *S. debilitatus*, which are sympatric with *S. allobrogus* in the west. However, specimens of *S. allobrogus* are generally larger, possess more shallowly impressed major punctation on metasomal tergum 1, a prominent submedian propodeal carina ventrally (fig. 43) and a more deeply emarginate female clypeus (fig. 58). In addition, males of *S. allobrogus* are easily separated from males of *S. connexus* by the length of antennal article 13. Specimens of *S. allobrogus* also resemble those of *S. angustatus*, but do not possess lengthened setae and have a shorter antennal article 13 in the male.

Description.—*Female*. Measurements of largest and smallest specimens given in Table 2. Taxonomically important character states given in Table 4.

*Male*. Measurements of largest and smallest specimens given in Table 2. Taxonomically important character states given in Table 4.

Geographical distribution and seasonal occurrence.—Known to range from continental Europe (excluding the Iberian Peninsula, western France, Belgium and Netherlands), east through Asia, to Magadan Oblast and Primorskij Krai in eastern USSR (fig. 76). **Austria**: distribution widespread, earliest seasonal record—Nordtirol, Innsbruck, Mittelgebg., 13.V.1920; latest seasonal record—Bad Aussee, Oberstressen, 10.VIII.1960. **Czechoslovakia**: Bohemia, Chodau; Nova Sedlica, 49.03N 22.30E, 22-26.VII.1967; Tatranská Kotlina, Bellacoque Alpen, 3000ft., 18.VI.1932. **Denmark**: Strandm., NEZ. **Finland**: distribution widespread in south, earliest seasonal record—Lojo [Lohja], 5.VI.1918; latest seasonal record—Kb., Kitee, Aconitumlunden, 2.VIII.1970; most northerly record—Ks., Kuusamo, 14.VII.1973. **France** distribution widespread in east, earliest seasonal record—Le Boreon, S.E. France, 13-15.VI.1964; latest seasonal record—Massif centrale, 1000-1500 m., 9.VIII.1977; most westerly records—Maisons Laffitte, Seine & Oise, 20.VI; Massif centrale, 1000-1500 m., 9.VIII.1971. **Germany (BRD & DDR)**: distribution widespread in south, earliest seasonal record—Munichen, 10.V.1857; latest seasonal record—Allgäuger Alpen, Umg. Oberstdorf, 11.VII.1949; most northerly record—Thale a. Harz [Mts.], Kaiserblick, 5.VI.1953. **Hungary**: Retyezáth, 1000-1300ft., 24.V-4.VI.1937, 19-24.VI.1937. **Italy**: Alto Adige, Val Gardena, Ortisei, VI.1942; Dobbiaco, BZ., V.S. Silvestro, 12.VIII.1970; M. di Campiglio, 26.VIII.1939; Val Genova, 5.VII.1950. **Norway**: Surendal, Moen., 10.VII.1926. **Romania** Transsylvania, Cibinsgeb, Hohe Rimie, 22.VII. **Sweden**: distribution widespread, earliest seasonal record—Vb., Bodarna, 5.V.1938; latest seasonal record—Ly. Lpm., Sorsele, 15.VIII.1928; most northerly record—T. Lpm., Björkliden, 20.VII.1941. **Switzerland**: distribution widespread, earliest seasonal record—Wallis, Lotschental, 6.VI.1919; latest seasonal record—Valais, La Sage, Val d'Herens, 1700 m., 26.VIII.1960. **Turkey**: Erzurum, 20 km. Ispir-Ikizdere Rd., 1700 m., 2.VI.1962; Trabzon, Hamsikoy, 1245 m., 23.V.1962; Trabzon, Zigana Dagi, 4200-6000ft., 13,14.VII.1960, 9,10,10-14.VIII.1959. **USSR** Alma Arasan, Zailijsk[ij] Alatau, 8.VII.1971; Altai, r. Chulyshman pod goroj koo, 11.VII.1980; Buryatskaya, A.S.S.R., Iuzh. Oereg oz. [lake] Baikal, Boyarskij, 6.VIII.1977; Dorpat [Tartu]; environs of Jakutskaja, 25.VI.1962; environs of Moscow, 26.VI.1928; Iu.V. [S.E.] Kazakhstan, Khr. [range] Ketmen, environs of Podgornoje, 22.VII.1968; Kazakh S.S.R., Alma Ata (hills), 10.VII.1976; Kostroma, Mittel Russe; Kurland, Jelowka, 5,9,23,VI.1917; Leningrad, 2.VI; N. Caucasus, Dombai [Dombaj], 7.VII.1978; Ösel, Abro [Saaremaa], 3.VII.1899; Primore, environs of Anisimovki, 1.VII.1974; r. Omolon, 180 km. nizhe p. Omolon, Chukotka [Magadan Obl.], 17,23.VII.1976; Stavropolve, Teberda, 25.VII.1981; Ushch [canyon] Turgen, Zailijsk[ij] Alatau, 23,24.VII.1971; Zailijsk[ij] Alatau, bol, Alma Atinsk uiz., 21.VI.1972.

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Tentatively considered the sister species of *S. cristatus*, from which it differs only slightly.

### 5.1.3.1.3.25 *S. (Symmorphus) cristatus* (Saussure)

*Odynerus (Protodynerus) cristatus* Saussure, 1855 (BMNH).

*Odynerus (Protodynerus) pumilus* Saussure, 1855 (MHNG). **New synonymy.**

*Odynerus (Protodynerus) philadelphiae* Saussure, 1857 (MHNG).

*Nortonia nevadaensis* Cameron, 1905 (USNM).

*Symmorphus hornii* Cameron, 1909 (BMNH).

*Symmorphus cristatus nevadaensis* (Cameron); Bohart, 1951.

? *Symmorphus trisulcatus* Cameron, 1906 (? loc.). **New synonymy.**

Notes about synonymy.—Saussure (1855) described *S. pumilus* (p. 197, no. 93) from Cayenne, directly after describing *S. cristatus* (p. 196, no. 92) from North America. I have examined the apparently mislabelled holotype of *S. pumilus* (see below under "Type material examined") and regard it as conspecific with the holotype of *S. cristatus*. Since both nominal species have the same date of publication, *S. pumilus* is hereby selected as a junior synonym of *S. cristatus* according to Article 24(a) of the International Code of Zoological Nomenclature.

Although a male specimen from Nevada in the Cameron collection in BMNH is labelled as the type of *S. trisulcatus* Cameron, the location of the real type described from New Mexico is unknown (Soika, 1941; Bohart, 1965). Bohart (1965) determined the specimen in the BMNH as *S. meridionalis* Viereck, listing *S. trisulcatus* as a junior synonym of the former name. I have examined this specimen and regard it as conspecific with the holotype of *S. cristatus*. Since it agrees with Cameron's description, I tentatively consider *S. trisulcatus* a junior synonym of *S. cristatus*.

In addition, examination of the holotype of *S. nevadaensis* (Cameron) confirms Bohart's (1951) placement of this nominal species under *S. cristatus*. However, subspecific recognition of a yellow color form based on this type, as opposed to the white coloration observed in typical *S. cristatus*, is considered unwarranted, given that color pattern varies continuously over the range of the species (see below under "Variation") and populations distinguished on this basis alone are not distinct structurally.

Type material examined.—*Odynerus (Protodynerus) cristatus* Saussure, HOLOTYPE, female labelled: "Type [circular red bordered label]"; "Odynerus/ cristatus/ [female symbol] Sauss. [blue label in Saussure's handwriting]"; "B.M. TYPE/ HYM./ 18.528" (BMNH).

*Odynerus (Protodynerus) pumilus* Saussure, HOLOTYPE, male labelled: "HOLOTYPUS [red label]"; "[circular green label]"; "Symmorphus/ pumilus/ (Sauss.)/ type [male symbol]"; "Symmorphus/ cristatus (Sauss.)/ = pumilus (Sauss.)/ det. J.v.d.Vecht 1977"; "R.M. Bohart (i.l)/ agrees that this is/ a syn. of cristatus/ J.v.d.Vecht 1977"; "HOLOTYPE [underlined in red]/ Odynerus/ pumilus Saus./ [male symbol]" (MHNG).

Comparison of Saussure's original description of *O. pumilus* in 1855, with his subsequent redescription in 1875, suggests that both were based on the same male specimen or specimens. In the original description Saussure states that the specimen or specimens were collected from Cayenne and were deposited in the Museum of Neuchatel. However, in 1875 Saussure recorded *O. pumilus* from Peru only and indicated his personal collection as the type depository. No specimen with this name could be found in the Museum of Neuchatel (Vecht, personal communication), although a male specimen under the label "pumilus Sauss. Pérou" is present in Saussure's collection in MHNG. This specimen, which is without locality data, agrees well with both descriptions and is therefore probably the specimen Saussure had before him. Since this male belongs to the Nearctic species *S. cristatus* (Saussure), the records from Cayenne and Peru are considered incorrect[5].

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[5] Zavattari (1912b) additionally refers to two supposed specimens of *O. pumilus*

*Odynerus (Protodynerus) philadelphiae* Saussure, LECTOTYPE (here designated), female labelled: "[square metallic colored label]"; "Pensylv[anie]."; "TYPUS [red label]"; "LECTO-/ TYPE/ [female symbol] philadelphiae/ Sss./ (RMB) [red label] [unpublished invalid designation]" (MHNG). My lectotype label "LECTOTYPE [underlined in red]/ Odynerus [female symbol]/ philadelphiae Sauss./ des. J.M. Cumming 1984 [black bordered label]" has been attached to this specimen.

PARALECTOTYPES: Pensylv[anie].-2 females (MHNG, MNHP). The specimen in the collection of MNHP additionally bears the label "Odyner./ Philadel/ phiae [female symbol]/ Sss. n. sp./ Et Unis" in Saussure's handwriting. My paralectotype labels have been attached to these specimens.

Saussure (1857) apparently described *O. philadelphiae* from a series of specimens from Pennsylvania, without selecting a holotype. Two females from this locality, including the lectotype designated herein, reside under this name in Saussure's collection in MHNG. A third female from Pennsylvania, determined by Saussure, is in the collection of MNHP.

*Nortonia nevadaensis* Cameron, HOLOTYPE, male labelled: "Ormsby Co. Nev/ July, Baker"; "3453"; "Nortonia/ nevadaensis/ 3453 Cam. n.sp."; "HOLOTYPE [red label]" (USNM).

*Symmorphus hornii* Cameron, HOLOTYPE, female labelled: "Gunnison/ Col. Baker"; "5350"; "5349"; "Symmorphus/ hornii Cam./ Type Canada"; "P. Cameron Coll./ 1914-110"; "B.M. TYPE/ HYM./ 18.531" (BMNH).

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[5](cont'd) housed in the collection of ZMHB. The first, a female collected from Alasia, Chilial by Krause (not Hlascia, Chili, as indicated by Zavattari), is a white marked specimen of *S. cristatus*. As Alasia (or Hlascia) could not be located in Chile or elsewhere and since some of Zavattari's Neotropical records have been shown to be in error (Bequaert, 1941), I believe Krause collected the specimen in North America or perhaps Mexico. The second, a headless yellow marked male apparently collected from Cuba by Riehl, may also belong to *S. cristatus*, although Cuba is well outside the known range of this Nearctic species.

Recognition.—Distinguished from other New World members by features given in the key to species and subspecies of *S. (Symmorphus)*. Specimens of *S. cristatus* are exceedingly similar to those of *S. allobrogus* from the Palearctic region. They are generally differentiated by the shorter male antennal article 13 and larger more dense major mesoscutal punctation (particularly anteriorly) in *S. cristatus*. In addition, specimens over much of the range of *S. cristatus* have white to ivory markings (see below under "Variation"), while those of *S. allobrogus* are marked with yellow.

Description.—*Female*. Measurements of largest and smallest specimens given in Table 2. Taxonomically important character states given in Table 4.

*Male*. Measurements of largest and smallest specimens given in Table 2. Taxonomically important character states given in Table 4.

Variation.—Specimens from the northern and eastern portion of the range have primarily white to ivory markings (those from the southeastern portion of the range may have very light yellow markings). In the western portion of the range, from Montana, Idaho and Washington south, both specimens with white or yellow markings occur. Those with yellow markings predominate at lower elevations and throughout California, while those with white markings appear to occur at higher elevations.

Geographical distribution and seasonal occurrence.—Known transcontinentally in North America, from Alaska, Yukon Territory, Northwest Territories and Labrador in the north, to California, Arizona, New Mexico and North Carolina in the south (fig. 77). **Newfoundland**: Deer Lake, 28 mi. NW., 29.VI.1966; Donovan's, Avalon Peninsula, 21.VII.1954; Gander, 11.VIII.1949; Goose Bay, Labr., 23.VIII.1948. **Prince Edward Island** Dalvay House, Can. Nat. Pk., 19,22.VII.1940; Souris, VII.1967. **Nova Scotia** distribution widespread, earliest seasonal record—Victoria Co., Beinn Bhreagh, Baddeck, 26-28.VI.1977; latest seasonal record—Baddeck, 27.VIII.1926. **New Brunswick** Dalhousie, 24.VII.1915;

Fredericton; Nerepis, 22.VIII; North Minto, 19.VII.1978; St. John, 14.VII. **Quebec** distribution widespread in south, earliest seasonal record—Montreal, 29.IV.1908; latest seasonal record—St. Anne de la Porcatiere, 7.VIII.1914; most northerly records—Cap Shat, 8.VII.1954; Gracefield, 10.VI.1937; Laniel, 21.VI.1944; St. Anne de la Porcatiere, 7.VIII.1914; Stoneham, 21.VI.1938. **Ontario**: distribution widespread, earliest seasonal record—Trenton, 28.V.1896; latest seasonal record—Thor Lake, 20-30.VIII.1927; most northerly records—Berens River, 5 mi. S. Lake Pikangikum, 8.VII.1958; Black Sturgeon Lake, 25.26.VI.1962; Kenora, 17-27 mi. S.E., 17,19,25.VII.1968, 26.VII.1976, 5.VIII.1967, 8.VIII.1968, 9.VIII.1972, 11.VIII.1970; Sudbury, 15.VI.1889, 16,18.VI.1892, 12.VII.1889; Thor Lake, 20-30.VIII.1927. **Manitoba** distribution widespread in south, earliest seasonal record—Shilo, 5 mi. S.W., 28.V.1958; latest seasonal record—Audy Lake, Riding Mtn. Nat. Pk., 12.VIII.1958; most northerly records—Cedar Lake, 29.VI.1940, VII.1936; Gillam, 22.VII.1949; Gypsumville, VI.1967; Husavik, 5.VII.1910. **Saskatchewan**: distribution widespread in south, earliest seasonal record—Regina, 30.VI.1979; latest seasonal record—8.VIII.1975; most northerly records—Prince Albert Nat. Pk., 23.VII.1937; Saskatoon, 9.VII.1957, 22.VII.1937, 1.VIII.1960; Wallwort, 17.VII.1942; Waskesiu Lake, 15.VI.1938, 1,2.VIII.1939. **Alberta** distribution widespread, earliest seasonal record—Edmonton, 20.V.1937; latest seasonal record—Lethbridge, 13.IX.1924; most northerly records—McMurray, 22.VI.1953; Slave Lake, 25.VIII.1924. **Northwest Territories** Aklavik, 8,15,25.VII.1931; Enterprise, 28.VII.1967; Fort Simpson, 20.VII.1950; Fort Smith, 18.VIII.1950; Fort Wrigley, McKenzie R., 31.VII.1922; Ft. McPherson, 4.VII.1957; Ft. Providence, 1.VIII.1907; Norman Wells, 28.VII.1949; Rae, 26.VII.1968. **Yukon Territory**: Dawson, 14 mi. E., 1300ft., 2.VIII.1962; Gravel Lake, 58 mi. E. Dawson, 2050ft., 13.VIII.1962; Rampart House, 16.VII.1951; Ross River, 61.56N, 3000ft., 22.VI.1960. **British Columbia**: distribution widespread, earliest seasonal record—Lower Post, 17.VI.1920; latest seasonal record—Terrace, IX.1920; most northerly records—Atlin, 9.VII.1929, 30.VII.1955, 2.VIII.1955, 12.VIII.1929; Lower Post, 17.VI.1948; Summit Lake, 7,16-19,27.VII.1959. **Alaska**: Anchorage, 15.VI.1921; Ft. Richardson, 16.VII.1948; Haines, 17.VII.1954; Ketchikan; Matanuska, 20.VII.1945; Shaw Crk., m289 Rich. Hwy., 12.VII.1951; Skagway, 1,23,29.VII.1923. **Arizona:** Grand Canyon, N. Rim, 7000ft., 4.VI.1946; Greer, Phelps M., 9000ft., 23.VII.1953; Kaibab, 26.VI.1937; Jacobs Lake, 18.VI.1958; nr. Alpine, 24.V.1947; Ramsay Canyon, 15 mi. S. Sierra Vista, Huachuca Mts., 6000ft., 5.VI.1968. **California**: distribution widespread in north, earliest seasonal record—Berkeley, 3.V.1947; latest seasonal record—Alpine Co., Iceberg Meadow, 6400ft., 24.VIII.1976; most southerly records—Chino, 25.V.1904; Glacier Lodge, Inyo Co., 30.VII.1953. **Colorado** distribution widespread in west, earliest seasonal record—Boulder, 8.V.1934; latest seasonal record—Steamboat Springs, 6800ft., 1.X.1950; most easterly records—Boulder, 8.V.1934, 14.V.1919, 11.VI.1904, 14.VI.1919, 16,18.VI.1924, 13.VII.1922; Conejos Co., 17.VII.1932; Evergreen, 2.VII.1941; Florissant, 22.VI.1902, 26.VI.1907, 16.VII; Fremont Co., 6 mi. S. Coaldale, 7500ft., 10.VIII.1964; Ft. Collins, 11.V.1904, 11.VI.1904. **Connecticut** Colebrook, VIII.1918; Lakeville, 18.VII.1938, 12.VIII.1939. **Idaho** distribution widespread, earliest seasonal record—Webb, Nez Perce Co., 29.III.1951; latest seasonal record—Franklin Co., Cub River Can., 12.VIII.1973. **Illinois** Algonquin, 26.V.1894, 14.VI.1895; Chicago, 30.V.1899. **Indiana**: [no additional data]. **Maine**: distribution widespread, earliest seasonal record—Aroostock Co., 10 mi. N. Houlton, 24.VI.1966; latest seasonal record—Kokadjo, Piscataquis Co., 24.VII.1973. **Maryland** N.W. Branch Pk., Mont. Co., 18.VII.1976. **Massachusetts**: distribution widespread, earliest seasonal record—Ashburnham, 18.V.1918; latest seasonal record—Laurel Mt., 17.VII.1914. **Michigan:** distribution widespread, earliest seasonal record—Ann Arbor, 20.V.1962; latest seasonal record—Keweenaw Co., Isle Royale, 25.VIII.1938. **Minnesota** distribution widespread in north, earliest seasonal record—Houston Co., 21.V.1938; latest seasonal record—Itasca Co., I-58, R-24, S-35, 11.VII.1973; most southerly records—Houston Co., 21,23.V.1938; Itasca, VII.1908; Red Lake Falls, 9.VI.1934. **Montana**: distribution widespread, earliest seasonal record—Flathead Nat. Forest, 16.VII.1946; latest seasonal record—Madison River, Gallatin Nat. Forest, 17.VIII.1948. **Nebraska**: West Point. **Nevada**: distribution widespread, earliest seasonal record—Reno, Washoe Co., 9.V.1959; latest seasonal record—Cobb Crk., 6 mi. S.W. Mtn. City, Elko Co., 6550ft., 24.VII.1935. **New Hampshire**: distribution widespread, earliest seasonal record—Nelson, 15.VI.1907; latest seasonal record—Northwood, Rockingham Co., 7.VIII.1957. **New Jersey**: Bergen Co., Tenafly. **New Mexico**: Bear Trap Camp, 28 mi. S.W. Magdalena, Socorro Co., 8500ft., 10-12.VIII.1965; Little Tesuque Cañon, vic. Santa Fe, 9200ft., 27.VII,10.VIII.1932; San Miguel Co., 4 km S. Cowles at Jct. Nora and Pecos rivers, 2408m, 4.VII.1978; Taos Hondo Can., 9000ft., 15-24.VI.1930. **New York**: distribution widespread, earliest seasonal record—Tompkins Co., 6-mile Crk., S.E. Ithaca Reservoir, 26.V.1968; latest seasonal record—Heart Lake, Essex Co., 30.VII.1940. **North Carolina**: Black Mt., V; Highlands, 3800ft., 6.VI.1957. **Ohio**: Franklin Co., 7.VI.1942; Licking, V.1926. **Oregon**: distribution widespread, earliest seasonal record—Benton Co., 5 mi. N.W. Corvallis, 11.V.1973; latest seasonal record—Greater Lake Pk., Sun Meadow Crk., 6500-7000ft., 3.IX.1930. **Pennsylvania**: Oak Station, Alleg. Co., Pittsburg; Perry Co., 1.8 mi. N.W. New Bloomfield, 28.VI.1969. **South Dakota**: Custer; Flynn Crk., 8 mi. N. Pringle, 5400ft., 8,9.VII.1961; Harney Peak, 21,22.VII.1924, Lawrence Co., Savoy, 5.VIII.1972. **Utah**: distribution widespread, earliest seasonal record—Wellsville, 10.V.1949; latest seasonal record—Mt. Logan, 9000ft., 18.VIII.1955. **Vermont**: Cornwall; Fairlee, L. Morey; Newport, 12.VII.1891; Stowe, Lamoille Co.; W. Danville, Caledonia Co., 8.VIII.1957. **Virginia**: Glencarlyn, 17.VI. **Washington**: distribution widespread, earliest seasonal record—Asotin, 4.VI.1930; latest seasonal record—Mt. Ranier, 4700ft., 17.VIII.1940. **West Virginia**: Cheat Mt., 2000ft., VI; Cranberry Glades, 13.VI.1955; nr. Greenland Gap, Grant Co., 16.VII.1937; Pocahontas Co., Cranberry Glades, 1.VII.1967. **Wisconsin**: Sauk Co., Sauk City - hills across river, 16.VI.1961; Tenderfoot Lake, Vilas Co., VII.1912. **Wyoming**: distribution widespread, earliest seasonal record—Wawona, Yellowstone Nat. Pk., 21.V.1938; latest seasonal record—Nash Crk., Medicine Bow NF, S.W. Albany Co., 11.VIII.1967.

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Probably the sister species of *S. allobrogus*.

### 5.1.3.1.3.26 *S. (Symmorphus) gracilis* (Brullé)

*Odynerus gracilis* Brullé, 1832. Lectotype, male, designated by Blüthgen, 1963 (MNHP).

*Odynerus elegans* Wesmael, 1833 (IRSN).

*Symmorphus elegans libanicus* Soika, 1963 (BMNH). **New synonymy**.

*Symmorphus gracilis libanicus* Soika; Vecht and Fischer, 1972.

? *Odynerus elegans* Herrich-Schaeffer, 1838. Homonym of *Odynerus elegans* Wesmael, 1833 (destroyed).

Notes about synonymy.—[illegible]hgen (1938, 1952, 1963) listed *S. elegans* (Wesmael), described in 1833 from Belgium, as a junior synonym of *S. gracilis* (Brullé), described in 1832 from Greece, although he expressed doubt about the identity of *S. gracilis* in 1961. I have examined the lectotype of *S. gracilis* (by designation of Blüthgen, 1963) and regard it as conspecific with the lectotype of *S. elegans* (Wesmael).

Although the type of *S. elegans* (Herrich-Schaeffer) appears to have been destroyed with the Herrich-Schaeffer collection (Vecht and Fischer, 1972), this nominal species is probably also conspecific with *S. gracilis*, based on the description given by Herrich-Schaeffer in 1838.

In addition, subspecific recognition of the densely punctate Middle Eastern population described by Soika (1963) as *S. elegans libanicus*, is considered unwarranted, given that punctation varies continuously over the range of *S. gracilis* (see below under "Variation") and numerous intermediate forms exist between this peripheral population and more typical *S. gracilis*.

Type material examined.—*Odynerus gracilis* Brullé, LECTOTYPE (by designation of Blüthgen, 1963), male labelled: "Museum Paris/ Morée [Pelopónnisos]/ Brullé 4187-33"; "Odynerus/ gracilis Br/ Morée"; "TYPE/ de O. gracilis"; "HOLOTYPE [red label]"; "Odynerus/ gracilis [male symbol]/ Brullé Lecto-/ Blüthgen det. 1962/ [on reverse side] holotypus" [antennae each without articles 4-13] (MNHP).

PARALECTOTYPE: Morée [Pelopónnisos]-male [right antenna without articles 2-13] (MNHP).

*Odynerus elegans* Wesmael, LECTOTYPE (here designated), female labelled: "Type Wesmael"; "O. elegans mihi [in Dubois' handwriting]/ dét. C. Wesmael"; "Symmorphus/ elegans Wesm: [female symbol]/ rév. Ed. Dubois 1920" (IRSN). My lectotype label "LECTOTYPE [underlined in red]/ Odynerus [female symbol]/ elegans Wesmael/ des. J.M. Cumming 1984 [black bordered label]" has been attached to this specimen.

PARALECTOTYPES: [without locality labels, same labels as lectotype]-female [smaller than lectotype], 3 males (IRSN). My paralectotype labels have additionally been attached to these specimens.

Wesmael (1833) based his description of *O. elegans* on an undetermined number of female and male specimens from Belgium. Although a number of specimens from the Wesmael collection in IRSN bear this name, most do not agree with the detailed original description and were probably added later. In addition to the lectotype and paralectotypes designated herein, two other specimens (a female and a male) agree with the original description and could potentially be considered syntypes. However, each bears the determination label "O. elegans Wesm" rather than "O. elegans mihi/ dét. C. Wesmael" suggesting they were determined subsequent to Wesmael's description.

*Symmorphus elegans libanicus* Soika, HOLOTYPE, female labelled: "N. Lebanon/ Cedars/ 4.7.[19]60"; "HOLOTYPUS/ Symmorphus/ elegans/ libanicus G.S. [red label]"

(BMNH).

ALLOTYPE, male labelled: "N. Lebanon/ Cedars/ 6.7.[19]60"; "ALLOTYPUS/ Symmorphus/ elegans/ libanicus G.S. [red label]" (BMNH).

PARATYPE: N. Lebanon, Cedars, 6.VII.[19]60-male (ZSBS).

Recognition.—Very similar to *S. paralleliventris* as discussed under "Recognition" of that species. In addition to features given in the key to species and subspecies of *S. (Symmorphus)*, specimens of *S. gracilis* are distinguished from those of most other species of *Symmorphus* by the moderately projected nearly acute to acute humeral angle of the pronotum (fig. 17).

Description.—*Female*. Measurements of largest and smallest specimens given in Table 2. Taxonomically important character states given in Table 4.

*Male*. Measurements of largest and smallest specimens given in Table 2. Taxonomically important character states given in Table 4.

Variation.—Specimens from Lebanon, one of the most southerly parts of the range of *S. gracilis*, have larger more dense punctation on the dorsal mesepisternum and metasomal tergum 2, than specimens from localities to the northwest or northeast, with intermediate specimens occurring in both Turkey and Iran. In addition, specimens from southern Spain, the southern most portion of the range in the west, also have relatively large dense punctation on metasomal tergum 2.

Geographical distribution and seasonal occurrence.—Known to range from Europe, east through western Asia, to the Soviet Tien Shan and Himalaya of northwestern India (fig. 78). **Austria**: distribution widespread, earliest seasonal record—Salzburg, Parsch, 29.V.1969; latest seasonal record—Styria, Tragöss-oberort, 18.VIII.1977. **Belgium**: distribution widespread, earliest seasonal record—Celles, 11.V.1897; latest seasonal record—Houyet, 2.VIII.1952. **Czechoslovakia:** Bohemia centr., Zavist, 11.VI.1964; Chlum u Trˇeb. Bohemia, 16,22.VI.1962, 4.VII.1970, 18,30.VII.1960, 19.VII.1962; CSR Slovakia, Jablonn, 1937. **Denmark**: distribution widespread, earliest seasonal record—Hareskov, 14.VI.1932; latest seasonal record—Kongsón, 27.VII.1941. **France**: distribution widespread, earliest seasonal record—Ollioules, 2.V.1954; latest seasonal record—St. Enimie, Anvergne, 5.IX.1958. **Germany (BRD & DDR)**: distribution widespread, earliest seasonal record—Saxonia, Leipzig, Connewitzer Holz, 31.V.1947; latest seasonal record—Umg. Starnberg, 24.VIII.1939. **Greece** distribution widespread in north, earliest seasonal record—Delphi, 12.IV.1963; latest seasonal record—Timfristos, 4700ft., 17.VII.1976; most southerly record—Peloponnes[us]. **Hungary:** Baranya-megya, Nagyharsany, 22.VI.1963; Budapest, 29.VIII.1960. **India:** Kashmir, Gulmarg [34.03N 74.23E], Summer of 1913. **Iran**: Elburs, 75 km. S. Chalus, 2400 m., 13.VII.1977. **Italy**: Lazio, Gerouio, 15.V.1944; Pracchia, 650 m., 15-20.VI.1955; Sicily, Piano Battaglia, Pa., 5000ft., 3.VII.1972; Trentino Segadi Ala. **Lebanon:** N. Lebanon, Cedars, 3,25,29,30.VI.1960, 3,4,6.VII.1960; N. Lebanon, Kadisha, 25.VI.1960. **Netherlands** distribution widespread, earliest seasonal record—Epen, Z.L., 20-30.V.1946; latest seasonal record—Epen, Z.L., 9.VII.1924. **Poland:** Muszkowice, pow Zabkowice Sl., 30.VI.1952. **Portugal**: Lisboa [Lisbon], 19.IV.1946. **Romania**: Comana Vlasca. **Spain**: distribution widespread, earliest seasonal record—Granada, Rio Guadalfeo, Orgiva, 300 m., 19.IV.1966; latest seasonal record—Camprodón, VII.1919; most southerly records—Granada, Rio Guadalfeo, Orgiva, 300 m., 19.IV.1966; Granada, Rio Lanjaron, near Lanjaron, 600 m., 14-16.VII.1982; S. Spain, Ronda, 1000 m., 1-5.VI.1974. **Sweden**: distribution widespread in south, earliest seasonal record—Båstad, 10.VI.1937; latest seasonal record—Ol., Gärdslosa Bägby, 9.VIII.1970; most northerly records—Björkö Uppl., 4,7,8,22.VII.1936; Vstm., Köping, 25.VI.1973, 3,VII.1973, 10.VII.1977. **Switzerland** distribution widespread, earliest seasonal record—Canton de Vaud, Cudrefin, 435 m., 30.VI.1972; latest seasonal record—Stalden, Wallis, 20.VII.1928. **Turkey:** distribution widespread, earliest seasonal record—Aydin [district], Bozdogan, 200 m., 22.IV.1962; latest seasonal record—Arguslu, above

Niksar, 2100ft., 28.VII.1959; most southerly records—Amanus Mts., Sertavul Gecidi, 4500ft., 22.VI.1960; Ankara [Antalya district], Karagol, 1200 m., 22.VI.1962; Ankara [Antalya district], Karagol Lake, 3500ft., 26.VI.1960; Aydin [district], Bozdogan, 200 m., 22.IV.1962. **United Kingdom (& Ireland)**: distribution widespread in England and Wales, north to southern Scotland, earliest seasonal record—Bricketwood, Herts., 22.V.1927; latest seasonal record—Porthcawl [Mid Glamorgan], 3.VIII.1903; most northerly record—Rx. [Roxburgh], 4.VII.1944. **USSR**: Borisowka, Ukraine, Russ. mer., 14.VI.1927; environs of Kiev, Feofaniya, 5.VI.1979; Kazakh S.S.R., Alma Ata (Medeo), 24.VII.1976; Krym Pionerskoe [? location], 21.VI.1976, 3.VII.1976; Monastero[.] Gherard [collector ?], Armenia, 19.VII.1963; Turkestan Merid. Capus, 1881; Zapov. Aksu-Dzhabagly, Iu. [S.] Kazakhstan, Chimkentskaya Obl., 15.VI.1965, 15.VI.1966, 1.VII.1966, 13.VII.1965. **Yugoslavia** Bistra Planina, nr. Mavrovo, 1700 m., Macedonia, 25.VI.1965; Katlanovska Banja, Macedonia, 5,6.VI.1965; Montenegro, Durmitor, 1894, 1904; Stolac.

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Inferred to be the sister species of *S. paralleliventris*.

### 5.1.3.1.3.27 *S. (Symmorphus) paralleliventris* Soika

*Symmorphus paralleliventris* Soika, 1953 (NHMV).

? *Odynerus allobrogus* Saussure *sensu* Dusmet, 1928. **Misidentification.**

Notes about synonymy.—Dusmet (1928) records a female specimen of *S. allobrogus* (Saussure), identified for him by Schulthess, from Tunisia. This specimen probably belongs to *S. paralleliventris* Soika, the only member of the genus known from Tunisia, as specimens of *S. allobrogus* have not been found south of Turkey.

Type material examined.—HOLOTYPE, female labelled: "Tunis/ Graeffe 1905"; "HOLOTYPUS/ Symmorphus/ paralleliventris/ A. Giordani Soika [red label]" (NHMV).

PARATYPE: Maroc, G[ran]d Atlas, Ijoukak, 9.V.1947, J. de Beaumont-female (MSNV).

Recognition.—Most similar to *S. gracilis*. Other than the shape of metasomal sternum 2 and differences in distribution, specimens of *S. paralleiiventris* are most readily distinguished from those of all but the most southerly occurring populations of *S. gracilis*, by the more closely spaced deeply impressed foveolate major punctures of metasomal tergum 2.

Description.—*Female*. Measurements of largest and smallest specimens given in Table 2. Taxonomically important character states given in Table 4.

*Male*. Measurements of largest and smallest specimens given in Table 2. Taxonomically important character states given in Table 4.

Geographical distribution and seasonal occurrence.—Known from the Atlas Mountains of northern Africa (fig. 78). In addition to the holotype, which is without seasonal data, and the paratype, which was collected in May, 17 male and five female specimens have been examined. **Morocco**: Asni bij Marrakech, 28.V.1953 (RNHL); Grand Atlas, Idni, 8.V.1944 (BMNH, MSNV); Haut Atlas, Jb. Ayachi, Mikdane, Maison Forestière, Cedar forest S. of M.F., 2700 m., 10.VII.1963 (BMNH); Idni, 1750 m., 28.V.1983 (GUIC, JMCU); Moyen Atlas, Ifrane, VI.1949 (MNHP); **Tunisia**: Alin Draham [Ain Draham], 1600 m., 18.V.1981 (PAGC); N. Tunisia, D.J.B. Kornine, 1500ft., 4.VI.1980 (GUIC, JMCU); N. Tunisia, Zaghouan, 600ft., 13.VI.1980 (GUIC); Tunis, 20.V (MNHP).

Chorological affinities.—See Tables 5 and 6.

Phylogenetic relationships.—Apparently most closely related to *S. gracilis*.

## 5.2 Species Excluded from *Symmorphus* Wesmael

*Odynerus (Symmorphus) latipennis* Smith (1857) and *Odynerus (Symmorphus) cilicius* Cameron (1901) (see Meade-Waldo, 1910), known only from females and both described from Sarawak, are excluded from the genus *Symmorphus* Wesmael because members of both species lack a longitudinal furrow and distinct transverse carina on metasomal tergum 1. In my opinion these two species belong to a yet undescribed genus.

# 6. EVOLUTIONARY HISTORY

## 6.1 Phylogenetic Interpretation

### 6.1.1 Monophyly of *Symmorphus* and relationships to remainder of Eumeninae

The monophyly of *Symmorphus* is supported by the development of both a transverse carina and median longitudinal furrow on metasomal tergum 1, widely separated or enlarged cephalic foveae filled with setae and a simple male antennal apex, linking members of the genus. However, as discussed by Carpenter and Cumming (1985) in their analysis of 43 eumenine character systems and Cumming and Leggett (1985) in a study of the cephalic foveae, these apotypic states occur in, or are approached by, those of other Eumeninae.

Development of a median longitudinal furrow on metasomal tergum 1 occurs only in *Symmorphus*, although as indicated by Carpenter and Cumming (1985) a transverse carina has evolved a number of times within the Eumeninae. The furrow however, appears to be an apotypic modification of a slight apical medial indentation present in many genera, that is probably part of the ground-plan of the subfamily (Carpenter and Cumming, 1985). Cephalic foveae similar to those in *Symmorphus*, apparently are present only in some species of *Paralastor* and many but not the most plesiotypic members of a monophyletic clade containing *Odynerus*, *Pterocheilus* and related genera (Cumming and Leggett, 1985). Thus these similar foveal states most probably evolved independently in each distinctly different group. In addition, most eumenine genera, including those considered very plesiotypic for the subfamily, are characterized by a hooked and/or coiled male antennal apex, or occasionally by reduction in size or number of terminal articles (Carpenter and Cumming, 1985). A few genera however, have males like *Symmorphus* that possess 13 articles and an unhooked or uncoiled apex (e.g.

*Raphiglossa, Psiliglossa, Raphiglossoides, Hypancistrocerus*, some *Pterocheilus* and some *Hypalastoroides*). However, the terminal articles in these taxa are either modified in shape, unlike those in *Symmorphus* and are probably not homologous, or if similar, belong to taxa (e.g. *Raphiglossoides*) that on the basis of other characters are presumably quite distantly related to *Symmorphus* (see Carpenter and Cumming, 1985). Therefore together the apotypic states discussed above, although not necessarily unique to *Symmorphus*, clearly indicate the monophyly of the genus.

The phylogenetic position of *Symmorphus* within the Eumeninae is less clear than the question of monophyly. Judging from the diagram of generic affinities published by Soika (1941 p. 160) and the classifications employed in catalogues of Palearctic (Vecht and Fischer, 1972) and Nearctic (Krombein, 1979) Eumeninae, a relationship near *Ancistrocerus* has generally been assumed. Evidence for this relationship is based entirely on possession of a similar transverse carina on metasomal tergum 1 in members of both genera. However as Carpenter and Cumming (1985) demonstrate, this carina has evolved independently numerous times within the subfamily and although useful in delimiting genera, is decidedly unreliable when attempting to relate them.

Unable to find convincing synapotypies linking *Symmorphus* to any other eumenine group, Carpenter and Cumming (1985) tentatively hypothesized a sister group relationship to a monophyletic clade containing *Odynerus, Pterocheilus* and related genera, based on possession of similar apotypic states of the cephalic foveae. However, subsequent detailed examination of this character system by Cumming and Leggett (1985) indicates that these foveal modifications most probably developed convergently within the *Odynerus-Pterocheilus* lineage as well as in a few species of *Paralastor*.

Presence in *Symmorphus* of a simple male antennal apex, in addition to use of larval curculionid provisions by some species, could potentially be interpreted as evidence for an extremely early eumenine origin. A simple male antennal apex is present in all non-eumenine

Vespidae, except some Polistinae (Carpenter and Cumming, 1985), while *Euparagia*, the most plesiotypic extant vespid (Carpenter, 1981), mass-provisions with curculionid larvae (Williams, 1927; Clement and Grissell, 1968).

As discussed by Carpenter and Cumming (1985) however, a hooked male antennal apex is widespread in Eumeninae including those genera considered very plesiotypic on the basis of other characters. Therefore the condition of the male antenna in *Symmorphus* most probably represents an apotypic reversal to the state seen in other vespids rather than a plesiotypic retention, with the hook, coil or perhaps other apical modification having been lost. Similar transformations are clearly indicated within a few eumenine genera such as *Pterocheilus* and *Hypalastoroides*, where males of a few species lack either an apical hook or coil. Furthermore, although a few species of *Symmorphus* are reported to mass-provision with curculionid larvae similar to *Euparagia*, all except *S. fuscipes* (known from only a single report on nesting behavior) additionally use chrysomelid and/or microlepidopterous larvae, like other species of *Symmorphus* in which nesting behavior has been studied. Considering that use of lepidopterous prey is inferred to be plesiotypic in Eumeninae (Kurzenko, 1980; Carpenter and Cumming, 1985), occasional use of curculionid larvae by a few species of *Symmorphus* cannot be considered a primitive trait and is more likely opportunistic.

Although an extremely early eumenine origin for *Symmorphus* and close relationship with either *Ancistrocerus* or the *Odynerus-Pterocheilus* clade are rejected here, alternate hypotheses concerning the phylogenetic position of *Symmorphus*, such as the one proposed below, should be considered tentative given the lack of convincing synapotypies linking the genus to other eumenine groups.

In a cladistic analysis of the Eumeninae based primarily on Nearctic genera, Carpenter and Cumming (1985) hypothesize an early origin for the lineages that include the 'Zethinae' (including *Ctenochilus*) and 'Raphiglossinae' (including *Raphiglossoides*) of authors. This complex of genera, which they refer to as the 'stem group' of the Eumeninae (fig. 79), contains overall the most plesiotypic genera in the subfamily. The remaining genera correspond to the 'Eumeninae' of authors and are considered by Carpenter and Cumming (1985) to be composed of two major lineages. The first is equivalent to *Eumenes sensu lato* (i.e. *Eumenes* in the old sense, including all genera that have been removed from it) and retains in its members many of the plesiotypies found in the stem group. The second corresponds to Carpenter and Cumming's *Montezumia-Microdynerus* component established on the basis of Nearctic genera, although probably containing nearly all remaining eumenine genera when additional faunal regions are considered (see discussions in Carpenter and Cumming, 1985 and Cumming and Leggett, 1985). The monophyly of this large group of genera although supported by a basomedian longitudinal sulcus on metasomal sternum 2, five-toothed female mandible and dentiform hind coxal carina, is substantiated primarily by the presence of cephalic foveae in females, although secondary loss or reduction must be inferred in each of these states in various included taxa (Carpenter and Cumming, 1985; Cumming and Leggett, 1985).

Presence of female cephalic foveae and a dentiform hind coxal carina in members of *Symmorphus* clearly indicate relationship within the so-called *Montezumia-Microdynerus* lineage, even though the basomedian sulcus of metasomal sternum 2 is lacking and females of *S. (Parasymmorphus)* possess only four teeth on each mandible. The phylogenetic position of *Symmorphus* in this assemblage however, is more uncertain.

Presence of a posteriorly produced propodeal valvula that is free distally from the posterolateral projection of the submarginal carina in members of *S. (Parasymmorphus)*, potentially suggests a link with a diverse group of included genera referred to by Carpenter and Cumming (1985) as the *Stenodynerus-Microdynerus* component, since many members also possess a similar submarginal carina and valvula (Carpenter and Cumming, 1985). However, this apotypic condition exhibits considerable homoplasy throughout Eumeninae (Carpenter and Cumming, 1985) and is probably not part of the ground-plan of *Symmorphus*, but an independent apotypy of *S. (Parasymmorphus)*, as discussed below under "Characters and states".

Furthermore, if ground-plan states of *Symmorphus* are considered, the ancestor of the genus appears to have been at a very primitive grade of evolution compared with those of most other members of the *Montezumia-Microdynerus* lineage. As justified below under "Characters and states", members of a proto-*Symmorphus* stock probably possessed a four-toothed female mandible, male antenna with tyloids, complete epicnemial carina and depressed apical margin on both metasomal tergum 1 and segment 2. These states are possessed by no other (e.g. tyloids) or relatively few members of the *Montezumia-Microdynerus* assemblage, although they are widespread in the stem group of the Eumeninae and *Eumenes sensu lato* (Soika, 1969, 1978; Carpenter and Cumming, 1985). In addition, unlike most genera in the *Montezumia-Microdynerus* lineage, all members of *Symmorphus* lack a basomedian longitudinal sulcus on metasomal sternum 2 as do the plesiotypic taxa of the Eumeninae and all other vespids (Carpenter and Cumming, 1985).

Although loss of the basomedian sulcus of metasomal sternum 2 and reduction from five to four female mandibular teeth are both indicated in some included taxa of the *Montezumia-Microdynerus* assemblage (Carpenter and Cumming, 1985), explanations relying on homoplasy in the form of reversal for all these potentially plesiotypic states in *Symmorphus*, seem highly unlikely given the number of different characters involved. Reversal in the majority of these characters is additionally improbable, because with the exception of the mandibular teeth and sternal sulcus, none involves regression through loss or reduction, so that each structural feature would have to have been re-acquired once lost.

The evidence therefore, although far from overwhelming, suggests a relatively early origin for *Symmorphus* near the base of the *Montezumia-Microdynerus* assemblage (fig. 79), presumably before the evolution of the apotypies that distinguish many of the major component lineages of this extremely diverse group of eumenine genera. Greater resolution of both the ground-plan of *Symmorphus* and the evolutionary transformations of characters involved near the base of the *Montezumia-Microdynerus* lineage, will hopefully be attained when relationships of the genera of this large group are analyzed on a world-wide basis.

### 6.1.2 Reconstructed phylogeny of *Symmorphus*

#### 6.1.2.1 Methods used for phylogenetic reconstruction

The hypothetico-deductive approach used here to reconstruct the phylogenetic relationships of the component taxa of *Symmorphus* follows the cladistic method originally elaborated by Hennig (1965, 1966). This method, which has undergone subsequent development by numerous authors, is fully discussed in its contemporary form by both Nelson and Platnick (1981) and Wiley (1981). Character states were defined for each character and inferred to be ancestral (plesiotypic), or derived (apotypic) through outgroup comparison. Monophyletic groups (*sensu* Hennig, 1966) were then recognized on the basis of shared derived states (synapotypies) arranged into a succession of nested hierarchies, in an attempt to produce a cladogram of character evolution that maximized congruency and minimized homoplasy among the states being considered.

Since the phylogenetic position of *Symmorphus* within the Eumeninae is somewhat uncertain, with the exact sister group relationship still undetermined (see "Monophyly of *Symmorphus* and relationships to remainder of Eumeninae"), outgroup comparisons based on examination of over 475 species representing at least 125 (or over 75% of known remaining) eumenine genera, were conducted over the course of this study. In addition, much of the character analysis drew heavily upon the results of a study by Carpenter and Cumming (1985), in which states of approximately 1100 species of Eumeninae were examined. Remaining members of the *Montezumia-Microdynerus* lineage provided outgroup comparisons to a closely related group, while together members of *Eumenes sensu lato* and the stem group of the Eumeninae provided more phylogenetically removed comparisons (fig. 79). States found in some members of *Symmorphus* and most members of the *Montezumia-Microdynerus* assemblage were generally considered plesiotypic, especially if they were also present in members of *Eumenes sensu lato* or the stem group. In addition, members of *S.* *(Parasymmorphus)* or *S.* *(Symmorphus)*, were each considered as part of the outgroup of the alternate subgenus (similar to the functional ingroup/ functional outgroup analysis described by Watrous and Wheeler, 1981) when polarities were determined for states important at lower hierarchical levels (i.e. within each subgenus). Outgroup comparisons however, did not always yield unequivocal determinations of character state polarity, depending on the variability or distribution of states in the outgroup. In these instances distribution of states within *Symmorphus* and other criteria, such as Dollo's principle that structures once lost are seldom regained, were sometimes helpful is assessing the direction of change.

Of the 37 characters listed in Tables 3 and 4, 28 are considered suitable for phylogenetic analysis. The remaining characters although useful diagnostically, are excluded from the analysis because polarities of the states could not be determined, or exhibit too much variation within species to be considered important indicators of relationship, or the derived state is confined to a single species. Beyond exclusion of certain characters, a rigorous character weighting system, such as that proposed by Hecht and Edwards (1977), has not been used. Rather, the phylogenetic reliability of incongruous characters is evaluated with discussion of alternative schemes of relationships, where appropriate.

### 6.1.2.2 Characters and states

Characters considered suitable for phylogenetic analysis are denoted in Tables 3 and 4 by a "†", and are fully listed with all their included states. For each character the inferred plesiotypic state is given as "0", with hypothesized transformation series depicted by successive numbering of apotypic states, in both a positive and negative direction away from "0" when separate transformation series are involved. A state denoted by an "*" is inferred to be an apotypic loss of a more plesiotypic state, without indication of the exact state lost. Justifications for the polarities of states of these characters as presented in Tables 3 and 4, including other possible alternative interpretations, are given below. However, characters used primarily to infer relationships among species within the *S. (Symmorphus) murarius* group only (i.e. characters 1, 7, 9, 12, 13, 19, 27, 36, 37), are not included in this discussion, since a rigorous phylogenetic analysis of this species group will not be forthcoming until the published version of the present work (see below under section 6.1.2.3).

Ocellar diameter (character 5).—In most species of *Symmorphus* the ocelli are relatively large (figs. 3, 14), with the maximum diameter of the median ocellus greater than 1.15 trans-scutal sulcus length. Small ocelli (fig. 10), with the maximum diameter of the median ocellus 0.75 to 0.89 trans-scutal length, occur only in *S. momunganensis* and *S. negrosensis*. Although size of ocelli varies throughout the Eumeninae, ocellar diameters similar to the relatively large ocelli of most species of *Symmorphus*, occur in the vast majority of Eumeninae and are therefore considered plesiotypic. Small ocelli similar to those seen in *S. momunganensis* and *S. negrosensis*, do occur in some species of a few other genera (e.g. *Zethus*, *Cephalodynerus* and *Leptochilus*), often in association with tubercles or other elevated modifications of the vertex.

Interocellar area (character 6).—Like the majority of eumenines, the area between the ocelli of most species of *Symmorphus* is not significantly raised above the remainder of the vertex (figs. 45-47). In *S. momunganensis* and *S. negrosensis* this area is abruptly elevated directly posteriad of the anterior ocellus, such that this ocellus is nearly oriented vertically (fig. 10). Although raised interocellar tubercles and swellings occur in some species of a number of eumenine genera (Carpenter and Cumming, 1985), these states are not very similar to the condition in *S. momunganensis* and *S. negrosensis*, which is undoubtedly derived and possibly unique within Eumeninae. The association of this state with reduced ocelli in both species, suggests that these states together form a structural complex, as apparently occurs in species of *Leptochilus* with interocellar swellings (Parker, 1966) and probably other genera.

Occipital carina (character 10).—The occipital carina in both *S. parvilineatus* and *S. ambotretus* is interrupted by two submedial incisions that delimit a median tooth (fig. 13), unlike other species in the genus and the remainder of the Eumeninae, which possess a non-incised carina (fig. 14). Although clearly apotypic, the incisions in *S. parvilineatus* delimit a sharp median tooth, while those in *S. ambotretus* delimit a blunt tooth (fig. 14), suggesting that each may be due to homoplasy.

Female mandible (character 11).—Four teeth are present on the mandible of females of *S. (Parasymmorphus)*, whereas females of *S. (Symmorphus)* possess five teeth. A four-toothed mandible appears to be part of the ground-plan of the Eumeninae, characterizing both the stem group, *Eumenes sensu lato* and males of many species of the *Montezumia-Microdynerus* group (Carpenter and Cumming, 1985). Apparent emargination of the basal tooth to form a five-toothed mandible, is an apotypic development that is shared by females of most members of the *Montezumia-Microdynerus* lineage, even though reversal to a smaller number of teeth appears to have occurred several times (Carpenter and Cumming, 1985).

Determination of the ancestral state in *Symmorphus* however, is problematic. As a member of the *Montezumia-Microdynerus* group, a female mandible with five teeth could reasonably be postulated as plesiotypic for the genus, with subsequent loss of a tooth in females of *S. (Parasymmorphus)*. However, if *Symmorphus* originated near the base of this assemblage, as suggested by other characters (see "Monophyly of *Symmorphus* and relationships to remainder of Eumeninae"), a five-toothed female mandible could have evolved independently from the four-toothed condition in both *S. (Symmorphus)* and other members of the *Montezumia-Microdynerus* group.

Support for the latter hypothesis is based on comparison of the position and relative size of the teeth in Eumeninae. In most members of *Eumenes sensu lato* with reduced teeth, as well as in many of the genera of the *Montezumia-Microdynerus* group in which similar reductions occur, mandibular teeth appear to have been lost or progressively reduced from the base to the apex (e.g. in *Pseudomicrodynerus*, some *Pterocheilus*, and possibly some *Leptochilus*). If such a trend was involved during the evolutionary history of *Symmorphus*, a small basal tooth followed by three larger apical teeth would be the expected form of the four-toothed mandibular state. This is because the five-toothed female mandible of *S. (Symmorphus)*, from which this regressive state would have been derived, possesses two small basal teeth followed by three larger apical teeth. However, the four-toothed female mandible characteristic of *S. (Parasymmorphus)* is made up of four similar sized equally spaced teeth (see Cumming and Vecht, 1986 figs. 1a, 2a), suggesting this state indeed is plesiotypic for the genus.

Pronotal carina (character 14).—A complete carina extended along the crest of the anterior face of the pronotum is present in most species of *Symmorphus* (figs. 13, 45-47). The carina is dorsolaterally or dorsomedially obsolete in a few species and entirely obsolete dorsally in *S. declivis, S. gracilis* and *S. paralleliventris* (fig. 17). A complete pronotal carina is considered plesiotypic in *Symmorphus* (with partial and complete regression inferred as apotypic within this transformation series), because this is the state in most Eumeninae, although similar regressive trends are apparent within many genera (Carpenter and Cumming, 1985).

Notaulus (character 17).—The notauli (figs. 5, 6) exhibit considerable homoplasy in Eumeninae. Carpenter and Cumming (1985) consider a complete notaulus to be plesiotypic, because of the widespread distribution of this state throughout the subfamily, with loss or partial regression having occurred numerous times, most often within genera. Such a trend is apparent within *Symmorphus*, with the notauli having become partially obsolete in *S. parvilineatus*, all members of the *S. hoozanensis* group and in some individuals of certain species.

Female epicnemial carina (character 18).—An epicnemial carina is present on the mesepisternum of most species of *Symmorphus* (figs. 4, 9, 16), being more prominent in males than in females. Members of *S. (Parasymmorphus)* possess a complete carina that is extended dorsally to the posterolateral margin of the pronotum (fig. 9), in contrast with members of *S. (Symmorphus)* in which the carina is dorsally (figs. 4, 16) or entirely (fig. 21) obsolete.

An epicnemial carina is part of the ground-plan of the Eumeninae, with loss having occurred independently in numerous groups (Carpenter and Cumming, 1985). When present, the carina is generally complete in the stem group and *Eumenes sensu lato* and dorsally obsolete in the *Montezumia-Microdynerus* lineage. The dorsal portion of this carina may have been re-acquired (i.e. representing a reversal) in members of *S. (Parasymmorphus)*, if a dorsally obsolete carina is considered primitive in *Symmorphus*. However, it seems more reasonable to assume that the complete state represents one of a number of plesiotypic retentions in *Symmorphus* (see "Monophyly of *Symmorphus* and relationships to remainder of Eumeninae"), with the carina having become dorsally and then entirely obsolete within *S. (Symmorphus)*.

Propodeal superior shelf (character 21).—Although a short nearly horizontal superior shelf is present on the propodeum of some members of the *Montezumia-Microdynerus* assemblage and a few members of the stem group (e.g. some *Zethus*), lack of this shelf is quite widespread and probably a ground-plan trait of the Eumeninae. However, a short superior shelf occurs in most species of *Symmorphus*, in each subgenus and species group, suggesting that this state is plesiotypic for *Symmorphus*, with further modification of the length of the shelf, including occasional loss, evident in some species.

Propodeal submedian carina (character 22).—Some type of ridge or carina extended along the ventral portion of the posterior face of the propodeum, from the submarginal carina towards the lateral ridge, is present in many members of the *Montezumia-Microdynerus* lineage, as well as some members of the stem group (e.g. some *Zethus*) and *Eumenes sensu lato* (e.g. some *Delta*). This ridge, which in its more complete form has been referred to as the submedian carina by Bohart and Stange (1965), is absent from a great many Eumeninae however, and thus may not be part of the ground-plan of the subfamily. Most species of *Symmorphus*, including those from each subgenus and species group, possess a submedian carina ventrally (figs. 43, 44), although it may be quite short in certain species (e.g. *S. parvilineatus*). Given the widespread distribution of this state within *Symmorphus* and the equivocal polarity assessment afforded through outgroup comparison, presence of the carina ventrally is tentatively considered plesiotypic for the genus, with loss of the carina in *S. momunganensis* and *S. negrosensis* (which is not that dissimilar from the condition in *S. parvilineatus*) treated as a synapotypy. Presence of a complete carina extended along the dorsal margin of the posterior face of the propodeum (fig. 15), represents a separate apotypic development in *S. fuscipes*.

Propodeal valvula (character 23).—The propodeal valvula of members of *S. (Symmorphus)* is short posteriorly and fused distally to the posterolateral projection of the submarginal carina (fig. 51), whereas the valvula of members of *S. (Parasymmorphus)* is produced posteriorly and free distally from the submarginal carina (figs. 49, 50). A short, distally fused valvula is part of the ground-plan of the Eumeninae including the *Montezumia-Microdynerus* group, with a posteriorly produced distally free valvula having evolved independently at least a few times within the latter lineage, as well as in some members of the stem group (Carpenter and Cumming, 1985). Since members of *Symmorphus* do not share other group-defining apotypies with those taxa characterized by a posteriorly produced distally free valvula (see Carpenter and Cumming, 1985) and given that this character exhibits homoplasy, a short distally fused valvula is considered plesiotypic in *Symmorphus*.

Propodeal orifice (character 24).—Members of *S. (Parasymmorphus)* possess a propodeal orifice that is narrowly acute dorsally (figs. 49, 50). In contrast, members of *S. (Symmorphus)* have the orifice broadly rounded above (figs. 33, 34, 36), although in *S. foveolatus, S. glasunowi* and *S. sichuanensis* the orifice is moderately narrow dorsally (fig. 26) and somewhat intermediate. A broadly rounded propodeal orifice is plesiotypic in the Eumeninae, with a narrow dorsally acute orifice having evolved independently in some members of the stem group and a few members of the *Montezumia-Microdynerus* lineage, often in association with lengthening of the valvula (Carpenter and Cumming, 1985). Thus dorsal narrowing of the orifice is considered an apotypic trend in *Symmorphus*, with the narrowly acute orifice in *S. (Parasymmorphus)* possibly forming part of a structural complex with the elongate distally free valvula (see character 23) possessed by members of this subgenus.

Metasomal tergum 1 longitudinal furrow (character 28).—A median longitudinal furrow on metasomal tergum 1 is an autapotypy of *Symmorphus*, although as Carpenter and Cumming (1985) indicate the furrow appears to be a modification of a slight medial indentation present in many eumenines. This indentation, which is probably part of the ground-plan of the subfamily, is always shallow and generally restricted to the apical portion of the tergum, unlike the furrow in *Symmorphus*, which is also developed basally. In some taxa the indentation is represented only by a narrow medial sulcus (e.g. *Paranortonia*), although in most eumenines exhibiting this feature it is more broadly excavated.

In *Symmorphus*, members of *S. (Parasymmorphus)* and the *S. (Symmorphus) hoozanensis* group possess a longitudinal furrow that is broadly impressed and very shallowly to shallowly depressed (fig. 11). In contrast, members of the *S. (Symmorphus) declivis* and *S.*

*(Symmorphus) murarius* groups, with the exclusion of *S. violaceipennis*, have a furrow that is more sharply impressed as well as being shallowly to moderately depressed with a deeper narrow medial sulcus (fig. 12). The furrow of *S. violaceipennis* also contains a deep medial sulcus, but is somewhat broadly impressed and even more deeply depressed.

The longitudinal furrow characteristic of *S. (Parasymmorphus)* and the *S. (Symmorphus) hoozanensis* group is most probably plesiotypic in *Symmorphus*, because this state is distributed in both subgenera and is most similar in terms of depth to the presumed ground-plan medial indentation of the Eumeninae. The more sharply impressed generally deeper furrow seen in both *S. declivis* and *S. murarius* group members is considered apotypic, with the included narrow medial sulcus showing convergence in some other Eumeninae. A further modification of this state is apparent in the furrow of *S. violaceipennis*, which although somewhat broadly impressed secondarily, still possesses a narrow medial sulcus and is more deeply depressed than the longitudinal furrow of other species.

Metasomal tergum 1 apical margin (character 29).—As Carpenter and Cumming (1985) indicate, a depressed margin or lamella extended along the apex of metasomal tergum 1 is probably plesiotypic in the Eumeninae, being present in many members of the stem group and *Eumenes sensu lato*, as well as a few members of the *Montezumia-Microdynerus* lineage. Loss or reduction of this border has occurred independently within each of these groups, sometimes frequently (Carpenter and Cumming, 1985). This trend is evident within *Symmorphus*, with the distinct depressed apical margin present in *S. parvilineatus*, apparently having been reduced (traces of the margin may remain, fig. 29) or lost in all other species.

Metasomal sternum 1 sculpture (characters 30, 31 and 32).—As indicated by Carpenter and Cumming (1985) most members of the *Montezumia-Microdynerus* lineage possess a curved transverse ridge just posterior to the anterior margin of metasomal sternum 1. Based on position, the lateral and medial portions of this ridge are probably homologous with, respectively, the lateral oblique ridges and at least part of the basal carina found in

*Symmorphus* (fig. 8). Presence of these structures in *Symmorphus* is therefore inferred to be plesiotypic, as is (due to widespread distribution within the genus) the development of a median longitudinal ridge, with each considered to have subsequently undergone regression.

Interpretation of the primitive form of the basal carina however, is more difficult. In *S. (Parasymmorphus)* it is extended across the apex of the narrow basal portion of the sternum and is straight. This is similar to the condition of the medial portion of the presumed homologous transverse ridge in many members of the *Montezumia-Microdynerus* lineage, and thus is probably plesiotypic in *Symmorphus*. However, the form of the remainder of the scuplture of metasomal sternum 1 in *S. (Parasymmorphus)*, with the lateral oblique ridges either completely reduced or anteriorly obsolete, tends to support the notion that the entire sculpture of the sternum may be apotypic in this group. Nevertheless, given current knowledge, the deeply curved basal carina (fig. 8) characteristic of most species of *S. (Symmorphus)*, is most reasonably assumed an apotypic modification of the state in *S. (Parasymmorphus)*, because this posteriorly curved basal carina is unlike the medial portion of the transverse ridge in most other members of the *Montezumia-Microdynerus* group, even though in a few taxa (e.g. some *Stenodynerus* and *Parancistrocerus*) it may be slightly emarginate medially. In addition, further modification of the deeply curved state is apparent in *S. tukvarensis* and *S. nipteroides*, where the basal carina has become inflated and raised posteriorly (fig. 35).

Metasomal segment 2 base in profile (characters 33 and 34).—The form of the base of metasomal segment 2 in profile appears to to be of great phylogenetic significance in *Symmorphus*, even though determination of the ancestral condition in the genus is somewhat problematic. *S. (Parasymmorphus) parvilineatus*, as well as members of both the *S. (Symmorphus) hoozanensis* and *S. (Symmorphus) declivis* groups, have the base of the tergum obtusely angulate and the sternum abruptly truncate posteriad of the basal sulcus (fig. 52). *S. (Parasymmorphus) momunganensis* and *S. (Parasymmorphus) negrosensis* have the tergum gradually rounded basally and the sternum markedly convex posteriad of the basal sulcus (fig.

53). Similarly, members of the *S. (Symmorphus) murarius* group possess a gradually rounded tergum basally, but have the sternum slightly convex to nearly flat posteriad of the basal sulcus (fig. 54).

All three states associated with the base of metasomal sternum 2 are present in other members of the *Montezumia-Microdynerus* lineage with the markedly convex base and the truncate base both very widely distributed. Within the stem group and *Eumenes sensu lato* the base of the sternum is markedly convex to flat, but not abruptly truncate. A polarity decision based entirely on outgroup comparison therefore, although equivocal, does suggests that a sternum with a slightly convex to flat base is probably derived in *Symmorphus* and that of the remaining two states, a markedly convex base is more likely plesiotypic. In addition, association of the truncate state of the sternum with the obtusely angulate base of metasomal tergum 2, in species belonging to different subgenera and species groups, suggests that both states should have identical polarities if they form a structural complex. A tergum with an obtusely angulate base occurs only in some species of a few eumenine genera (e.g. *Pseudonortonia*), so that a gradually rounded tergum is probably plesiotypic in *Symmorphus*. Thus the condition of an obtusely angulate tergum and abruptly truncate sternum, is probably best considered apotypic in the genus given current knowledge.

Metasomal segment 2 apical margin (character 35).—Like metasomal tergum 1, a markedly developed depressed margin or lamella occurs at the apex of metasomal segment 2 in many members of the stem group and *Eumenes sensu lato*, as well as some members of the *Montezumia-Microdynerus* lineage, and is probably plesiotypic in the Eumeninae (Carpenter and Cumming, 1985). This state, which is also considered plesiotypic in *Symmorphus*, is present in members of *S. (Parasymmorphus)* (fig. 53), with subsequent reduction in the length of the margin evidently having given ris[illegible]the very similar state in the *S. (Symmorphus) hoozanensis* group (fig. 52). Continued regression may have lead to the condition in the *S. (Symmorphus) declivis* and *S. (Symmorphus) murarius* groups, where the margin in most species is shorter still and not depressed (figs. 41, 54, although it is slightly depressed on the tergum of *S. sichuanensis*).

### 6.1.2.3 Phylogenetic relationships

Monophyly and relationships of subgenera and species groups—Figures 80 and 81 are alternative cladistic hypotheses of relationships of the subgenera and species groups in *Symmorphus*, that differ only in the resolution of the *S. (Symmorphus) hoozanensis* group (see below). In both, *S. (Parasymmorphus)* is inferred to be the sister group of *S. (Symmorphus)*, with the monophyly of the former clearly indicated by the posteriorly produced distally free propodeal valvula (state 23.1) and narrowly acute propodeal orifice dorsally (state 24.2). Conversely the monophyly of *S. (Symmorphus)* is established primarily by the five-toothed mandible in females (state 11.1) and loss of at least the dorsal portion of the epicnemial carina (state 18.1 initially). It is possible though, that both these states could be considered part of the ground-plan of the genus and thus not indicative of relationship at the subgeneric level (see "Characters and states"). However, loss of the distinct depressed apical margin of metasomal tergum 1 (state 29.1), presence of a deeply curved basal carina on metasomal sternum 1 (state 30.1), as well as reduction in the length of the apical margin of metasomal segment 2 (state 35.1 initially) in *S. (Symmorphus)*, additionally support this clade, even though each state shows homoplasy (states 29.1 and 35.0/1), ~~or~~ is subsequently lost (state 30.*).

Overall, members of the *S. hoozanensis* group are among the most plesiotypic species included in *S. (Symmorphus)*, and are hypothesized to have arisen before the evolution of the synapotypies establishing the *S. declivis* group-*S. murarius* group clade. This latter clade is reasonably well supported by the sharply impressed longitudinal furrow on metasomal tergum 1, including a deeper narrow medial sulcus (state 28.1) and by the relatively short non-depressed apical margin on metasomal segment 2 (state 35.2), although the slightly depressed apical margin on the tergum of metasomal segment 2 (state 35.1/2) in *S. sichuanensis*, a member of the *S. murarius* group, must then be considered a reversal.

Further resolution of the relationships of the species groups of *S. (Symmorphus)* is dependent upon interpretation of the states associated with the base of metasomal segment 2. Members of the *S. hoozanensis* and *S. declivis* groups possess an abruptly truncate sternum (state 34.1) in conjunction with an obtusely angulate tergum (state 33.1), whereas those of the *S. murarius* group possess a slightly convex to nearly flat metasomal sternum (state 34.-1) and gradually rounded tergum (state 33.0).

Comparisons made with the outgroup indicate that an obtusely angulate tergum (state 33.1) is probably apotypic in the genus and although somewhat equivocal, additionally suggest that both the abruptly truncate and slightly convex to nearly flat states of the sternum (states 34.1 and 34.-1) represent independent modifications of the markedly convex condition (state 34.0) seen in *S. (Parasymmorphus) momunganensis* and *S. (Parasymmorphus) negrosensis* (see "Characters and states"). This interpretation (fig. 80) supports the monophyly of the three species groups in *S. (Symmorphus)* (not in doubt for the monobasic *S. declivis* group) and indicates a sister group relationship between the *S. declivis* and *S. murarius* groups, given their previously discussed close relationship. Such an hypothesis necessitates the independent development of an obtusely angulate tergum (state 33.1) and abruptly truncate sternum (state 34.1) at the base of metasomal segment 2 in both the *S. hoozanensis* and *S. declivis* groups, as must have additionally occurred in *S. (Parasymmorphus) parvilineatus*.

However, given the somewhat equivocal assessment of polarity of states associated with the base of metasomal segment 2, especially in states of the sternum, and the occurrence of an obtusely angulate tergum (state 33.1) and abruptly truncate sternum (state 34.1) in the more plesiotypic elements of the genus, it is distinctly possible that both of these states are actually part of the ground-plan of *Symmorphus*. Such a revised polarity assessment immediately allows for the possibility that the *S. hoozanensis* group is paraphyletic in relation to the remaining members of *S. (Symmorphus)* (fig. 81), as the only other potential synapotypy uniting members of this species group is the partial regression of notauli (state 17.1), a state that is prone to homoplasy. Under this interpretation the relationships of the remaining taxa are not altered from those previously discussed, although *S. declivis* is now indicated as the sister group of the *S. murarius* group because it retains more plesiotypies, with loss of the basal carina and median longitudinal ridge of metasomal sternum 1 (states 30.• and 31.1) its only remaining apotypies. In addition, the hypothesis presented in figure 81, requires considerable homoplasy in the notauli (states 17.0, 17.1) as well as independent development of a gradually rounded metasomal tergum 2 basally (state 33.0, reversal to the apparent plesiotypic eumenine condition) in both the *S. murarius* group and the *S. (Parasymmorphus) momunganensis-S. (Parasymmorphus) negrosensis* clade.

Although difficult to choose between these competing phylogenetic hypotheses, the interpretation of character evolution and relationships presented in figure 80, appears more parsimonious given current knowledge. The distinct possibility that an obtusely angulate tergum (state 33.1) and abruptly truncate sternum (state 34.1) form a structural complex at the base of metasomal segment 2 and thus share the same evolutionary development (see "Characters and states"), in conjunction with outgroup comparison indicating that an angulate tergum is probably derived, together support the notion that this condition of metasomal segment 2 (i.e. state 33.1 + 34.1), although exhibiting homoplasy, is indeed apotypic within *Symmorphus*.

Relationships of species of *S. (Parasymmorphus)*—Within *S. (Parasymmorphus)*, the relationships among the three included species are very well established (fig. 82). *S. momunganensis* and *S. negrosensis* are clearly indicated as sister species by the reduced ocelli (state 5.1), elevated interocellar area (state 6.1), loss of the superior shelf (state 21.2) and submedian carina (state 22.-1) of the propodeum, indistinct apical margin of metasomal tergum 1 (state 29.1), and loss of the median longitudinal ridge (state 31.1) plus lateral oblique ridges (state 32.1) of metasomal sternum 1. *S. parvilineatus* is inferred to be the sister group of this clade, because members of this species retain the structures that have regressed in both *S. momunganensis* and *S. negrosensis*, and lack an elevated interocellar area. Although plesiotypic in these features, *S. parvilineatus* possesses an incised occipital carina (state 10.1), partially obsolete notauli (state 17.1), and an obtusely angulate tergum (state 33.1) plus abruptly truncate sternum (state 34.1) at the base of metasomal segment 2. However these apotypies, although distinctive in *S. (Parasymmorphus)*, have also developed convergently within *S. (Symmorphus)*.

Relationships of species of the *S. (Symmorphus) hoozanensis* group—The distribution of characters amenable to phylogenetic analysis in the *S. hoozanensis* group, is inadequate to completely resolve relationships among all four included species (fig. 83). *S. hoozanensis* and *S. canlaonicus* are associated by two shared modifications, namely a dorsolaterally obsolete pronotal carina (state 14.1) and a ventrally faint to obsolete female epicnemial carina (state 18.1/2 initially). Both are regressive apomorphies and thus potentially unreliable indicators of relationship, with at least the epicnemial carina also exhibiting homoplasy in the *S. murarius* group. Incongruent with this distribution, is the presence of a slightly elongate potentially plesiotypic depressed apical margin on metasomal segment 2 (state 35.0/1) in *S. hoozanensis*. *S. ambotretus*, *S. alkimus* and *S. canlaonicus* possess a somewhat shorter potentially more derived margin (state 35.1) that could be considered indicative of close relationship between them. Nevertheless, a sister group relationship between *S. hoozanensis* and *S. canlaonicus* is more parsimonious in terms of total number of evolutionary transformations, so that the somewhat longer metasomal segment apical margin (state 35.0/1) in *S. hoozanensis* is tentatively considered a reversal towards a seemingly more plesiotypic condition (fig. 83). The exact relationships of *S. ambotretus* and *S. alkimus* to this lineage however, are left unresolved, because the only remaining apotypies possessed by these species (state 10.1—incised occipital carina in *S. ambotretus*, state 21.1—reduced propodeal superior shelf in *S. alkimus*), are not shared among other included members (fig. 83).

Relationships of species of the *S. (Symmorphus) murarius* group—A rigorous phylogenetic analysis of this species group will not be presented until the published version of the present work, due to time constraints imposed upon the completion of this dissertation and the complexity of the data involved. Instead, the most tenable relationships of the included species, apparent from the characters presented in Tables 3 and 4, are briefly discussed. Most characters used to infer relationships within the group, appear to exhibit considerable homoplasy throughout the genus, rather than congruent patterns of hierarchically nested synapotypies. Thus the relationships proposed below should be considered tentative, as they are seldom clearly supported.

A number of species of the *S. murarius* group possess lengthened setae on the head and mesosoma in addition to short pubescence (state 36.1). This apparent apotypy may have arisen only once within *Symmorphus*, however the relative dissimilarity of the species with lengthened setae as a group, suggests that this feature evolved separately in at least three lineages.

One of these lineages, which includes *S. murarius*, *S. foveolatus*, *S. glasunowi* and *S. sichuanensis*, is reasonably well established by enlarged cephalic foveae (state 7.1), elongation of male antennal article 13 (state 13.1 initially), lateral evanescence of the transverse carina of metasomal tergum 1 (state 27.1), loss of the basal carina of metasomal sternum 1 (state 30.[illegible]) and reduction of the median longitudinal ridge of metasomal sternum 1 (s[illegible] initially). Within this lineage, *S. sichuanensis*, *S. foveolatus*, and *S. glasunowi* are considered related by a narrowed propodeal orifice dorsally (state 24.1), with *S. foveolatus* and *S. glasunowi* inferred as sister species on the basis of both loss of male antennal tyloids (state 12.1) and the propodeal superior shelf (state 21.2).

*S. crassicornis*, *S. captivus*, *S. angustatus* and *S. albomarginatus* form a phenetically similar cluster of species that also possess lengthened setae (state 36.1). Although the exact relationships among these apparently closely related species is unresolved, they may together form the sister group to the less setose *S. decens*, on the basis of possession of a prominent cephalic foveal carina (state 9.0, a probable apotypic reversal in the *S. murarius* group) and loss of the basal carina of metasomal sternum 1 (state 30.•).

In addition, lengthened setae (state 36.1) also appear to have evolved separately in a lineage containing *S. violaceipennis* and *S. mizuhonis*. Both species are phenetically quite similar and appear distantly related to other taxa possessing lengthened setae. They are probably sister species, although no other synapotypies could be located.

Relationships among the remaining species of the *S. murarius* group are mainly unresolved, although a few sister species pairs are apparent. *S. tukvarensis* and *S. nipteroides* share an inflated posteriorly raised basal carina on metasomal sternum 1 (state 30.2) as well as a ventrally obsolete epicnemial carina (state 18.2), and are presumably closely related. Similarly, *S. gracilis* and *S. paralleliventris* appear to share a sister species relationship, on the basis of dorsal evanescence of the pronotal carina (state 14.2), development on the mesopleuron of a high reflexed border along the anterior margin of the pseudosternum (state 19.1) and loss of the basal carina of metasomal sternum 1 (state 30.•). In addition, *S. debilitatus* and *S. cliens*, *S. lucens* and *S. sublaevis*, as well as *S. allobrogus* and *S. cristatus*, probably represent three additional species pairs. Support for these sister relationships however, is base primarily on unanalyzed (phenetic) similarity, as species in each pair differ only slightly from one another.

The relationships of all these included lineages to one another and to the remaining species in the *S. murarius* group however, are at present unclear. Increased resolution of this group must await a complete analysis, with the possible inclusion of more data. Implementation of this analysis via computer programs such as PAUP and PHYSIS, written by D. L. Swofford and J. S. Farris respectively, should allow for a better understanding of the available data, while suggesting potentially overlooked alternative sets of relationships.

## 6.2 Zoogeographic Considerations

The approach taken here towards historical zoogeography involves an amalgamation of techniques employed by both dispersal and vicariance biogeographers. For example, although an attempt is made to invoke a minimum of dispersal versus vicariant explanations for the chorological patterns seen within *Symmorphus*, region of origin of the genus is considered despite some justifiable criticism of this concept by Croizat *et al.* (1974), Platnick and Nelson (1978) and Rosen (1978).

Estimates of the time of origin of *Symmorphus* are hampered by absence of knowledge about evolutionary rates within the genus and lack of a fossil record, in which vespids as a group are scarely represented (Burnham, 1978). The entire aculeate Hymenoptera, although known only as far back in the stratigraphic record as the Upper Cretaceous, exhibit enough diversity at this time to suggest that the group may have evolved as early as the Jurassic (Evans, 1966). The earliest known vespids, two species belonging to the extinct euparagiine genus *Curiovespa* Rasnitsyn, are from the Upper Cretaceous (Rasnitsyn, 1975). However, several vespids are known from Eocene and Oligocene beds in both North America and Europe, with those from the Oligocene mostly assignable to extant genera (Burnham, 1978). This perhaps indicates an earlier origin for the family than evidenced by appearance in the fossil record alone.

Such a notion is consistent with chorological patterns displayed by some subfamilies of the Vespidae, where the Masarinae and Polistinae are primarily Gondwanian and the Vespinae is predominantly Laurasian in distribution, suggesting that separation of both continents during the Mesozoic may have profoundly affected the evolutionary history of the family (Carpenter, 1981). Distributional patterns for the Eumeninae, which is the sister group to the Indomalayan Stenogastrinae and the Polistinae + Vespinae (Carpenter, 1981), are more complex. The stem group (fig. 79) is predominantly Gondwanian, whereas *Eumenes sensu lato* is cosmopolitan, as are some genera of the *Montezumia-Microdynerus* lineage. *Symmorphus* is unique in the

Eumeninae in exhibiting a cosmopolitan Laurasian distribution, which elsewhere in the family is seen only in the Vespinae (see Vecht, 1967).

That *Symmorphus* may nearly be as old as the Vespinae, which probably originated toward the end of the Mesozoic, is suggested by more than just similar extant distributions. Although ranked as a subfamily, the Vespinae exhibits similar diversity to *Symmorphus*, with approximately 55 species worldwide, even though its sister group the Polistinae is far more diverse (Spradbery, 1973). The vespine species are group into four genera, *Provespa*, *Vespa*, *Vespula* and *Dolichovespula*. *Provespa* is Indomalayan in distribution, *Vespa* occurs in both the Palearctic and Oriental regions (plus New Guinea) although it is much more diverse in the latter, whereas *Vespula* and *Dolichovespula* are Holarctic in distribution (Vecht, 1965, 1967). A rigorous phylogenetic analysis of these taxa is unfortunately lacking, but on the basis of structural and behavioral characters *Vespa* is generally thought to be the sister or stem group to *Vespula* and *Dolichovespula*, which together are considered a monophyletic group (Yamane, 1976; Greene, 1979). Phenetically, *Provespa* appears quite isolated from these three genera and so most likely shares a sister group relationship with this lineage, although this has yet to be established. Such a pattern for the Vespinae is entirely concordant with that observed in *Symmorphus*, whereby the broadly Indomalayan *S. (Parasymmorphus)* is the sister group of *S. (Symmorphus)*, which is made up basally of a primarily Oriental sister or stem group to a Holarctic clade (figs. 80, 81). Thus given the recurrent nature of this pattern in the family and the inference on structural grounds that *Symmorphus* is a relatively old member of the Eumeninae (see "Monophyly of *Symmorphus* and relationships to remainder of Eumeninae"), the genus is hypothesized to have originated in Laurasia at the end of the Mesozoic.

The Oriental distribution of *S. (Parasymmorphus)* in conjunction with the predominantly Oriental distribution of the *S. hqozanensis* group, the most basal species group of *S. (Symmorphus)* (figs. 80, 81), reasonably suggests that the ancestor of the genus originated within this region of Laurasia, even though *Symmorphus* exhibits greatest species richness in the Palearctic region. Divergence of S. *(Parasymmorphus)* from S. *(Symmorphus)* probably occurred in the earliest Cenozoic of the Oriental region, although the exact vicariant event involved cannot at present be inferred. Expansion of the range of S. *(Symmorphus)* north into Asia during the early Palaeocene, accompanied by a north-south vicariance, probably resulted in production of both the more southerly S. *hoozanensis* group lineage and the more northerly S. *declivis* group + S. *murarius* group clade. The relatively brief partial northern withdrawal of the Turgai Sea from Eurasia in the Paleocene (Adams, 1981; Milner, 1983), may have allowed westward expansion of this later clade into Europe. Subsequent re-establishment of this barrier in the early Eocene (Adams, 1981; Milner, 1983) could then have separated the ancestral stock of the S. *declivis* group in Europe from that of the S. *murarius* group in Asia.

Inadequate resolution of many of the relationships of the species included in these basal clades, greatly obscures historical events responsible for their present distributions, despite considerable allopatry between presumed related taxa suggestive of vicariant patterns. In addition, the distributions of most of the Oriental species are very incompletely known, since relatively few specimens have been collected from this area. Nevertheless, some explanation of the geographic history of these groups appears possible.

Within S. *(Parasymmorphus)*, S. *parvilineatus* is as phenetically divergent from the S. *momunganensis* + S. *negrosensis* clade as species groups are from each other within S. *(Symmorphus)*. This suggests that a relatively old, perhaps early mid-Tertiary, vicariant event was involved in the production of these two clades (fig. 82), assuming roughly equivalent evolutionary rates in both subgenera. Differentiation of S. *momunganensis* and S. *negrosensis* however, probably occurred much more recently, presumably during the Pleistocene when fluctuating sea levels joined and then separated many of the Philippine islands (Alcala, 1976).

Reconstruction of the geographic history of the S. *hoozanensis* group must await better resolution of the phylogenetic relationships among the included species. The somewhat tentative sister species relationship shared by *S. hoozanensis* from Taiwan and *S. canlaonicus* from the Philippines (fig. 83), is not strongly supported by geological evidence, since these islands apparently had no direct connection with each other in the past (Alcala, 1976). However, during the maximum regression of the Pleistocene seas, the Philippine islands appear to have been joined to the southeast Asian mainland via Borneo and Sumatra, while Taiwan was connected to southern China (Darlington, 1957; Alcala, 1976). Thus a wide ranging ancestral species could have become isolated on these islands during the early Pleistocene, with subsequent extinction of the mainland stock producing the pattern seen today. Similarly, a relatively recent restriction in the range of *S. alkimus* may have also resulted in its present disjunct distribution, where *S. alkimus alkimus* occurs in Sri Lanka and *S. alkimus dialeukus* is known only from northern Sumatra (fig. 62). During the Pleistocene both these islands were connected to the mainland (Darlington, 1957), suggesting that *S. alkimus* was probably distributed continuously around the Bay of Bengal at some time during this epoch. Extinction of the intervening populations to the north, perhaps as late as the last glacial maximum, presumably created the disjunction seen today.

Members of the *S. murarius* group are generally found to the north of their congeners, with those occurring in the southern portion of the group's range generally restricted to temperate habitats at higher elevation. Thus the group as a whole is more cool adapted than other members of the genus, suggesting that much of its evolution probably occurred in conjunction with the deterioration of warm climates in the northern hemisphere at the end of the Eocene (Wolfe, 1978). The permanent withdrawal of the Turgai Sea by this time (Adams, 1981; Milner, 1983) probably allowed for the first westward expansion of the group into Europe, possibly at the expense of the European *S. declivis* group lineage, of which *S. declivis* may be a relict. With the disappearance of the North Atlantic land connections between Europe and North America by the early Oligocene (Matthews, 1979) dispersal of the *S. murarius* group into North America was presumably via the Bering land bridge, perhaps beginning as early as the Oligocene when this connection appears to have become reasonably well established

(McKenna, 1975; Matthews, 1979).

The *S. murarius* - *S. sichuanensis* - *S. foveolatus* - *S. glasunowi* lineage may have been one of the earliest established within the *S. murarius* group, based on degree of phenetic divergence exhibited among the included species. The actual vicariant events involved in the evolutionary history of this lineage cannot presently be inferred, however an initial east-west Eurasian vicariance may have separated the ancestor of *S. murarius* in the west from the ancestor of the other three species in the east (compare figs. 64 and 65). A subsequent north-south vicariance in Asia probably resulted in the production of the *S. sichuanensis* lineage to the south and the *S. foveolatus* + *S. glasunowi* clade to the north, followed by an east-west separation of the latter two species, perhaps as recently as the Pleistocene (fig. 65).

Similarly, the vicariant events involved in the separation of *S. violaceipennis* and *S. mizuhonis*, as well as *S. tukvarensis* and *S. nipteroides*, may also have occurred reasonably early, assuming relatively constant evolutionary rates throughout the *S. murarius* group. Although the exact vicariances involved are unknown, distribution of three of these species in the Himalaya and *S. mizuhonis* to the north in Asia (figs. 69, 74), suggests that development of barriers between both sets of sister species may have been correlated with the orogeny of the Himalaya, which was most intense during mid-Miocene times (Adams, 1981). In addition, the vicariance that split *S. paralleliventris* in the Atlas Mountains of northern Africa from the western Palearctic *S. gracilis* (fig. 78), probably occurred only slightly later, given the phenetic divergence of these sister species. Although many European species of various groups are established in the Atlas Mountains, apparently having dispersed there via the Iberian Peninsula throughout the Quaternary (see for example Williams, 1985), the ancestor of these two species probably reached northern Africa in the late Miocene when Iberia and Africa were temporarily connected (Hsü, 1972). Opening of the Straits of Gibraltar in the early Pliocene (Hsü, 1972) then, presumably created the pattern observed today.

Origin of the very similar species in each of three sister species pairs, *S. debilitatus* + *S. cliens* (fig. 71), *S. lucens* + *S. sublaevis* (fig. 72) and *S. allobrogus* + *S. cristatus* (figs. 76, 77), as well as of the phenetically similar *S. crassicornis*, *S. captivus*, *S. angustatus* and *S. albomarginatus* (figs. 66, 67, 68), probably occurred rather recently in the latter part of the Pliocene and Pleistocene. During this time, interruptions of land connections between Asia and North America through Beringia (Matthews, 1979), as well as those between Japan and the mainland (Minato *et al.*, 1965), in addition to dramatic changes in climate, community composition and habitat type, undoubtedly provided ample opportunity for vicariant events and distributional shifts necessary to account for the chorological patterns seen in these species.

The presumed close relationship and phenetic similarity between *S. crassicornis* plus its relatives from the Palearctic and *S. albomarginatus* from the New World, as well as between *S. allobrogus* from the Palearctic and *S. cristatus* from the Nearctic, indicates that North America was invaded separately by both lineages during the late Pliocene or Pleistocene. Fragmentation of the range of *S. albomarginatus* during the late Pleistocene, may have resulted in the geographic variation encountered throughout the range of *S. albomarginatus albomarginatus* and in the isolation of *S. albomarginatus midas* in Central America (fig. 68). The ancestor of *S. canadensis* probably also dispersed into North America in the Pliocene or Pleistocene, as this Nearctic species appears to have close affinities with *S. debilitatus* from Europe and *S. cliens* from Japan. *S. projectus* the remaining Nearctic species, is phenetically isolated from other members of the *S. murarius* group and probably represents an earlier invasion from the Palearctic, perhaps during the Oligocene or Miocene.

The major historical zoogeographic events hypothesized to have occurred during the evolutionary history of *Symmorphus* are summarized in Fig. 84.

# 7. CONCLUDING REMARKS

It is hoped that this contribution will be a stimulus for further research, as much remains to be learned about *Symmorphus*. In particular greater resolution of the phylogenetic relationships of *Symmorphus* with the remainder of the Eumeninae, should allow for clearer interpretations of evolutionary transformations within the genus. Discovery of additional specimens of *S. (Parasymmorphus)*, especially males, or those of the *S. (Symmorphus) hoozanensis* group, could prove especially valuable in this regard.

The phylogenetic interrelationships of the species of *Symmorphus* are still mainly unresolved, particularly those of the *S. (Symmorphus) murarius* group. Clarification of these relationships will require a more thorough analysis, possibly implemented via computer programs such as PAUP and PHYSIS. Investigation of other character systems, including chromosomal features and more complete life history information, could increase the resolution of any subsequent phylogenetic analysis at the species level.

Continued collection of specimens is warranted, especially in such areas as the Oriental region and eastern Asia, where some taxa are currently known from only a few specimens. Such efforts will probably lead to the discovery of additional undescribed taxa, and provide a more complete understanding of chorological relationships among the currently recognized species, as well as information on intraspecific geographic variation.

The geographic variation exhibited by some species of *Symmorphus* (e.g. *S. albomarginatus*) appears to be exceedingly complex. Further investigation of this variation is required, including studies of ecophenotypic factors. In addition, techniques such as electrophoresis should be extremely useful in establishing patterns of gene flow among populations.

This study should be regarded as a preliminary organization of information about the species of *Symmorphus*. Although it has resolved some problems concerning the classification and evolution of the genus, many more remain to be answered. Hopefully this work will stimulate further research in some of these areas.

**Table 1. Measurements for *Symmorphus* species not fully described in text (part 1)**

Species abbreviations: **cr**, *S. crassicornis*; **cp**, *S. captivus*; **an**, *S. angustatus*; **al**, *S. albomarginatus*; **dn**, *S. decens*. **vi**, *S. violaceipennis*; **mi**, *S. mizuhonis*; **bi**, *S. bifasciatus*; **db**, *S. debilitatus*; **cl**, *S. cliens*; **co**, *S. connexus*; **lu**, *S. lucens*. Other symbols: "-" unknown; "T1" refers to metasomal tergum 1; "T2" refers to metasomal tergum 2; "S2" refers to metasomal sternum 2.

Based on largest and smallest specimens for both female and male of each species.

| Character | cr | cp | an | al | dn | vi | mi | bi | db | cl | co | lu |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **FEMALE** | | | | | | | | | | | | |
| Head: height/width | 0.96-0.97 | 0.96-0.99 | 0.95 | 0.96-1.00 | 0.91-0.95 | 1.00-1.05 | 1.00 | 0.96-0.98 | 1.00-1.05 | 1.09-1.13 | 1.04-1.05 | 1.04-1.05 |
| Clypeus: height/width | 0.66-0.67 | 0.69-0.72 | 0.67 | 0.67-0.72 | 0.58-0.61 | 0.66-0.67 | 0.67-0.69 | 0.61-0.62 | 0.67-0.68 | 0.64-0.68 | 0.64-0.65 | 0.65-0.69 |
| OOL/POL | 0.99-1.19 | 0.97-1.04 | 0.99-1.08 | 0.96-1.06 | 1.05-1.10 | 1.29-1.37 | 1.16-1.23 | 0.90-1.00 | 0.96-1.00 | 1.00-1.10 | 0.88-0.94 | 1.06-1.07 |
| LOL/POL | 0.49-0.51 | 0.46-0.48 | 0.52-0.54 | 0.52 | 0.53 | 0.53 | 0.52-0.55 | 0.53-0.60 | 0.56-0.58 | 0.50-0.54 | 0.59 | 0.56-0.60 |
| Foveal diameter/ trans-scutal sulcus length | 0.80-0.92 | 0.89-0.90 | 0.88-0.90 | 0.50-0.84 | 0.60-0.75 | 0.25-0.33 | 0.67-0.84 | 0.89-1.25 | 0.84-1.11 | 1.33 | 1.32-1.45 | 1.60-2.00 |
| Foveal interval/POL | 0.33-0.86 | 0.93-1.00 | 0.88-0.92 | 1.01-1.06 | 1.00-1.10 | 1.00-1.05 | 0.92-0.95 | 0.73-0.87 | 0.75-0.89 | 0.98-1.10 | 0.82-0.86 | 0.73-0.89 |
| Propodeal superior shelf length/ trans-scutal sulcus length | 1.10-1.33 | 1.33-1.40 | 0.80-1.34 | 0.75-1.38 | 1.50-1.60 | 2.50-3.11 | 1.38-1.67 | 1.33-2.33 | 1.38-1.67 | 1.33-2.23 | 1.50-1.83 | 1.65-1.75 |
| T1: postcarinal length/apical width | 0.50 | 0.49-0.52 | 0.52-0.62 | 0.46-0.51 | 0.57-0.58 | 0.73-0.77 | 0.63-0.67 | 0.75-0.77 | 0.66-0.67 | 0.67-0.71 | 0.61-0.63 | 0.63-0.71 |
| T1: carinal width/ apical width | 0.74-0.79 | 0.83-0.84 | 0.67-0.73 | 0.77-0.82 | 0.76-0.81 | 0.77-0.82 | 0.79-0.84 | 0.68 | 0.75-0.76 | 0.83-0.85 | 0.82-0.84 | 0.79-0.80 |
| T2: length/width | 0.84 | 0.80-0.86 | 0.84-0.89 | 0.87-0.89 | 0.86-0.90* | 1.00 | 0.95-0.96 | 0.90-0.91 | 0.95-0.96 | 1.00-1.02 | 0.87-0.89 | 0.94-0.98 |
| T2+S2 apical margin length/trans-scutal sulcus length | 0.40-0.46 | 0.50-0.56 | 0.50-0.53 | 0.33-0.50 | 0.60-0.80 | 0.67 | 0.67 | 0.67-1.00 | 0.75-0.89 | 1.00-1.77 | 0.89-0.94 | 1.00 |
| Body length to apex of T2 | 10.5-14.0 | 14.0-15.0 | 9.5-12.5 | 7.5-12.0 | 9.0-11.0 | 8.5-10.0 | 7.5-9.5 | 6.5-9.0 | 7.0-8.5 | 6.0-8.0 | 6.5-8.5 | 6.5-9.0 |

Table 1. Measurements for *Symmorphus* species (cont.)

| Character | cr | cp | an | al | dn | vi | mi | bi | db | cl | co | lu |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **MALE** | | | | | | | | | | | | |
| Antennal article 13: length/width | 0.98-1.07 | 1.06 | 1.00-1.07 | 1.00-1.20 | 0.89-1.00 | | 1.00-1.03 | 1.07-1.09 | 0.78-0.85 | 0.67-0.75 | 1.00-1.03 | 0.75-0.83 |
| Body length to apex of T2 | 8.0-12.0 | 11.0 | 6.5-9.5 | 6.0-10.5 | 7.0-8.0 | | 5.5-7.5 | 5.5-8.5 | 6.0-7.5 | 6.5-7.5 | 5.5-8.0 | 6.5-7.5 |

**Table 2. Measurements for *Symmorphus* species not fully described in text (part 2)**

Species abbreviations: **su**, *S. sublaevis*; **ca**, *S. canadensis*; **pr**, *S. projectus*; **tu**, *S. tukvarensis*; **ni**, *S. nipteroides*. **fu**, *S. fuscipes*; **ap**, *S. apiciornatus*; **ab**, *S. allobrogus*; **ct**, *S. cristatus*; **gr**, *S. gracilis*; **pl**, *S. parallelliventris*. Other symbols: "-" unknown; "T1" refers to metasomal tergum 1; "T2" refers to metasomal tergum 2; "S2" refers to metasomal sternum 2.

Based on largest and smallest specimens for both female and male of each species.

| Character | su | ca | pr | tu | ni | fu | ap | ab | ct | gr | pl |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **FEMALE** | | | | | | | | | | | |
| Head: height/width | 1.08-1.16 | 1.04-1.06 | 1.02-1.08 | 1.05-1.08 | 1.07 | 1.04-1.05 | 0.95-1.04 | 1.00-1.04 | 0.97-1.00 | 1.00-1.03 | 1.00-1.02 |
| Clypeus: height/width | 0.67-0.70 | 0.63-0.67 | 0.66-0.69 | 0.67-0.68 | 0.73 | 0.70-0.73 | 0.61-0.67 | 0.69-0.70 | 0.68 | 0.71-0.76 | 0.68-0.74 |
| OOL/POL | 0.93-1.00 | 0.98-1.10 | 0.95-1.00 | 1.04-1.20 | 1.13 | 1.06-1.08 | 1.12-1.13 | 0.97-1.17 | 1.00-1.22 | 0.95-1.06 | 1.04-1.06 |
| LOL/POL | 0.50-0.53 | 0.58-0.68 | 0.58-0.63 | 0.52-0.53 | 0.60 | 0.54-0.56 | 0.50-0.56 | 0.57-0.59 | 0.52-0.63 | 0.56 | 0.54-0.59 |
| Foveal diameter/ trans-scutal sulcus length | 1.43-1.60 | 1.17-1.50 | 1.20 | 0.88-1.13 | 1.32 | 1.35-1.50 | 0.86-1.50 | 0.89-1.00 | 0.89-1.67 | 1.00-1.17 | 2.07-2.17 |
| Foveal interval/POL | 0.80-0.84 | 0.64-0.70 | 0.75-0.84 | 0.89-0.98 | 0.87 | 0.70-0.75 | 0.69-0.79 | 0.83-0.84 | 0.69-0.99 | 0.74-1.03 | 0.74-0.81 |
| Propodeal superior shelf length/ trans-scutal sulcus length | 1.57-2.14 | 1.75-1.88 | 0.40-0.75 | 1.13-1.32 | 2.63 | 1.50-1.80 | 1.15-1.75 | 1.53-2.00 | 1.33-1.50 | 1.18-1.33 | 1.32-1.33 |
| T1: postcarinal length/apical width | 0.58-0.64 | 0.71-0.81 | 0.53-0.55 | 0.60-0.63 | 0.75 | 0.75-0.88 | 0.64-0.70 | 0.61-0.71 | 0.61-0.67 | 0.57 | 0.60-0.67 |
| T1: carinal width/ apical width | 0.78-0.82 | 0.71-0.72 | 0.75-0.90 | 0.83-0.87 | 0.77 | 0.64-0.65 | 0.70-0.82 | 0.71-0.78 | 0.70-0.78 | 0.79 | 0.83-0.89 |
| T2: length/width | 0.95-1.00 | 0.93-0.96 | 0.80-0.92 | 0.92-1.00 | 0.99 | 0.86-0.96 | 0.90 | 0.84-0.96 | 0.83-0.88 | 0.82-1.03 | 1.00-1.05 |
| T2+S2 apical margin length/trans-scutal sulcus length | 0.71-1.00 | 0.67-0.75 | 0.80-1.00 | 0.84-0.94 | 0.94 | 0.75-0.90 | 0.97-1.25 | 0.89-1.14 | 0.75-0.89 | 0.43-0.67 | 0.67-0.75 |
| Body length to apex of T2 | 7.5-9.0 | 5.0-9.0 | 6.5-8.5 | 7.0-8.5 | 7.5 | 6.5-9.0 | 6.0-9.5 | 8.5-10.5 | 6.5-11.0 | 8.0-11.5 | 8.5-10.0 |

Table 2. Measurements for *Symmorphus* species (cont.)

| Character | su | cn | pr | tu | ni | fu | ap | ab | ct | gr | pl |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **MALE** | | | | | | | | | | | |
| Antennal article 13: length/width | 0.78-0.80 | 0.75-0.90 | 0.91-0.93 | - | 1.00 | 1.00-1.13 | 0.60-0.67 | 0.67-0.75 | 0.58-0.59 | 0.98-1.00 | 0.86-0.87 |
| Body length to apex of T2 | 6.0-7.0 | 5.0-8.5 | 5.5-8.0 | - | 6.0 | 6.0-8.0 | 5.0-7.0 | 7.0-9.5 | 5.5-9.5 | 6.5-10.5 | 8.0-9.0 |

**Table 3. Character states in *Symmorphus* (part 1)**

Characters denoted by "†" are primary characters used to infer phylogenetic relationships among species in chapter 6.

Species abbreviations: **pa**, *S. parvilineatus*; **mo**, *S. momunganensis*; **ne**, *S. negrosensis*; **ho**, *S. hoozanensis*; **ak**, *S. alkimus*; **am**, *S. ambotretus*; **ca**, *S. canlaonicus*; **dc**, *S. declivis*; **mu**, *S. murarius*; **fo**, *S. foveolatus*; **gl**, *S. glasunowi*; **si**, *S. sichuanensis*; **cr**, *S. crassicornis*; **cp**, *S. captivus*; **an**, *S. angustatus*; **al**, *S. albomarginatus*; **da**, *S. decens*.

Other symbols: "-" state unknown; "*" state absent, route of transformation from plesiomorphic state not inferred; "1/2" intermediate between states 1 and 2; "1/*" similar to state 1 but nearly obsolete; "1,2" dimorphic, with both states 1 and 2; "1→2" states 1 through 2 including intermediates; "1→3" states 1 through 3 including intermediates.

| Character | pa | mo | ne | ho | ak | am | ca | dc | mu | fo | gl | si | cr | cp | an | al | da |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **HEAD** | | | | | | | | | | | | | | | | | |
| 1.† Female clypeal apex<br>-1-broadly and shallowly emarginate<br>0-shallowly emarginate<br>1'-some specimens 1, others 0/1<br>1-moderately emarginate<br>2-deeply emarginate | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1' | 1 | 1 | 1 | 1 | 1→2 | 1 | 1→2 | -1 |
| 2. Male clypeal apex<br>-1-broadly and shallowly emarginate<br>0-shallowly to moderately emarginate<br>1-deeply emarginate | - | - | - | - | 0 | 0 | - | 0 | 0 | 0→1 | 0 | 0 | 0 | 0 | 0 | 0→1 | -1 |
| 3. Female clypeal convexity<br>0-evenly convex<br>0'-as 0, but with apical teeth slightly reflexed anteriorly<br>1-markedly convex through apical third | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 4. Interantennal carina<br>0-prominent<br>1-very faint or absent | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 5.† Ocellar diameter<br>0-unreduced<br>1-reduced | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 6.† Interocellar area<br>0-not elevated<br>1-elevated | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 7.† Cephalic foveal diameter<br>0-small<br>1-moderate<br>2-large | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 3 | 2 | 2 | 2 | 1 | 1 | 1 | 0→1 | 0→1 |

Table 3. Character states in *Symmorphus* (cont.)

| Character | pa | mo | ne | ho | ak | am | ca | dc | mu | fo | gl | si | cr | cp | an | al | dn |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 3-very large | | | | | | | | | | | | | | | | | |
| 8. Cephalic foveal separation<br>0-widely spaced<br>1-moderately spaced<br>2-narrowly spaced | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 0→1 | 1 | 1 | 1→2 | 0 | 0→1 | 0 | 0 |
| 9.† Cephalic foveal carina<br>0-prominent<br>1-faint or absent | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0→1 | 0 | 0 | 0→1 | 0 |
| 10.† Occipital carina<br>0-without submedial incisions<br>1-with 2 submedial incisions | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 11.† Female mandible<br>0-four-toothed<br>1-five-toothed | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 12.† Male antennal tyloids<br>0-present<br>1-absent | - | - | - | - | 0 | 0 | - | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 13.† Male antennal article 13<br>-1-short<br>0-moderately long<br>1-long<br>2-very long | - | - | - | - | 0 | 0 | - | 0 | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 0→1 | 0 |
| **MESOSOMA** | | | | | | | | | | | | | | | | | |
| 14.† Pronotal carina<br>0-complete<br>1-dorsolaterally obsolete<br>1'-dorsomedially obsolete<br>2-dorsally obsolete | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 1' | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0→1' |
| 15. Female humeral angle<br>0-not or barely projected<br>0'-some specimens 0, others 0/1<br>1'-some specimens 1, others 0/1<br>1-slightly projected<br>2'-some specimens 2, others 1/2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1' | 0 | 0' | 0 | 0 | 0' | 0 | 0 | 0→1 | 0 |

Table 3. Character states in *Symmorphus* (cont.)

| Character | pa | mo | ne | ho | ak | am | ca | dc | mu | fo | gl | si | cr | cp | an | al | da |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2-moderately projected<br>3-greatly projected | | | | | | | | | | | | | | | | | |
| 16. Male humeral angle<br>0-barely to slightly projected<br>0'-some specimens 0, others 0/1<br>1-moderately projected<br>1'-some specimens 1, others 1/2<br>2-greatly projected | . | . | . | . | 0 | 0 | . | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0→1' | 0 |
| 17.† Notaulus<br>0-complete<br>1-partially obsolete | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0→1 | 0 | 0 | 0 | 0→1 | 0 | 0→1 | 0→1 | 0 |
| 18.† Female epicnemial carina<br>0-complete<br>1-dorsally obsolete<br>2'-some specimens 2, others 1/2<br>2-entirely obsolete | 0 | 0 | 0 | 2' | 1 | 1 | 1/2 | 1 | 2' | 2 | 2 | 1/2 | 1 | 1 | 2' | 1 | 2 |
| 19.† Pseudosternum, anterior margin<br>0-without high reflexed border<br>1-with high reflexed border | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 20. Metanotum<br>0-nearly vertical, dorsal surface narrow<br>0'-some specimens 0, others 0/1<br>1-not vertical, primarily oblique and/or dorsal surface expanded | 0/1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0/1 | 0/1 | 0/1 | 0/1 | 0/1 | 0' | 1 |
| 21.† Propodeal superior shelf<br>-1-moderately long<br>0-short<br>1-very short<br>2-absent | 0 | 2 | 2 | 0 | 1 | 0 | 0 | 0 | 0→1 | 2 | 2 | 0→1 | 0 | 0 | 0→1 | 0→1 | 0 |
| 22.† Propodeal submedian carina<br>-1-entirely absent<br>0-present ventrally, absent or faint and irregular dorsally<br>1-complete and sharply defined throughout | 0 | -1 | -1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

Table 3. Character states in *Symmorphus* (cont.)

| Character | pa | mo | ne | ho | ak | am | ca | dc | mu | fo | gl | si | cr | cp | aa | al | da |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 23.† Propodeal valvula<br>0-short posteriorly, fused distally to submarginal carina<br>1-produced posteriorly, free distally from submarginal carina | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 24.† Propodeal orifice<br>0-broadly rounded dorsally<br>1-somewhat narrowed dorsally<br>2-narrowly acute dorsally | 2 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| **METASOMA** | | | | | | | | | | | | | | | | | |
| 25. T1 postcarinal length<br>-1-short<br>0-moderate<br>1-long | 0 | -1 | -1 | 0 | -1 | -1→0 | -1 | 0 | -1→0 | 0 | 0 | 0→1 | -1 | -1 | -1→0 | -1 | 0 |
| 26. T1 postcarinal sides: amount convergent towards base<br>0-barely<br>1-slightly<br>2-moderately<br>3-markedly | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 1→2 | 1→2 | 2→3 | 2→3 | 2 | 2 | 1 | 2→3 | 1→2 | 1→2 |
| 27.† T1 transverse carina<br>0-complete<br>1-laterally faint or obsolete | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| 28.† T1 longitudinal furrow<br>0-broadly impressed, very shallowly to shallowly depressed, without deeper narrow medial sulcus<br>1-sharply impressed, shallowly to moderately depressed, with deeper narrow medial sulcus<br>2-broadly impressed, deeply depressed, with deeper narrow medial sulcus | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 29.† T1 depressed apical margin<br>0-distinct<br>1-indistinct | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |

Table 3. Character states in *Symmorphus* (cont.)

| Character | pa | mo | ne | ho | ak | am | ca | dc | mu | fo | gl | si | cr | cp | an | al | dn |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 30.† S1 basal carina<br>0-straight and transverse<br>1-deeply curved posteriorly, fused to lateral oblique ridges<br>1'-some specimens 1, others 1/•<br>2-inflated and raised posteriorly, fused to lateral oblique ridges<br>•-absent | 0 | 0 | 0 | 1 | 1 | 1 | 1 | • | • | • | • | • | • | • | • | • | • |
| 31.† S1 median longitudinal ridge<br>0-present<br>0'-some specimens 0, others 0/1<br>1'-some specimens 1, others 0/1<br>1-absent | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1' | 1 | 1 | 1 | 0' | 0' | 0 | 0 | 0 |
| 32.† S1 lateral oblique ridges<br>0-present<br>1-absent | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 33.† T2 base in profile<br>0-gradually rounded<br>1-obtusely angulate | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 34.† S2 base in profile<br>-1-slightly convex posteriad of basal sulcus<br>0-markedly convex posteriad of basal sulcus<br>1-abruptly truncate posteriad of basal sulcus | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | -1 | -1 | -1 | -1 | -1 | -1 | -1 | -1 | -1 |
| 35.† Segment 2 apical margin<br>0-depressed, markedly developed<br>1-depressed, moderately developed<br>2-not depressed, moderately to slightly developed | 0 | 0 | 0 | 0/1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 1/2 | 2 | 2 | 2 | 2 | 2 |
| **PUBESCENCE** | | | | | | | | | | | | | | | | | |
| 36.† Lengthened setae<br>0-absent<br>1'-some specimens 1, others 0/1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1' | 0 |

Table 3. Character states in *Symmorphus* (cont.)

| Character | pa | mo | ne | ho | ak | am | ca | dc | mu | fo | gl | si | cr | cp | an | al | dn |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1-present | | | | | | | | | | | | | | | | | |
| **BEHAVIOR** | | | | | | | | | | | | | | | | | |
| 37.† Prey type<br>0-external leaf feeding chrysomelid or rarely curculionid larvae<br>1-leaf-mining coleopterous or lepidopterous larvae | · | · | · | · | · | · | · | · | 0 | 0 | · | · | 0 | · | 0 | 0 | 0 |

**Table 4. Character states in *Symmorphus* (part 2)**

Characters denoted by "†" are primary characters used to infer phylogenetic relationships among species in chapter 6.

Species abbreviations: **vi**, *S. violaceipennis*; **mi**, *S. mizuhonis*; **bi**, *S. bifasciatus*; **db**, *S. debilitatus*; **cl**, *S. cliens*; **co**, *S. connexus*; **lu**, *S. lucens*; **su**, *S. sublaevis*; **ca**, *S. canadensis*; **pr**, *S. projectus*; **tu**, *S. tukvarensis*; **ni**, *S. nipteroides*; **fu**, *S. fuscipes*; **ap**, *S. apiciornatus*; **ab**, *S. allobrogus*; **ct**, *S. cristatus*; **gr**, *S. gracilis*; **pl**, *S. parallelíventris*.

Other symbols as in Table 3.

| Character | vi | mi | bi | db | cl | co | lu | su | ca | pr | tu | ni | fu | ap | ab | ct | gr | pl |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **HEAD** | | | | | | | | | | | | | | | | | | |
| 1.† Female clypeal apex<br>-1-broadly and shallowly emarginate<br>0-shallowly emarginate<br>1'-some specimens 1, others 0/1<br>1-moderately emarginate<br>2-deeply emarginate | 2 | 1 | 1 | 0 | 0/1 | 0 | 0→1 | 0 | 0→1 | 0→1 | 0 | 0 | 1' | 0→1 | 1 | 1' | 1' | 1' |
| 2. Male clypeal apex<br>-1-broadly and shallowly emarginate<br>0-shallowly to moderately emarginate<br>1-deeply emarginate | - | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 3. Female clypeal convexity<br>0-evenly convex<br>0'-as 0, but with apical teeth slightly reflexed anteriorly<br>1-markedly convex through apical third | 0' | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 4. Interantennal carina<br>0-prominent<br>1-very faint or absent | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0→1 |
| 5.† Ocellar diameter<br>0-unreduced<br>1-reduced | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 6.† Interocellar area<br>0-not elevated<br>1-elevated | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 7.† Cephalic foveal diameter<br>0-small<br>1-moderate<br>2-large<br>3-very large | 0 | 1 | 1→2 | 1 | 2 | 2 | 2 | 2 | 1→2 | 1 | 1 | 2 | 2 | 2 | 1 | 1→2 | 1 | 2 |

Table 4. Character states in *Symmorphus* (cont.)

| Character | vi | mi | bi | db | cl | co | lu | su | cn | pr | tu | ni | fu | ap | ah | ct | gr | pl |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 8. Cephalic foveal separation<br>0-widely spaced<br>1-moderately spaced<br>2-narrowly spaced | 0 | 0 | 1 | 1 | 0 | 1 | 0→1 | 1 | 1 | 1 | 0→1 | 1 | 1 | 1 | 1 | 0→1 | 0→1 | 1 |
| 9.† Cephalic foveal carina<br>0-prominent<br>1-faint or absent | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0→1 | 1 | 1 | 1 |
| 10.† Occipital carina<br>0-without submedial incisions<br>1-with 2 submedial incisions | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 11.† Female mandible<br>0-four-toothed<br>1-five-toothed | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 12.† Male antennal tyloids<br>0-present<br>1-absent | - | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 13.† Male antennal article 13<br>-1-short<br>0-moderately long<br>1-long<br>2-very long | - | 0 | 0 | -1→0 | -1 | 0 | -1→0 | -1→0 | -1→0 | 0 | - | 0 | 0 | -1 | -1 | -1 | 0 | 0 |
| **MESOSOMA**<br>14.† Pronotal carina<br>0-complete<br>1-dorsolaterally obsolete<br>1'-dorsomedially obsolete<br>2-dorsally obsolete | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 2 |
| 15. Female humeral angle<br>0-not or barely projected<br>0'-some specimens 0, others 0/1<br>1'-some specimens 1, others 0/1<br>1-slightly projected<br>2'-some specimens 2, others 1/2<br>2-moderately projected<br>3-greatly projected | 0/1 | 1 | 1' | 1→2 | 1' | 1 | 0/1 | 1' | 0' | 1→3 | 1 | 1 | 0' | 0' | 0' | 0→1 | 2' | 1 |

Table 4. Character states in *Symmorphus* (cont.)

| Character | vi | mi | bi | db | cl | co | lu | su | cn | pr | tu | ni | fu | ap | ab | ct | gr | pl |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 16. Male humeral angle<br>0-barely to slightly projected<br>0'-some specimens 0, others 0/1<br>1-moderately projected<br>1'-some specimens 1, others 1/2<br>2-greatly projected |  | 0→1 | 0' | 1' | 0' | 0→1 | 0' | 0→1 | 0 | 1→2 |  | 0/1 | 0 | 0 | 0' | 0→1 | 1' | 0/1 |
| 17.† Notaulus<br>0-complete<br>1-partially obsolete | 0→1 | 0→1 | 0→1 | 0 | 0 | 0 | 0→1 | 0 | 0 | 0 | 0 | 0 | 0→1 | 0→1 | 0→1 | 0 | 0 | 0 |
| 18.† Female epicnemial carina<br>0-complete<br>1-dorsally obsolete<br>2'-some specimens 2, others 1/2<br>2-entirely obsolete | 2 | 1/2 | 1 | 1 | 1 | 1 | 1 | 1→2 | 1 | 2' | 2 | 2 | 1 | 1 | 2' | 1→2 | 1 | 1/2 |
| 19.† Pseudosternum, anterior margin<br>0-without high reflexed border<br>1-with high reflexed border | 0 | 0 | 0/1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| 20. Metanotum<br>0-nearly vertical, dorsal surface narrow<br>0'-some specimens 0, others 0/1<br>1-not vertical, primarily oblique and/or dorsal surface expanded | 0/1 | 0' | 0' | 0 | 0' | 0' | 0' | 0 | 0' | 0 | 0 | 0/1 | 0' | 0' | 0' | 0' | 0/1 | 0/1 |
| 21.† Propodeal superior shelf<br>-1-moderately long<br>0-short<br>1-very short<br>2-absent | -1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | -1→0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 22.† Propodeal submedian carina<br>-1-entirely absent<br>0-present ventrally, absent or faint and irregular dorsally<br>1-complete and sharply defined throughout | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 23.† Propodeal valvula | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0' | 0 | 0 | 0 | 0 | 0 |

Table 4. Character states in *Symmorphus* (cont.)

| Character | vi | mi | bi | db | cl | co | lu | su | cn | pr | tu | ni | fu | ap | ab | ct | gr | pl |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0-short posteriorly, fused distally to submarginal carina<br>1-produced posteriorly, free distally from submarginal carina | | | | | | | | | | | | | | | | | | |
| 24.† Propodeal orifice<br>0-broadly rounded dorsally<br>1-somewhat narrowed dorsally<br>2-narrowly acute dorsally | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **METASOMA** | | | | | | | | | | | | | | | | | | |
| 25. T1 postcarinal length<br>-1-short<br>0-moderate<br>1-long | 0→1 | 0 | 0→1 | 0 | 0 | 0 | 0 | 0 | 0→1 | -1 | 0 | 0 | 0→1 | 0 | 0 | 0 | 0 | 0 |
| 26. T1 postcarinal sides: amount convergent towards base<br>0-barely<br>1-slightly<br>2-moderately<br>3-markedly | 1→2 | 1→2 | 2 | 2 | 1 | 1 | 1→2 | 1→2 | 2 | 0→2 | 1 | 2 | 3 | 1→2 | 2 | 2 | 2 | 0→1 |
| 27.† T1 transverse carina<br>0-complete<br>1-laterally faint or obsolete | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 28.† T1 longitudinal furrow<br>0-broadly impressed, very shallowly to shallowly depressed, without deeper narrow medial sulcus<br>1-sharply impressed, shallowly to moderately depressed, with deeper narrow medial sulcus<br>2-broadly impressed, deeply depressed, with deeper narrow medial sulcus | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 29.† T1 depressed apical margin<br>0-distinct<br>1-indistinct | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 30.† S1 basal carina | 1 | 1' | 1' | 1' | 1 | 1 | 1 | 1' | 1 | 1 | 2 | 2 | • | 1 | 1' | 1' | • | • |

**Table 4.** Character states in *Symmorphus* (cont.)

| Character | vi | mi | bi | db | cl | co | lu | su | ca | pr | tu | ni | fu | ap | ab | ct | gr | pl |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0-straight and transverse<br>1-deeply curved posteriorly, fused to lateral oblique ridges<br>1'-some specimens 1, others 1/•<br>2-inflated and raised posteriorly, fused to lateral oblique ridges<br>•-absent | | | | | | | | | | | | | | | | | | |
| 31.† S1 median longitudinal ridge<br>0-present<br>0'-some specimens 0, others 0/1<br>1'-some specimens 1, others 0/1<br>1-absent | 0 | 0' | 0' | 0' | 0' | 0 | 0' | 0→1 | 0 | 0 | 0/1 | 0 | 0→1 | 0' | 0' | 0' | 0→1 | 1 |
| 32.† S1 lateral oblique ridges<br>0-present<br>1-absent | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 33.† T2 base in profile<br>0-gradually rounded<br>1-obtusely angulate | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 34.† S2 base in profile<br>-1-slightly convex posteriad of basal sulcus<br>0-markedly convex posteriad of basal sulcus<br>1-abruptly truncate posteriad of basal sulcus | -1 | -1 | -1 | -1 | -1 | -1 | -1 | -1 | -1 | -1 | -1 | -1 | -1 | -1 | -1 | -1 | -1 | -1 |
| 35.† Segment 2 apical margin<br>0-depressed, markedly developed<br>1-depressed, moderately developed<br>2-not depressed, moderately to slightly developed | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| **PUBESCENCE** | | | | | | | | | | | | | | | | | | |
| 36.† Lengthened setae<br>0-absent<br>1'-some specimens 1, others 0/1<br>1-present | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

Table 4. Character states in *Symmorphus* (cont.)

| Character | vi | mi | bi | db | cl | co | lu | su | cn | pr | tu | ni | fu | ap | ab | ct | gr | pl |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **BEHAVIOR** | | | | | | | | | | | | | | | | | | |
| 37.† Prey type<br>0-external leaf feeding chrysomelid or rarely curculionid larvae<br>1-leaf-mining coleopterous or lepidopterous larvae | - | - | 0 | 1 | - | 1 | - | - | 1 | - | - | - | - | - | 0 | 0 | 0 | - |

**Table 5. Chorological affinities in *Symmorphus* (part 1)**

Species abbreviations: **pa**, *S. parvilineatus*; **mo**, *S. momunganensis*; **ne**, *S. negrosensis*; **ho**, *S. hoozanensis*; **aka**, *S. alkimus alkimus*; **akd**, *S. alkimus dialeukus*; **am**, *S. ambotretus*; **ca**, *S. canlaonicus*; **dc**, *S. declivis*; **mu**, *S. murarius*; **fo**, *S. foveolatus*; **gl**, *S. glasunowi*; **si**, *S. sichuanensis*; **cr**, *S. crassicornis*; **cp**, *S. captivus*; **an**, *S. angustatus*; **ala**, *S. albomarginatus albomarginatus*; **alm**, *S. albomarginatus midas*; **dn**, *S. decens*.

A—species that are allopatric. S—species that are broadly sympatric. S*—species that are questionably or narrowly sympatric.

| Species | pa | mo | ne | ho | aka | akd | am | ca | dc | mu | fo | gl | si | cr | cp | an | ala | alm | da |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *S. parvilineatus* | - | | | | | | | | | | | | | | | | | | |
| *S. momunganensis* | A | - | | | | | | | | | | | | | | | | | |
| *S. negrosensis* | A | A | - | | | | | | | | | | | | | | | | |
| *S. hoozanensis* | A | A | A | - | | | | | | | | | | | | | | | |
| *S. alkimus alkimus* | A | A | A | A | - | | | | | | | | | | | | | | |
| *S. alkimus dialeukus* | A | A | A | A | A | - | | | | | | | | | | | | | |
| *S. ambotretus* | S | A | A | A | A | A | - | | | | | | | | | | | | |
| *S. canlaonicus* | A | A | S | A | A | A | A | - | | | | | | | | | | | |
| *S. declivis* | A | A | A | A | A | A | A | A | - | | | | | | | | | | |
| *S. murarius* | A | A | A | A | A | A | A | A | S | - | | | | | | | | | |
| *S. foveolatus* | A | A | A | A | A | A | A | A | A | S | - | | | | | | | | |
| *S. glasunowi* | A | A | A | A | A | A | A | A | A | S | A | - | | | | | | | |
| *S. sichuanensis* | A | A | A | A | A | A | S | A | A | A | A | A | - | | | | | | |
| *S. crassicornis* | A | A | A | A | A | A | A | A | S | S | A | S | A | - | | | | | |
| *S. captivus* | A | A | A | A | A | A | A | A | A | A | S | A | A | A | - | | | | |
| *S. angustatus* | A | A | A | A | A | A | A | A | S | S | S | A | A | S | A | - | | | |
| *S. albomarginatus albomarginatus* | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A | - | | |
| *S. albomarginatus midas* | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A | - | |
| *S. decens* | A | A | A | A | A | A | A | A | A | A | S | A | A | A | S | A | A | A | - |
| *S. violaceipennis* | S | A | A | A | A | A | S | A | A | A | A | A | A | A | A | A | A | A | A |
| *S. mizuhonis* | A | A | A | S | A | A | S | A | A | S | S | A | S | S* | S | S | A | A | S |
| *S. bifasciatus* | A | A | A | A | A | A | A | A | S | S | S | S | A | S | S | S | A | A | S |
| *S. debilitatus* | A | A | A | A | A | A | A | A | S | S | A | A | A | S | A | S | A | A | A |
| *S. cilens* | A | A | A | A | A | A | A | A | A | A | S | A | A | A | S | A | A | A | S |
| *S. connexus* | A | A | A | A | A | A | A | A | S* | S | A | S* | A | S | A | S | A | A | A |
| *S. lucens* | A | A | A | A | A | A | A | A | A | S | S | A | A | S | S | S | A | A | S |
| *S. sublaevis* | A | A | A | A | A | A | A | A | A | S | A | S | A | S | A | A | A | A | A |
| *S. canadensis* | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A | S | A | A |
| *S. projectus* | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A | S | A | A |
| *S. tukvarensis* | S | A | A | A | A | A | S | A | A | A | A | A | A | S | A | A | A | A | A |
| *S. nipteroides* | A | A | A | A | A | A | A | A | A | A | A | A | A | S | A | A | A | A | A |
| *S. fuscipes* | A | A | A | A | A | A | A | A | S* | S | S | A | A | S | A | S | A | A | A |
| *S. apiciornatus* | A | A | A | A | A | A | S* | A | A | S | S | A | S* | A | S | S | A | A | S |
| *S. allobrogus* | A | A | A | A | A | A | A | A | S | S | S | S* | A | S | A | S | A | A | A |
| *S. cristatus* | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A | S | A | A |
| *S. gracilis* | A | A | A | A | A | A | A | A | S | S | A | S | A | S | A | S | A | A | A |
| *S. paralleliventris* | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A |

**Table 6. Chorological affinities in *Symmorphus* (part 2)**

Species abbreviations: vi, *S. violaceipennis*; mi, *S. mizuhonis*; bi, *S. bifasciatus*; db, *S. debilitatus*; cl, *S. cliens*; co, *S. connexus*; lu, *S. lucens*; su, *S. sublaevis*; cn, *S. canadensis*; pr, *S. projectus*; tu, *S. tukvarensis*; ni, *S. nipteroides*; fu, *S. fuscipes*; ap, *S. apiciornatus*; ab, *S. allobrogus*; ct, *S. cristatus*; gr, *S. gracilis*; pl, *S. parallelliventris*.

A—species that are allopatric. S—species that are broadly sympatric. S*—species that are questionably or narrowly sympatric.

| Species | vi | mi | bi | db | cl | co | lu | su | cn | pr | tu | ni | fu | ap | ab | ct | gr | pl |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *S. violaceipennis* | : | | | | | | | | | | | | | | | | | |
| *S. mizuhonis* | A | - | | | | | | | | | | | | | | | | |
| *S. bifasciatus* | A | S | - | | | | | | | | | | | | | | | |
| *S. debilitatus* | A | A | S | - | | | | | | | | | | | | | | |
| *S. cliens* | A | S | S | A | - | | | | | | | | | | | | | |
| *S. connexus* | A | S* | S | S | A | - | | | | | | | | | | | | |
| *S. lucens* | A | S | S | A | S | S | - | | | | | | | | | | | |
| *S. sublaevis* | A | A | S | A | A | S | A | - | | | | | | | | | | |
| *S. canadensis* | A | A | A | A | A | A | A | A | - | | | | | | | | | |
| *S. projectus* | A | A | A | A | A | A | A | A | S | - | | | | | | | | |
| *S. tukvarensis* | S | A | A | A | A | A | A | A | A | A | - | | | | | | | |
| *S. nipteroides* | A | A | A | A | A | A | A | A | A | A | A | - | | | | | | |
| *S. fuscipes* | A | S | S | S | A | S | S | A | A | A | A | A | - | | | | | |
| *S. apiciornatus* | A | S | S | A | S | A | S | A | A | A | A | A | S | - | | | | |
| *S. allobrogus* | A | S | S | S | A | S | S | S | A | A | A | A | S | S | - | | | |
| *S. cristatus* | A | A | A | A | A | A | A | A | S | S | A | A | A | A | A | - | | |
| *S. gracilis* | A | A | S | S | A | S | A | S | A | A | A | A | S | A | S | A | - | |
| *S. parallelliventris* | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A | |

**Figures 1 to 8.** Structures, terms and measurements in *Symmorphus*. Scale bars = 200 μm. Abbreviations: **aw**, apical width of metasomal tergum 1; **bc**, basal carina; **bs**, basal sulcus of metasomal sternum 2; **cl**, clypeus; **clh**, clypeal height; **clw**, clypeal width; **cw**, carinal width of metasomal tergum 1; **dmes**, dorsal mesepisternum; **epc**, epicnemial carina; **fv**, cephalic foveae; **fvi**, cephalic foveal interval; **hh**, head height; **hw**, head width; **iac**, interantennal carina; **LOL**, lateral ocellar line; **lor**, lateral oblique ridge; **mem**, mesepimeron; **mlr**, median longitudinal ridge; **mn**, metanotum; **mtp**, metapleuron; **no**, notaulus; **pc**, pronotal carina; **pcl**, postcarinal length of metasomal tergum 1; **pd**, propodeum; **pds**, propodeal superior shelf; **pn**, pronotum; **POL**, posterior ocellar line; **OOL**, ocular ocellar line; **sc**, mesoscutum; **scl**, mesoscutellum; **tc**, transverse carina; **tg**, tegula; **tsa**, trans-scutal articulation; **tss**, trans-scutal sulcus; **vmes**, ventral mesepisternum.

**Figure 1.** *S. projectus*, frontal view of female head.

**Figure 2.** *S. decens*, frontal view of female frons and clypeus.

**Figure 3.** *S. projectus*, dorsal view of female vertex.

**Figure 4.** *S. connexus*, lateral view of mesosoma.

**Figure 5.** *S. connexus*, dorsal view of mesosoma.

**Figure 6.** *S. decens*, dorsal view of mesonotum.

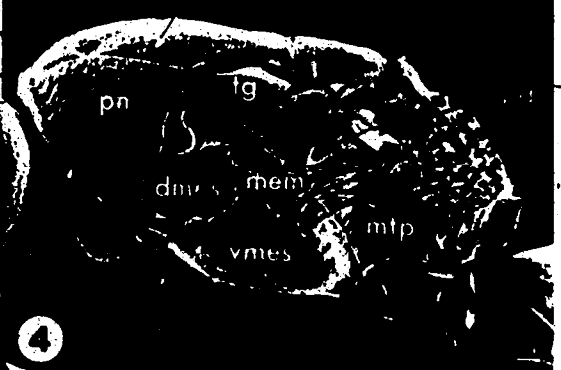
**Figure 7.** *S. albomarginatus*, dorsal view of metasomal segment 1.

**Figure 8.** *S. albomarginatus*, ventral view of metasomal segment 1.


hw
d
1


clw
ch
2


OOL
LOL
POL
3


pn
tg
dmes
mem
mtp
vmes
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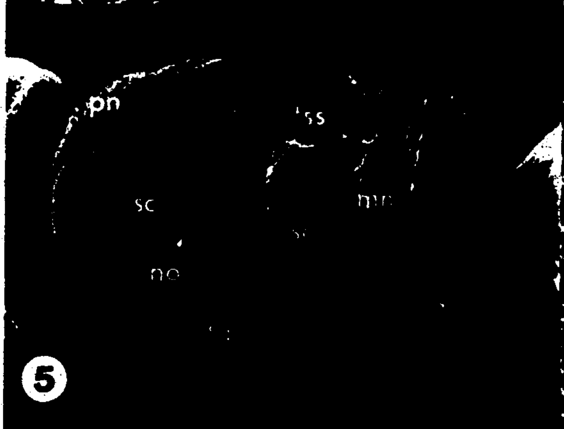
pn
tss
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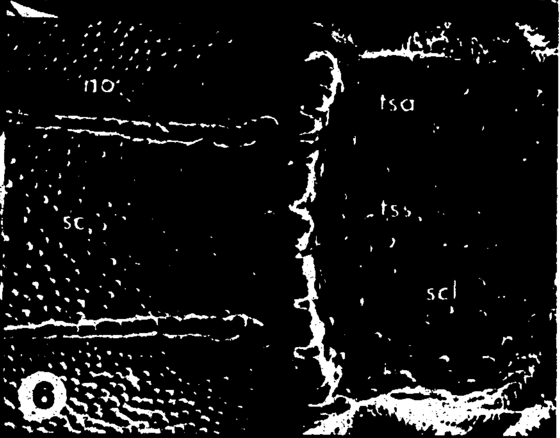
5


no
sc
tsa
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cw
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8

Figures 9 to 16. Structures and terms in *Symmorphus*. Scale bars = 400 μm. Abbreviations: **dmes**, dorsal mesepisternum; **epc**, epicnemial carina; **fvc**, cephalic foveal carina; **ioa**, interocellar area; **lf**, longitudinal furrow; **ms**, medial sulcus; **oc**, occipital carina; **pc**, pronotal carina; **pn**, pronotum; **smc**, submedian carina; **tc**, transverse carina; **t2**, metasomal tergum 2.

**Figure 9.** *S. momunganensis*, lateral view of mesosoma.

**Figure 10.** *S. negrosensis*, oblique dorsal view of female head.

**Figure 11.** *S. ambotretus*, dorsal view of metasomal segments 1 and 2.

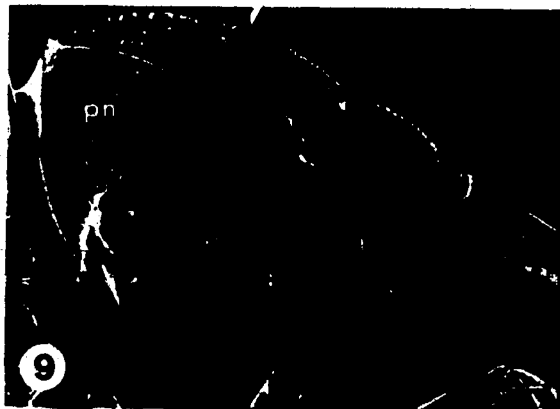
**Figure 12.** *S. canadensis*, oblique dorsal view of metasomal segments 1 and 2.

**Figure 13.** *S. ambotretus*, dorsal view of male head and pronotum.

**Figure 14.** *S. decens*, dorsal view of female vertex.

**Figure 15.** *S. fuscipes*, posterior view of propodeum.

**Figure 16.** *S. fuscipes*, lateral view of mesosoma.



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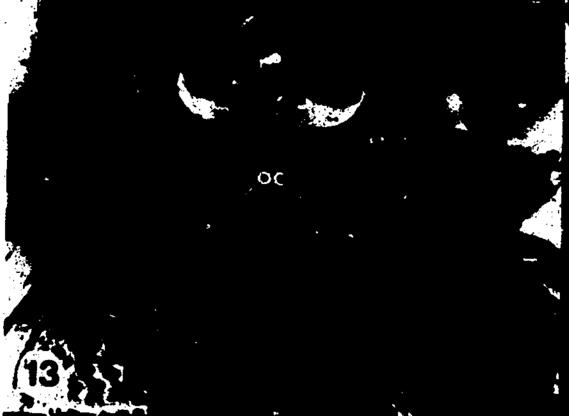

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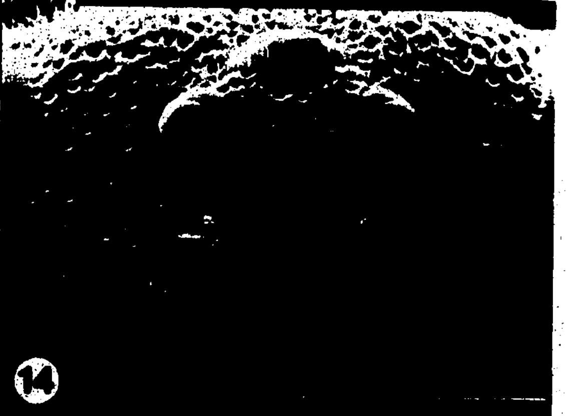

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Figures 17 to 24. Structures and terms in *Symmorphus*. Scale bars = 400 µm. Abbreviations: **amps**, anterior margin of pseudosternum of mesopleuron; **bs**, basal sulcus of metasomal sternum 2; **ioa**, interocellar area; **lor**, lateral oblique ridge; **mlr**, median longitudinal ridge; **pn**, pronotum; **psc**, posterolateral projection of submarginal carina; **sc**, mesoscutum; **t1**, metasomal tergum 1; **vl**, propodeal valvula; **vmes**, ventral mesepisternum.

**Figure 17.** *S. gracilis*, oblique dorsal view of female head and mesosoma.

**Figure 18.** *S. gracilis*, ventral view of mesosoma.

**Figure 19.** *S. albomarginatus*, ventral view of mesosoma.

**Figure 20.** *S. albomarginatus*, ventral view of metasomal segment 1.

**Figure 21.** *S. foveolatus*, lateral view of mesosoma.

**Figure 22.** *S. mizuhonis*, lateral view of mesosoma.

**Figure 23.** *S. mizuhonis*, lateral view of propodeum.

**Figure 24.** *S. murarius*, lateral view of propodeum.

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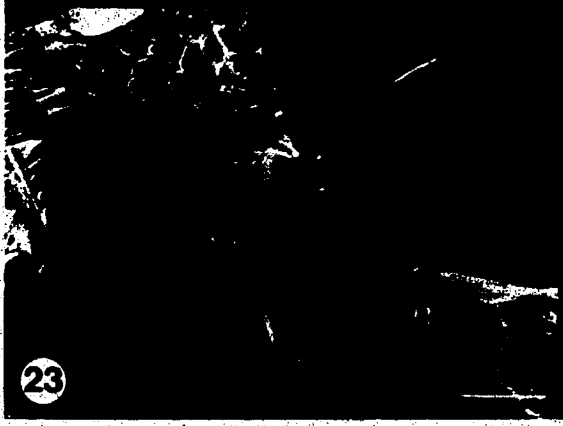

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Figures 25 to 32. Structures and terms in *Symmorphus*. Scale bars = 400 μm, except figure 28 where scale bar = 200 μm. Abbreviations: **fv**, cephalic foveae; **mtp**, metapleuron; **pd**, propodeum; **pdo**, propodeal orifice; **tc**, transverse carina; **ty**, tyloids; **t2**, metasomal tergum 2; **vl**, propodeal valvula.

Figure 25. *S. murarius*, posterolateral view of propodeum and metasomal segment 1.

Figure 26. *S. foveolatus*, posterolateral view of propodeum and metasomal segment 1.

Figure 27. *S. murarius*, dorsal view of female vertex.

Figure 28. *S. sublaevis*, male antennal apex.

Figure 29. *S. canadensis*, dorsal view of metasomal segment 2.

Figure 30. *S. angustatus*, dorsal view of metasomal segment 1.

Figure 31. *S. angustatus*, lateral view of propodeum.

Figure 32. *S. crassicornis*, lateral view of propodeum.

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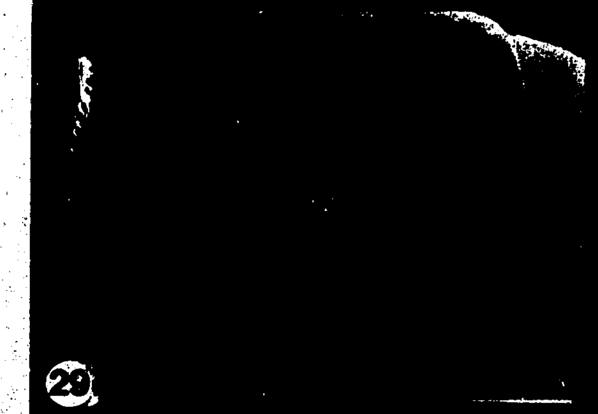

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**Figures 33 to 40**. Structures and terms in *Symmorphus*. Scale bars=400 $\mu$m. Abbreviations: **bc**, basal carina; **bs**, basal sulcus of metasomal sternum 2; **dmes**, dorsal mesepisternum; **dpds**, medial depression of propodeal superior shelf; **lor**, lateral oblique ridge; **mtp**, metapleuron; **pdo**, propodeal orifice; **vmes**, ventral mesepisternum.

**Figure 33**. *S. angustatus*, posterior view of female propodeum.

**Figure 34**. *S. crassicornis*, posterior view of female propodeum.

**Figure 35**. *S. tukvarensis*, oblique ventral view of metasomal segment 1.

**Figure 36**. *S. apiciornatus*, posterolateral view of propodeum.

**Figure 37**. *S. apiciornatus*, lateral view of propodeum.

**Figure 38**. *S. bifasciatus*, lateral view of mesosoma.

**Figure 39**. *S. allobrogus*, lateral view of mesosoma.

**Figure 40**. *S. debilitatus*, lateral view of mesosoma.

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**Figures 41 to 48.** Structures and terms in *Symmorphus*. Scale bars = 400 μm. Abbreviations: **amg**, apical margin of metasomal segment 2; **ha**, humeral angle of pronotum; **iac**, interantennal carina; **pc**, pronotal carina; **sc**, mesoscutum; **smc**, submedian carina; **t1**, metasomal tergum 1; **t2**, metasomal tergum 2.

**Figure 41.** *S. sublaevis*, oblique dorsal view of metasoma.

**Figure 42.** *S. lucens*, oblique dorsal view of metasoma.

**Figure 43.** *S. allobrogus*, oblique posterior view of propodeum.

**Figure 44.** *S. connexus*, oblique posterior view of propodeum.

**Figure 45.** *S. debilitatus*, oblique dorsal view of female head and mesosoma.

**Figure 46.** *S. connexus*, oblique dorsal view of female head and mesosoma.

**Figure 47.** *S. bifasciatus*, oblique dorsal view of female head and mesosoma.

**Figure 48.** *S. projectus*, frontal view of frons and clypeus.

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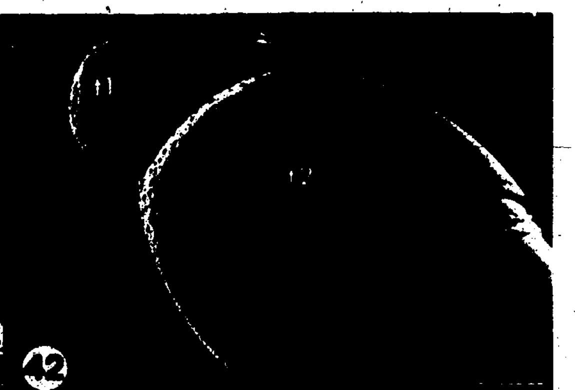

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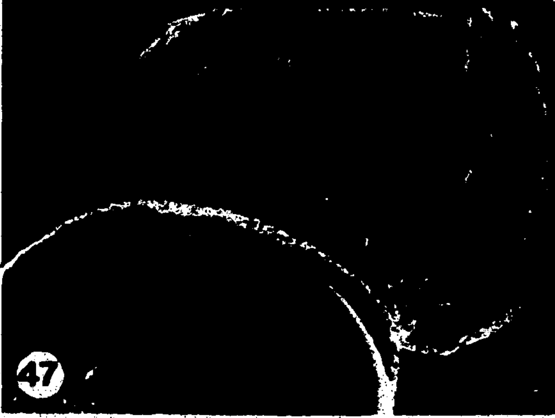

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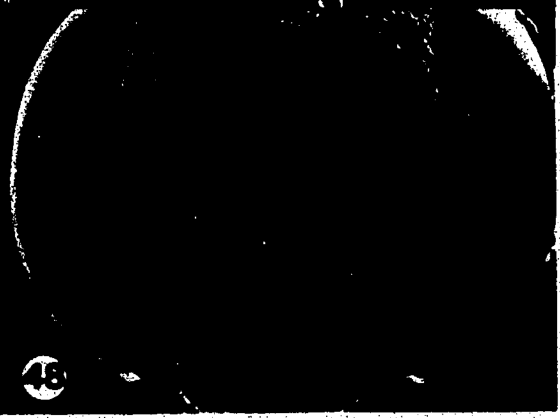

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**Figures 49 to 54**. Structures and terms in *Symmorphus*. Scale bars = 1.0 mm. Abbreviations: **amg**, apical margin of metasomal segment 2; **bs**, basal sulcus of metasomal sternum 2; **pdo**, propodeal orifice; **psc**, posterolateral projection of submarginal carina; **t2**, metasomal tergum 2; **vl**, propodeal valvula.

**Figure 49**. *S. momunganensis*, posterolateral view of propodeum.

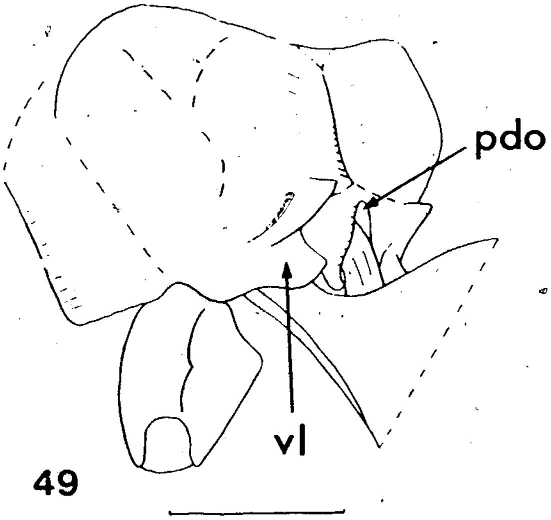
**Figure 50**. *S. negrosensis*, posterolateral view of propodeum.

**Figure 51**. *S. alkimus*, posterolateral view of propodeum.

**Figure 52**. *S. alkimus*, lateral view of metasomal segments 1 and 2.

**Figure 53**. *S. momunganensis*, lateral view of metasomal segments 1 and 2.

**Figure 54**. *S. gracilis*, lateral view of metasomal segments 1 and 2.



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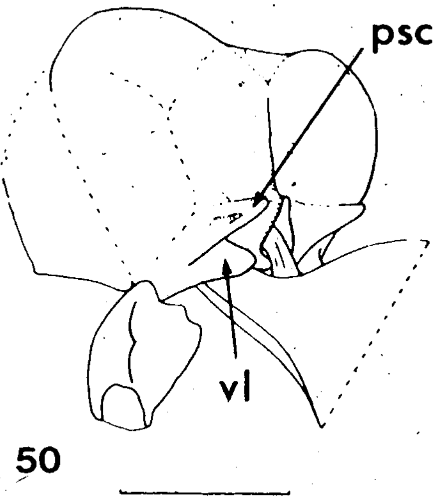

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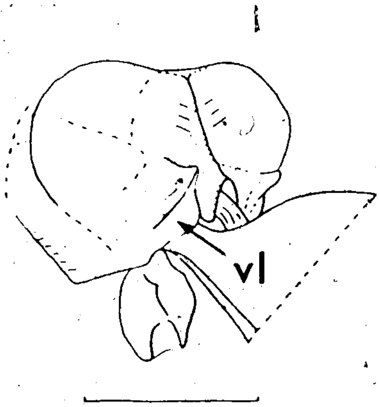

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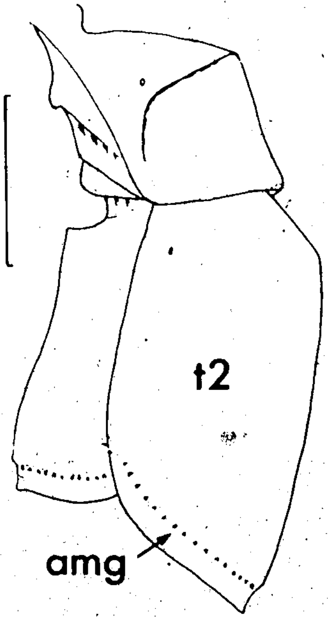

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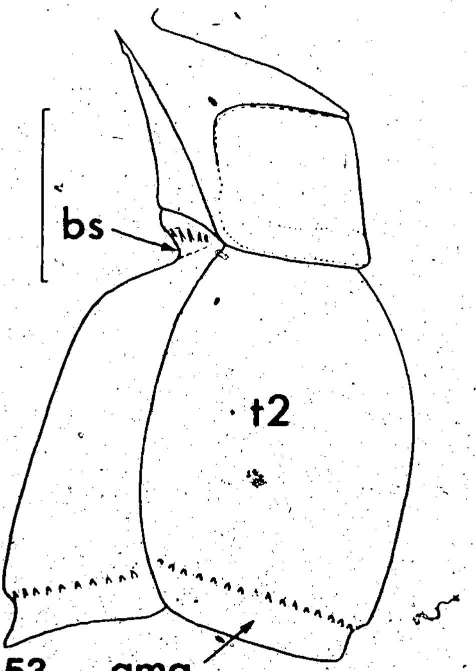

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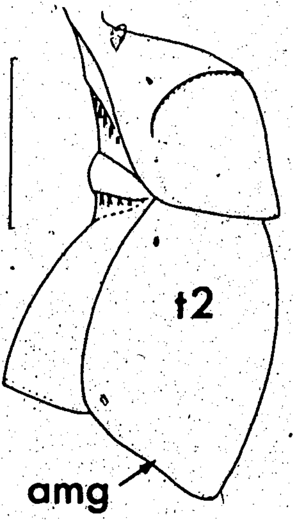


54

Figures 55 to 60. Structures and terms in *Symmorphus*. Scale bars = 0.5 mm, except figure 55 where scale bar = 1.0 mm. Abbreviations: **cl**, clypeus; **pc**, pronotal carina.

**Figure 55.** *S. momunganensis*, anterior face of pronotum.

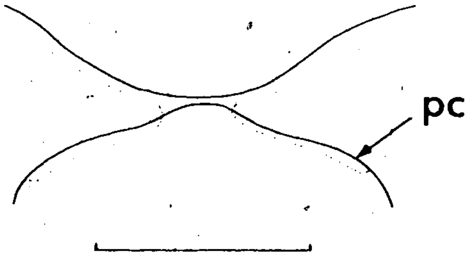
**Figure 56.** *S. decens*, male clypeus.

**Figure 57.** *S. alkimus*, female clypeus.

**Figure 58.** *S. allobrogus*, female clypeus.

**Figure 59.** *S. violaceipennis*, female clypeus.

**Figure 60.** *S. connexus*, lateral view of female head.



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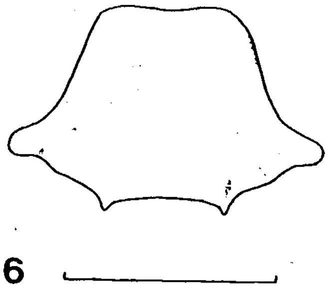

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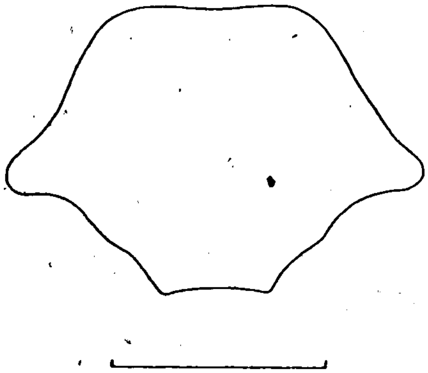

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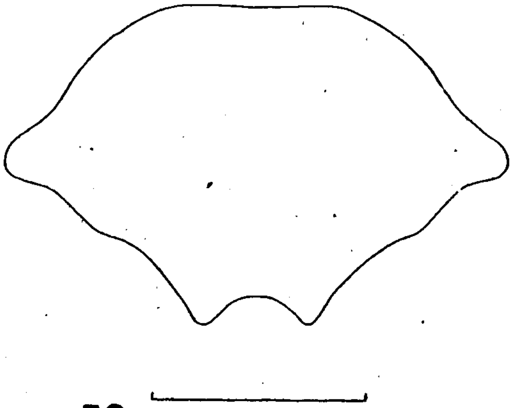

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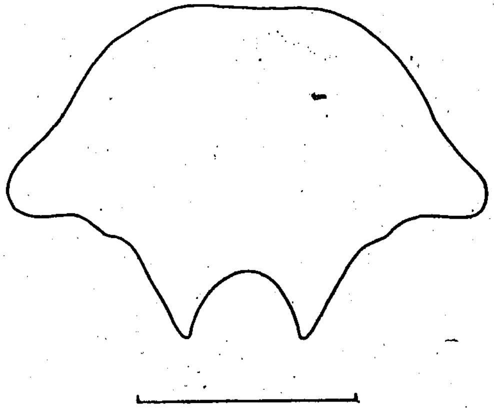

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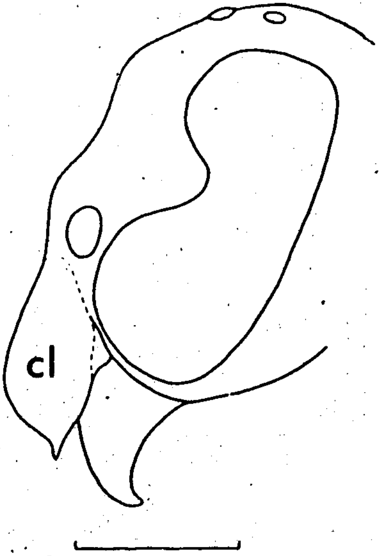

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**Figure 61**. Geographical distribution of *S. parvilineatus*, *S. momunganensis* and *S. negrosensis*.

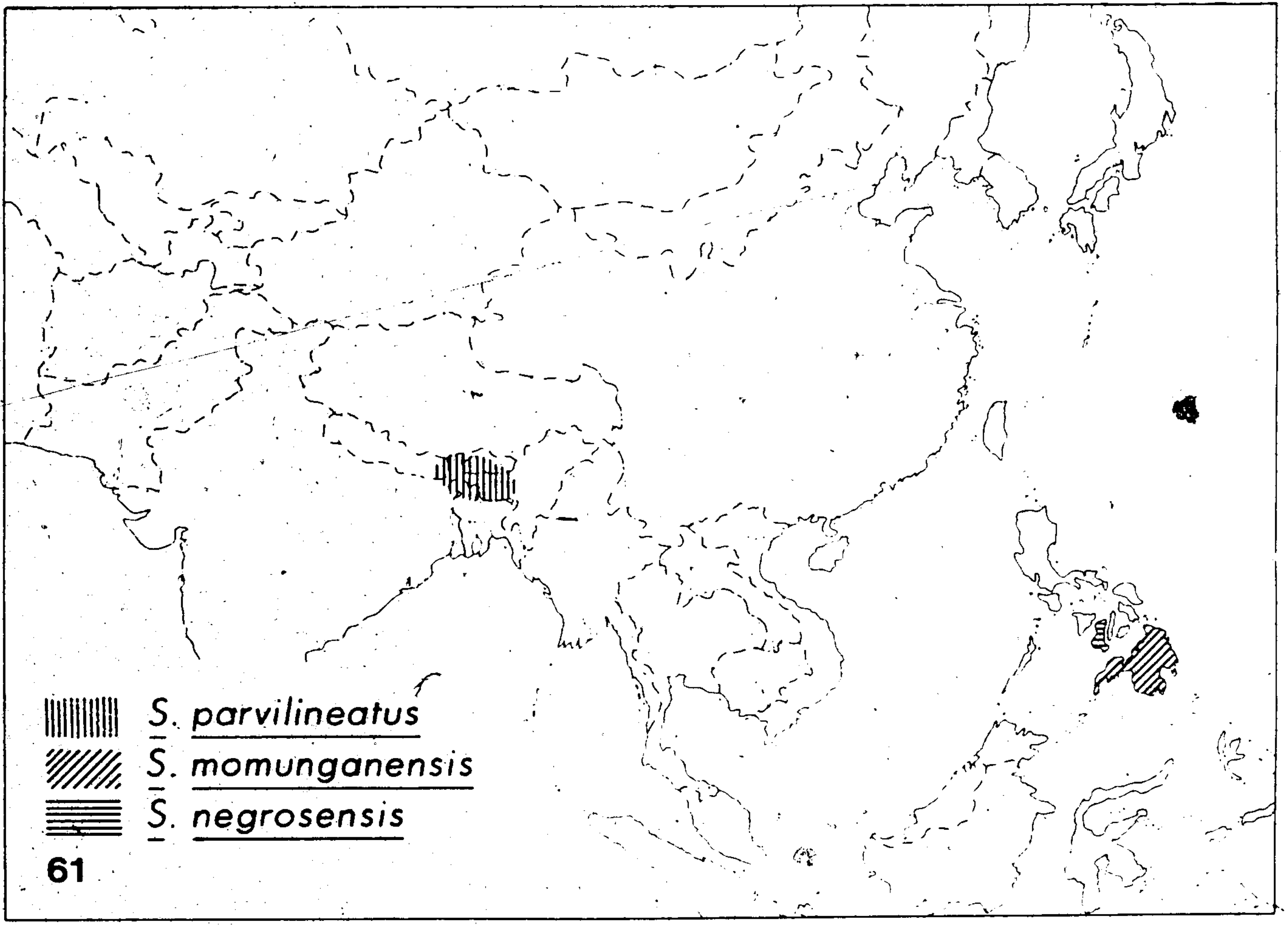

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**Figure 62**. Geographical distribution of *S. hoozanensis* and *S. alkimus*.

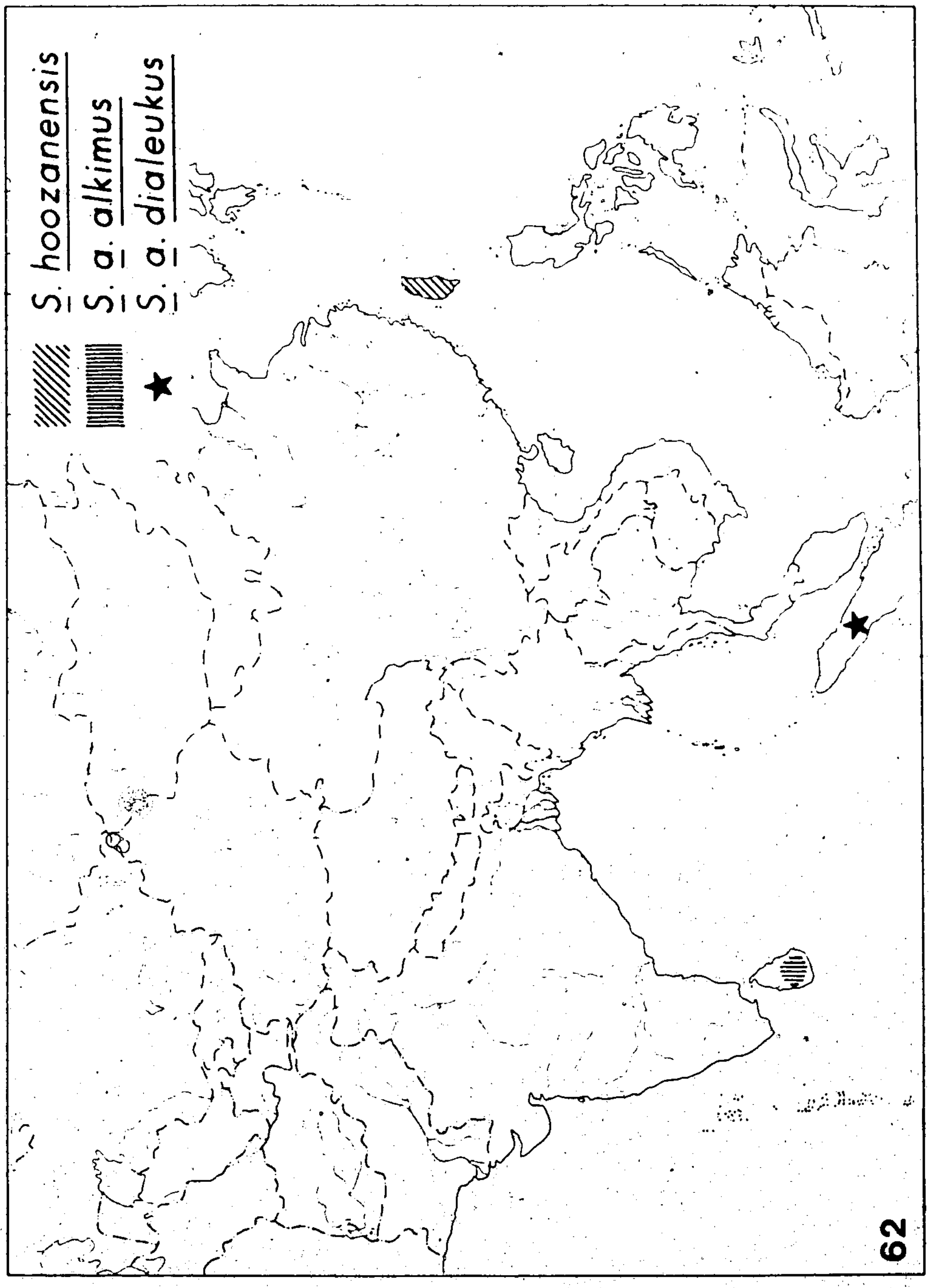

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Figure 63. Geographical distribution of *S. ambotretus* and *S. canlaonicus*.

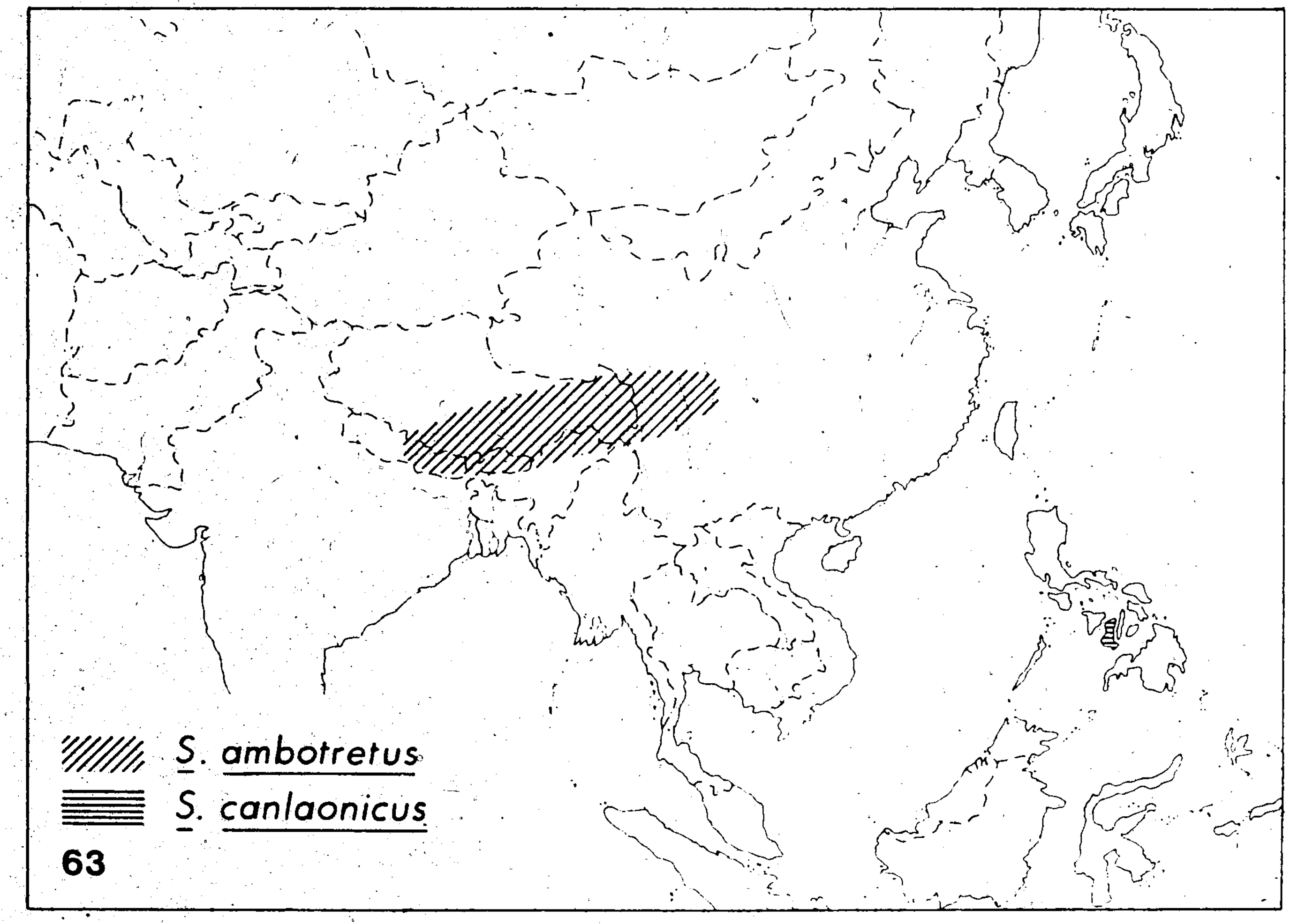
▨ S. ambotretus
▤ S. canlaonicus
63

Figure 64. Geographical distribution of *S. declivis* and *S. murarius*.

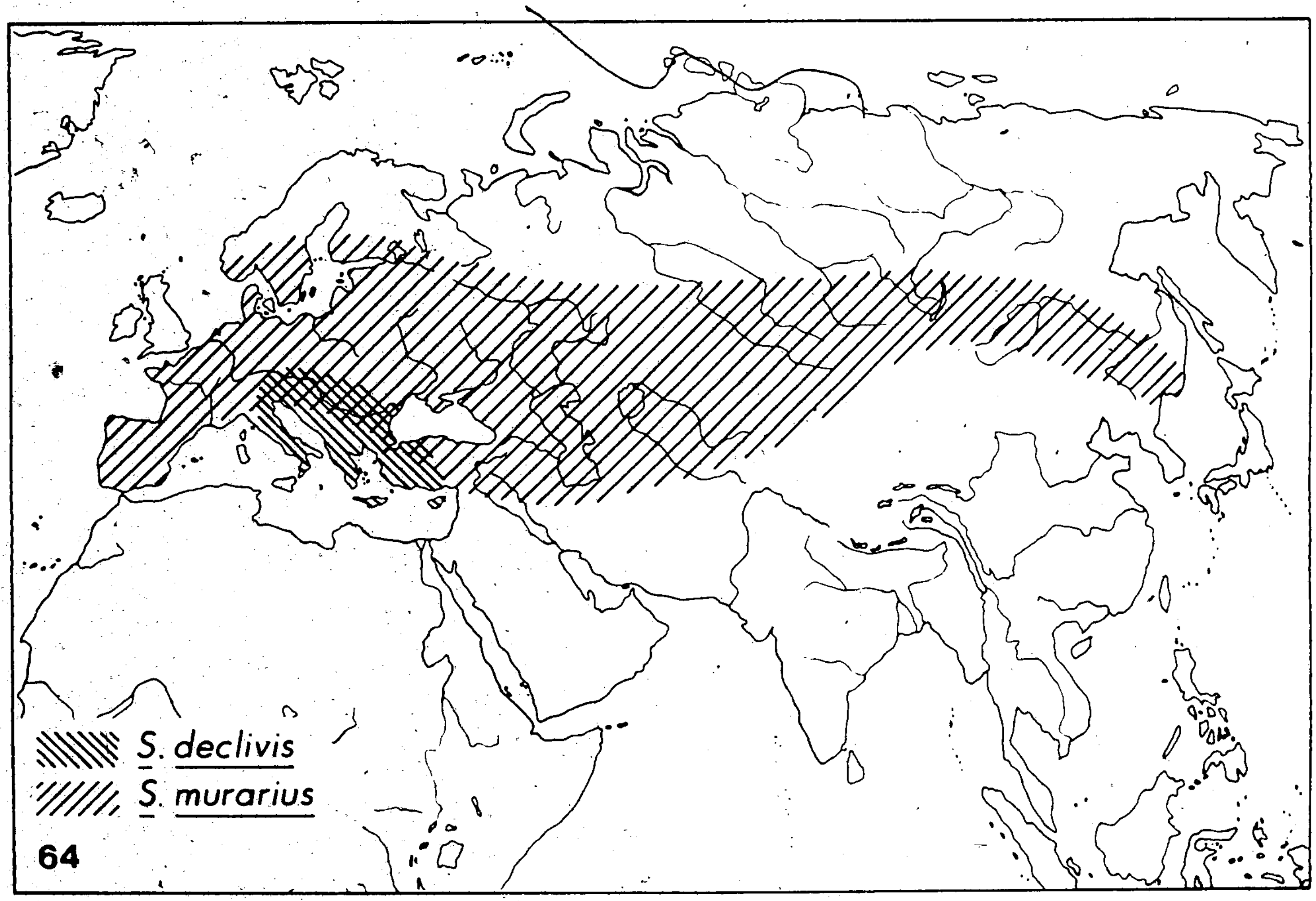
S. declivis
S. murarius
64

**Figure 65**. Geographical distribution of *S. foveolatus*, *S. glasunowi* and *S. sichuanensis*.

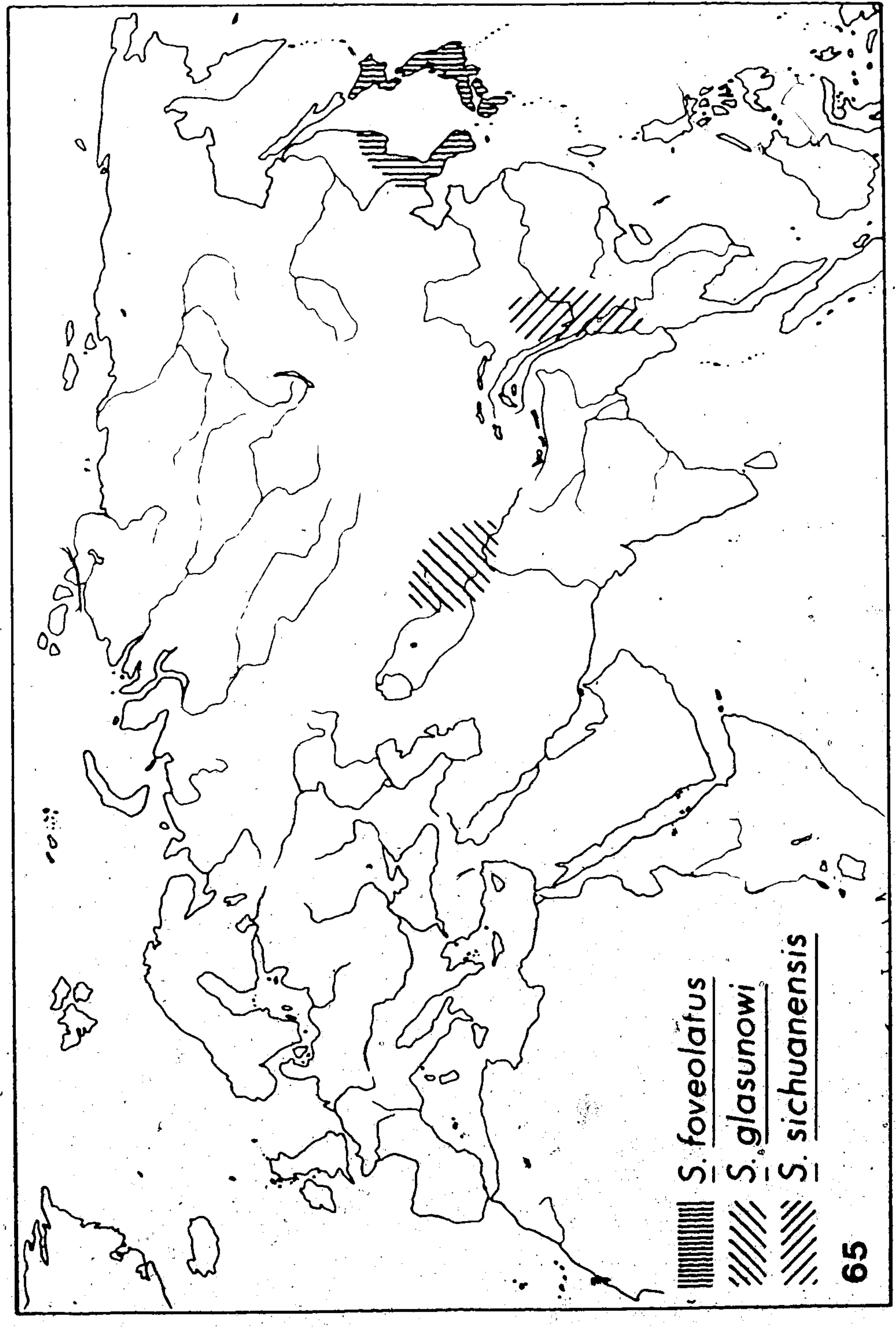

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Figure 66. Geographical distribution of *S. crassicornis* and *S. captivus*.

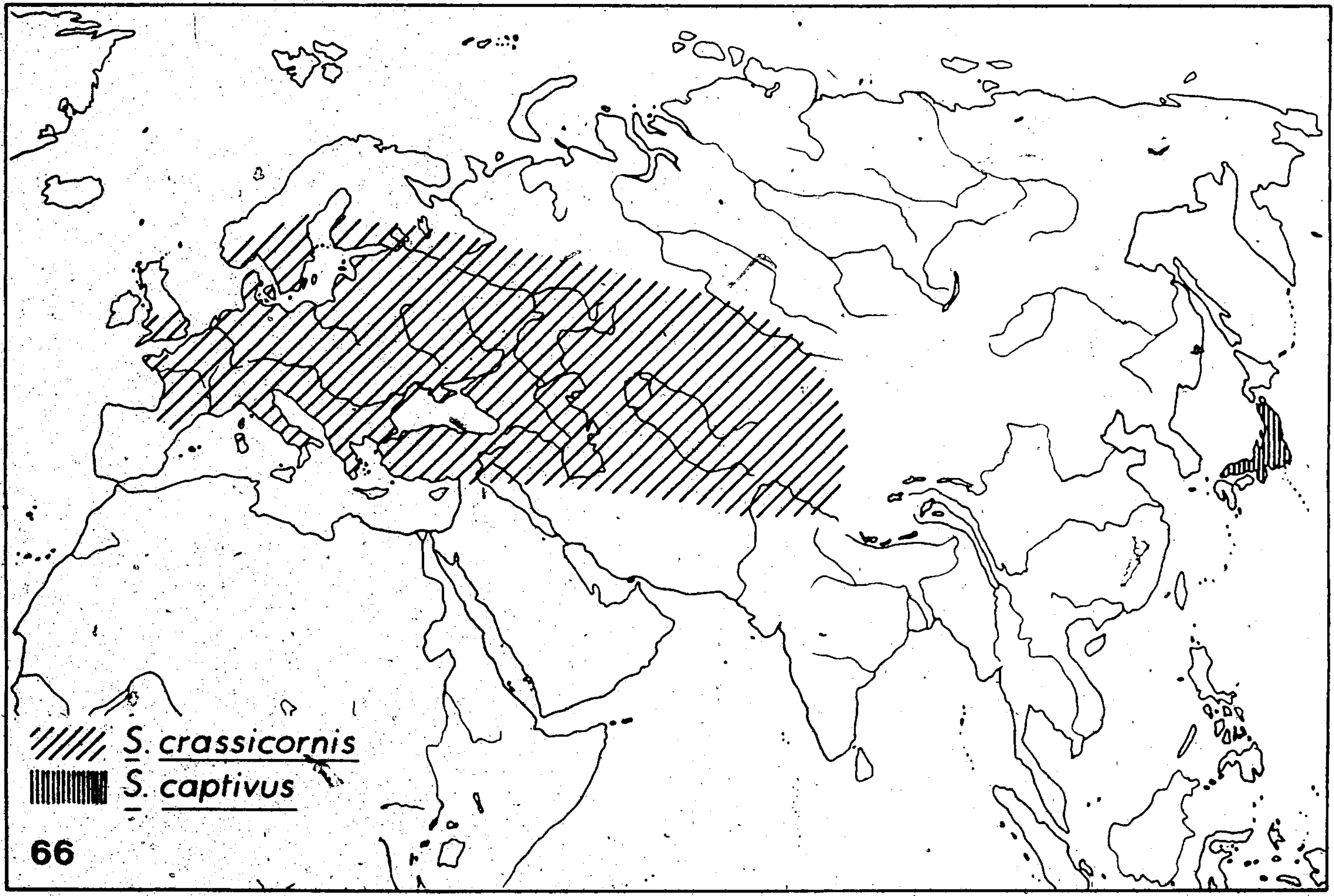

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**Figure 67**. Geographical distribution of *S. angustatus* and *S. decens*.

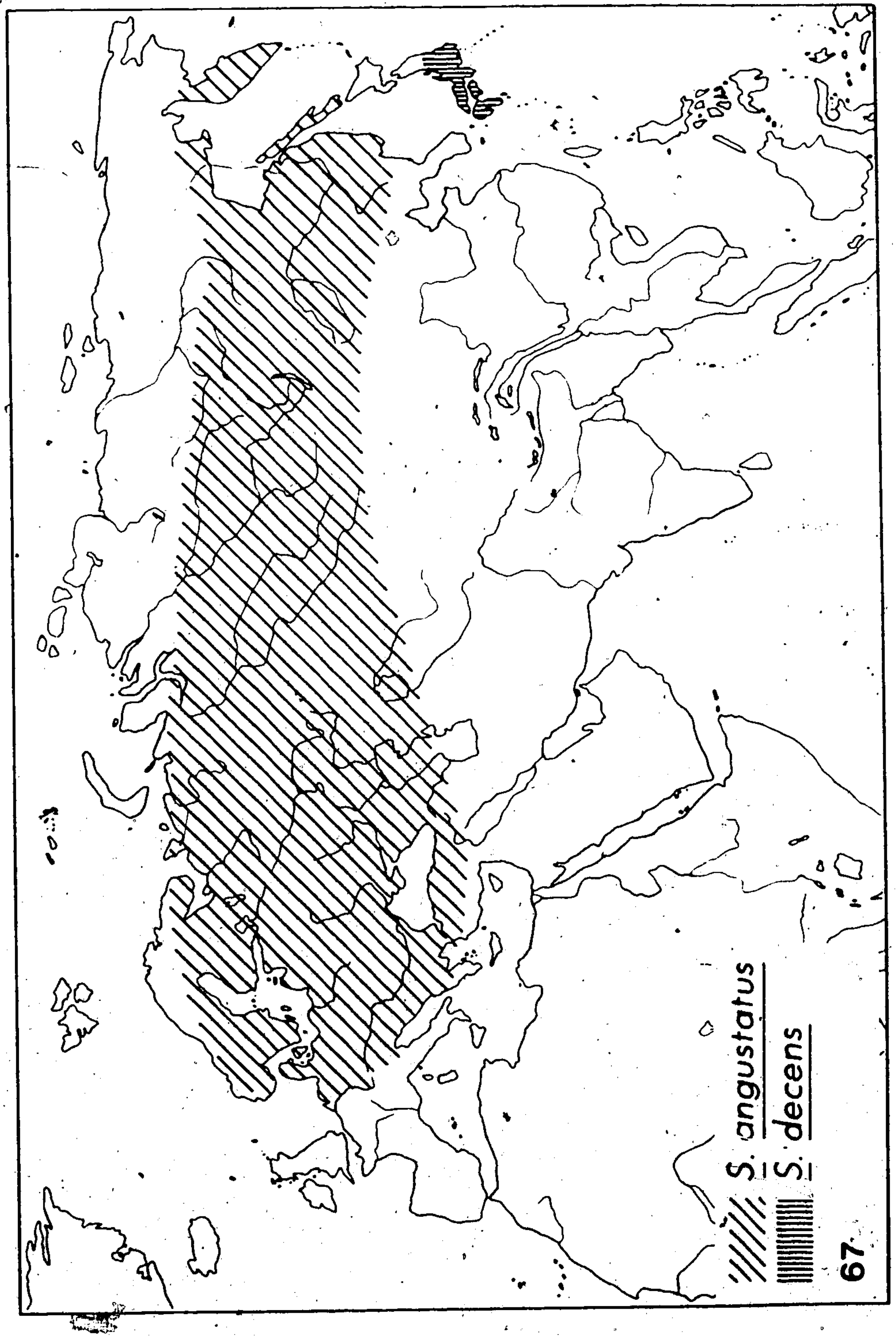
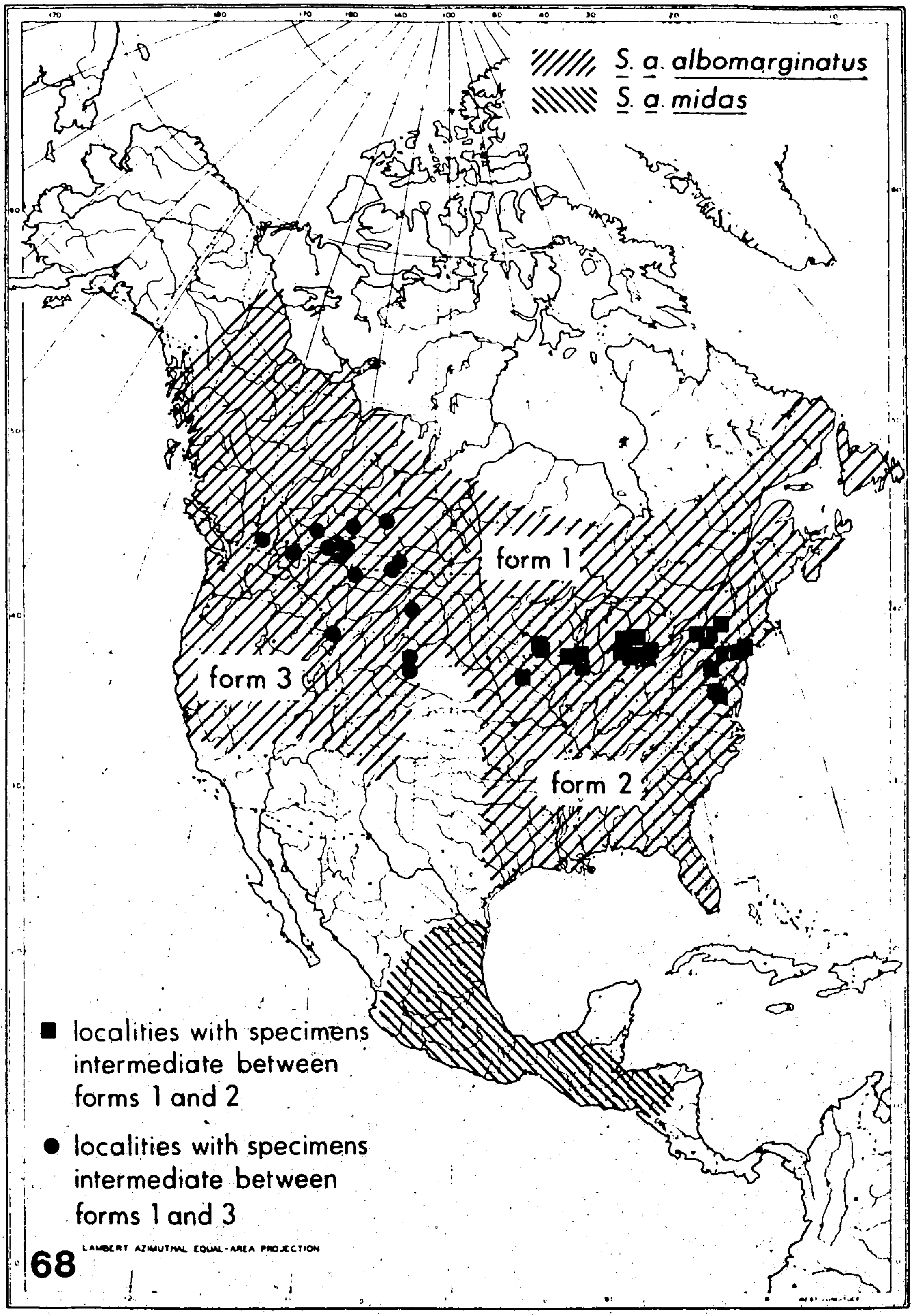

S. angustatus
S. decens
67

**Figure 68**. Geographical distribution of *S. albomarginatus*.



▨ S. a. albomarginatus
▧ S. a. midas
form 1
form 2
form 3
■ localities with specimens intermediate between forms 1 and 2
● localities with specimens intermediate between forms 1 and 3
68
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION

**Figure 69**. Geographical distribution of *S. violaceipennis* and *S. mizuhonis*.

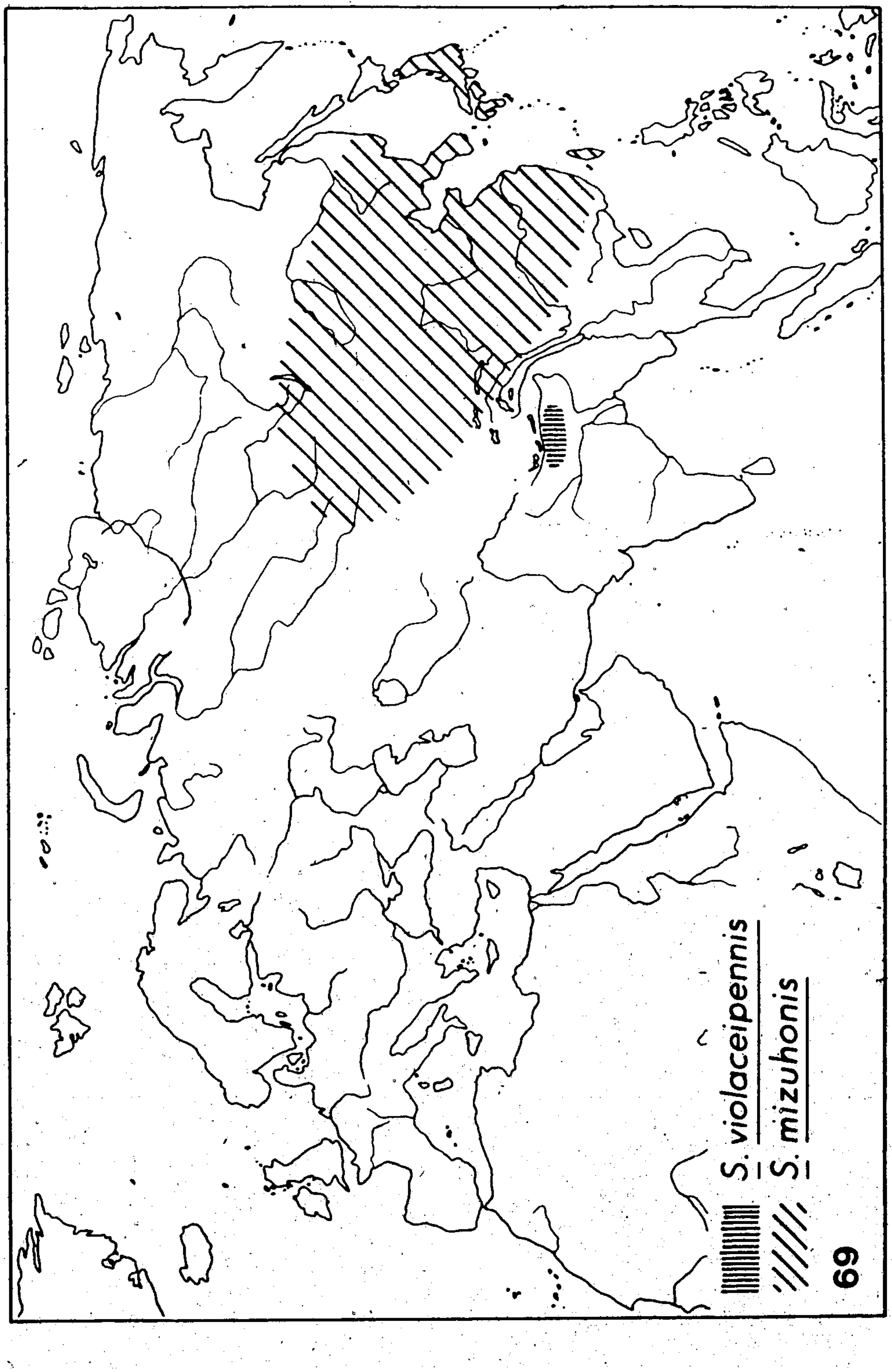
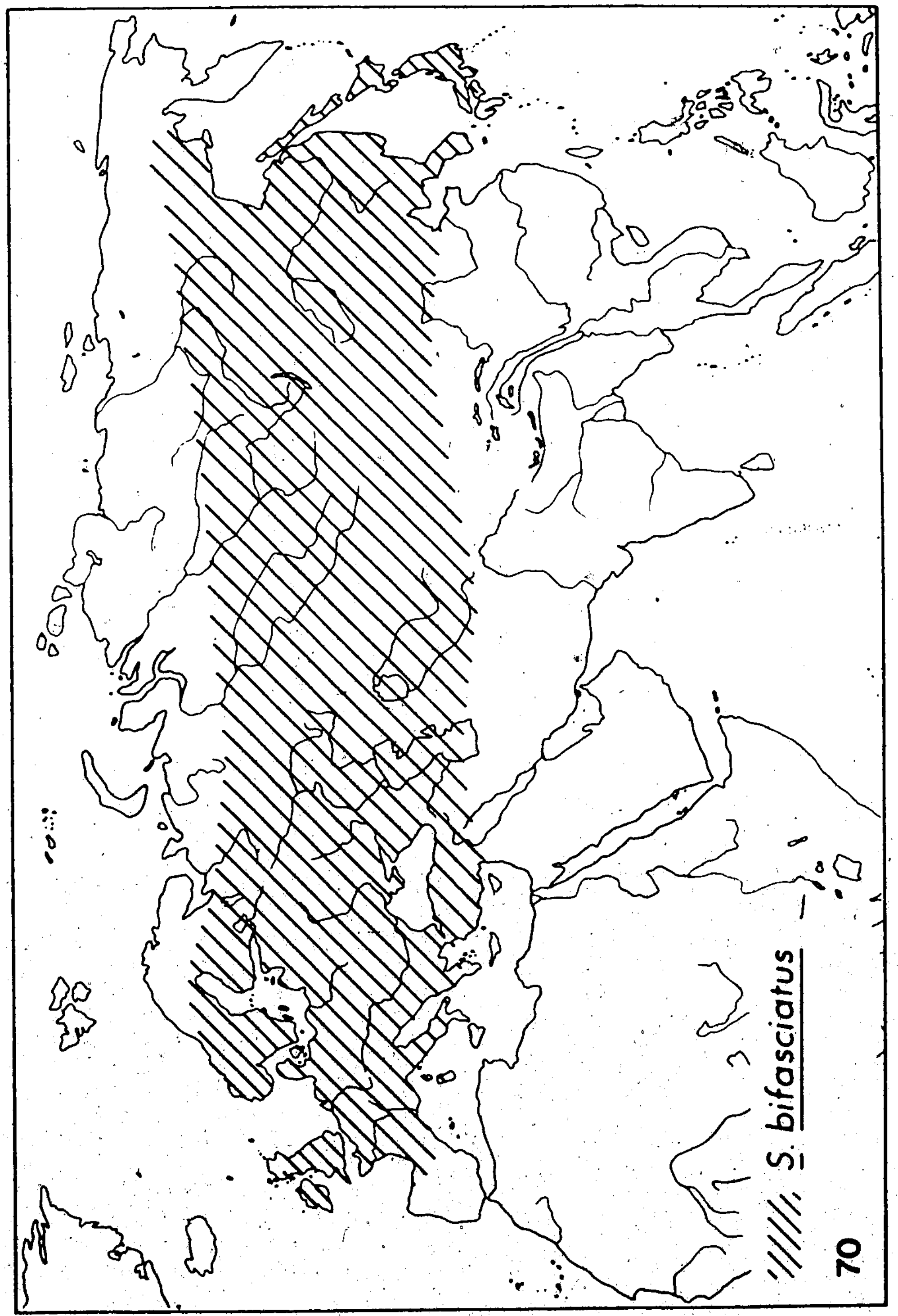

S. violaceipennis
S. mizuhonis
69

Figure 70. Geographical distribution of *S. bifasciatus*.



70

**Figure 71**. Geographical distribution of *S. debilitatus* and *S. cliens*.

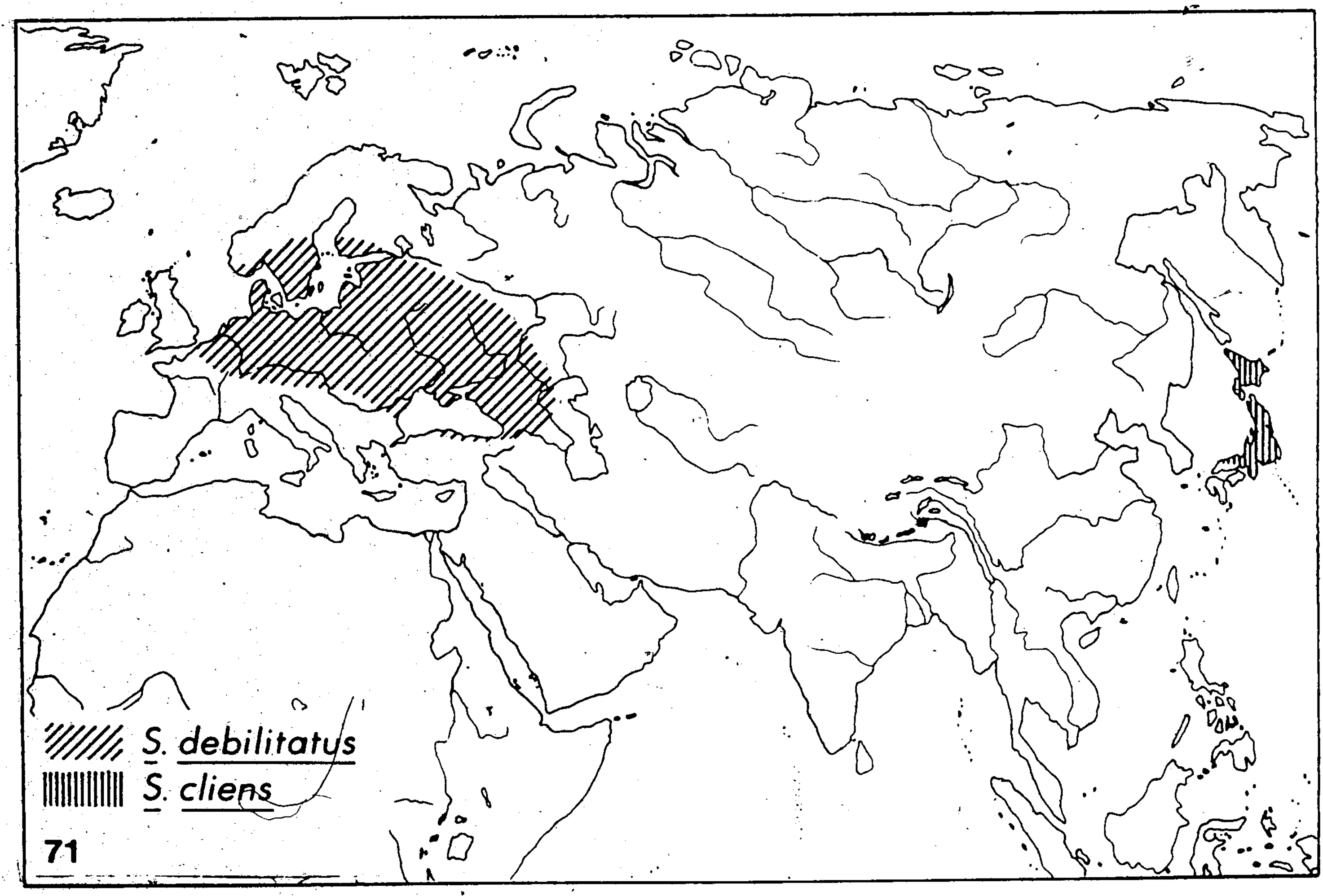
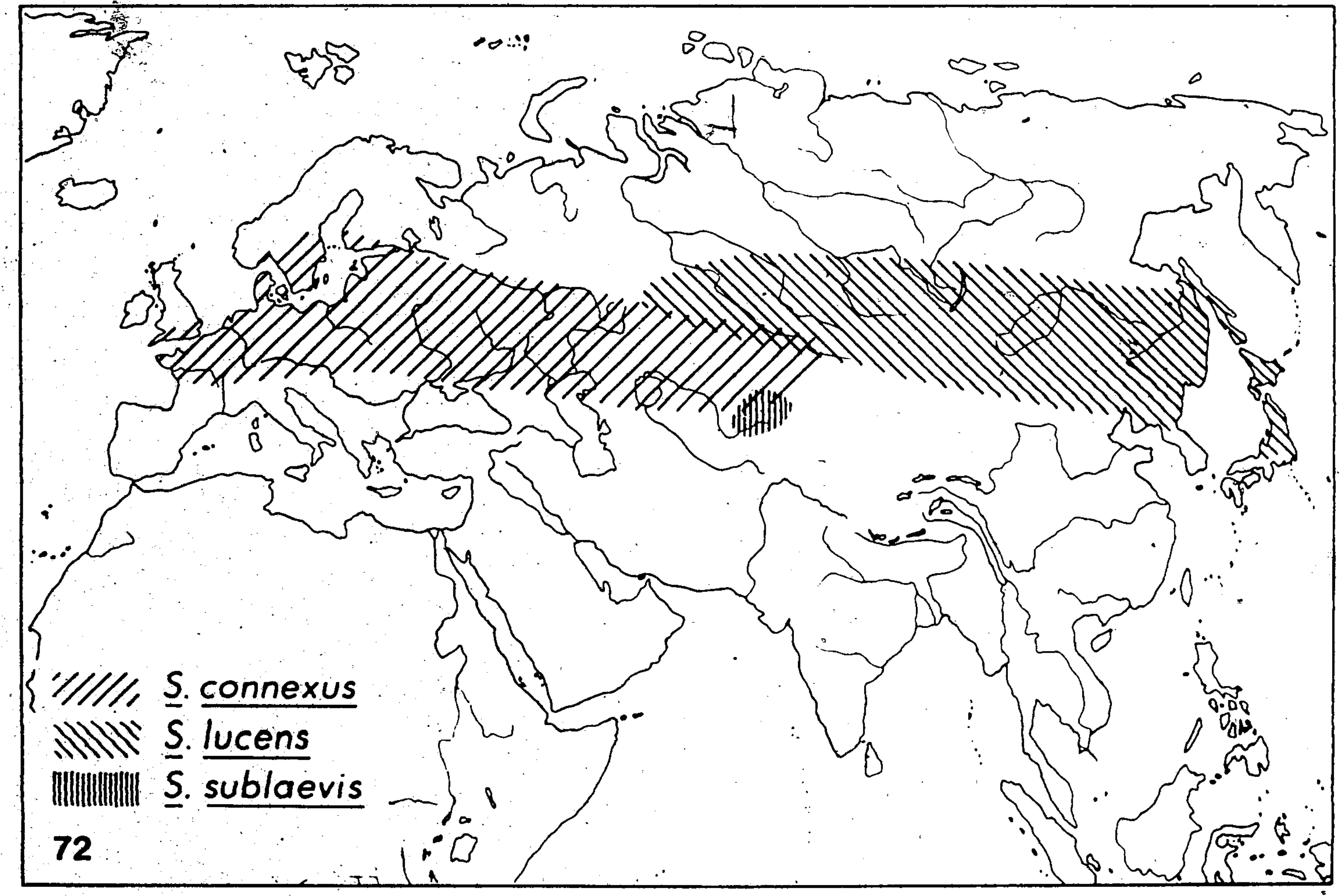

S. debilitatus
S. cliens
71

Figure 72. Geographical distribution of *S. connexus*, *S. lucens* and *S. sublaevis*.



72

Figure 73. Geographical distribution of *S. canadensis* and *S. projectus*.

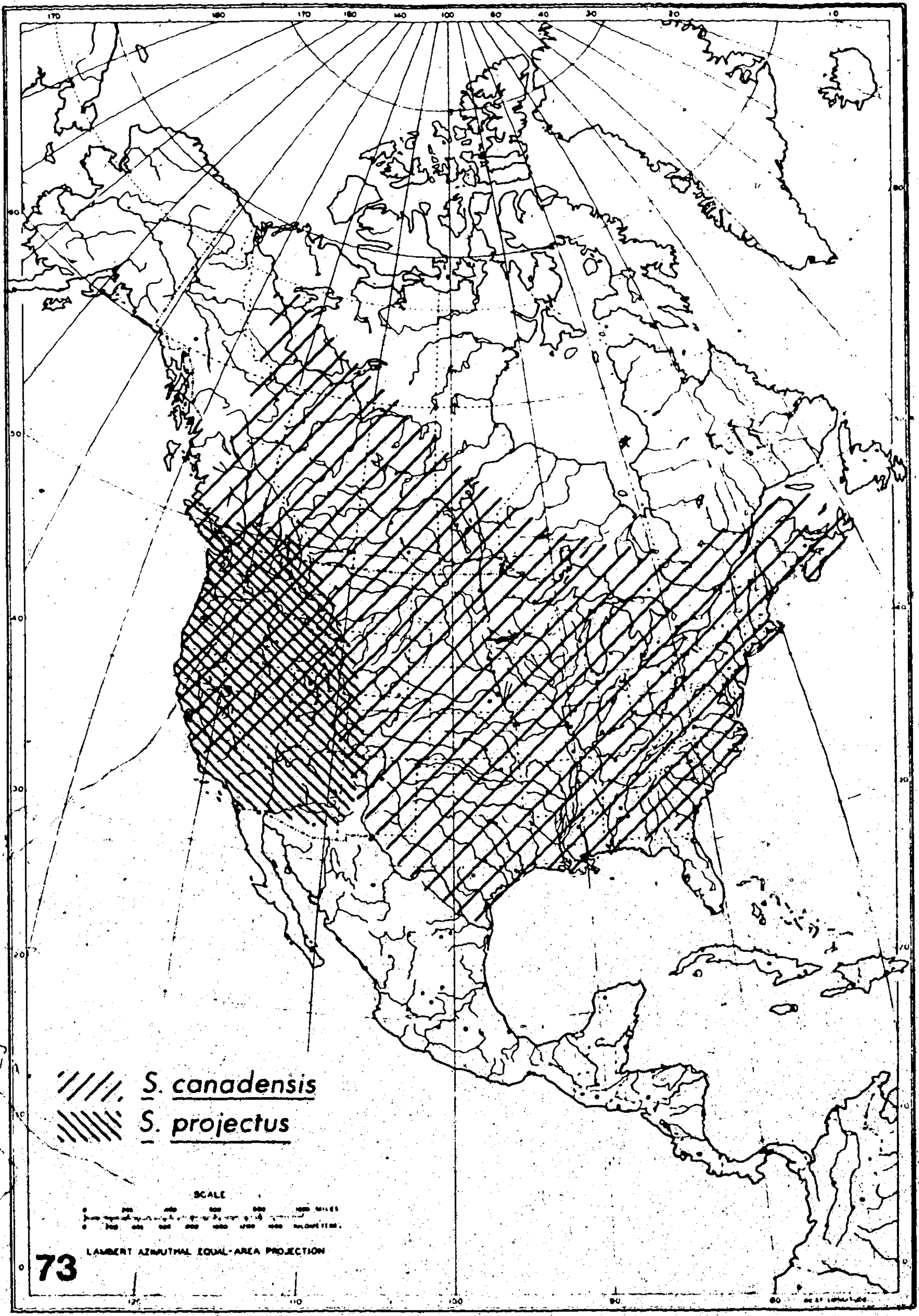

S. canadensis
S. projectus
SCALE
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
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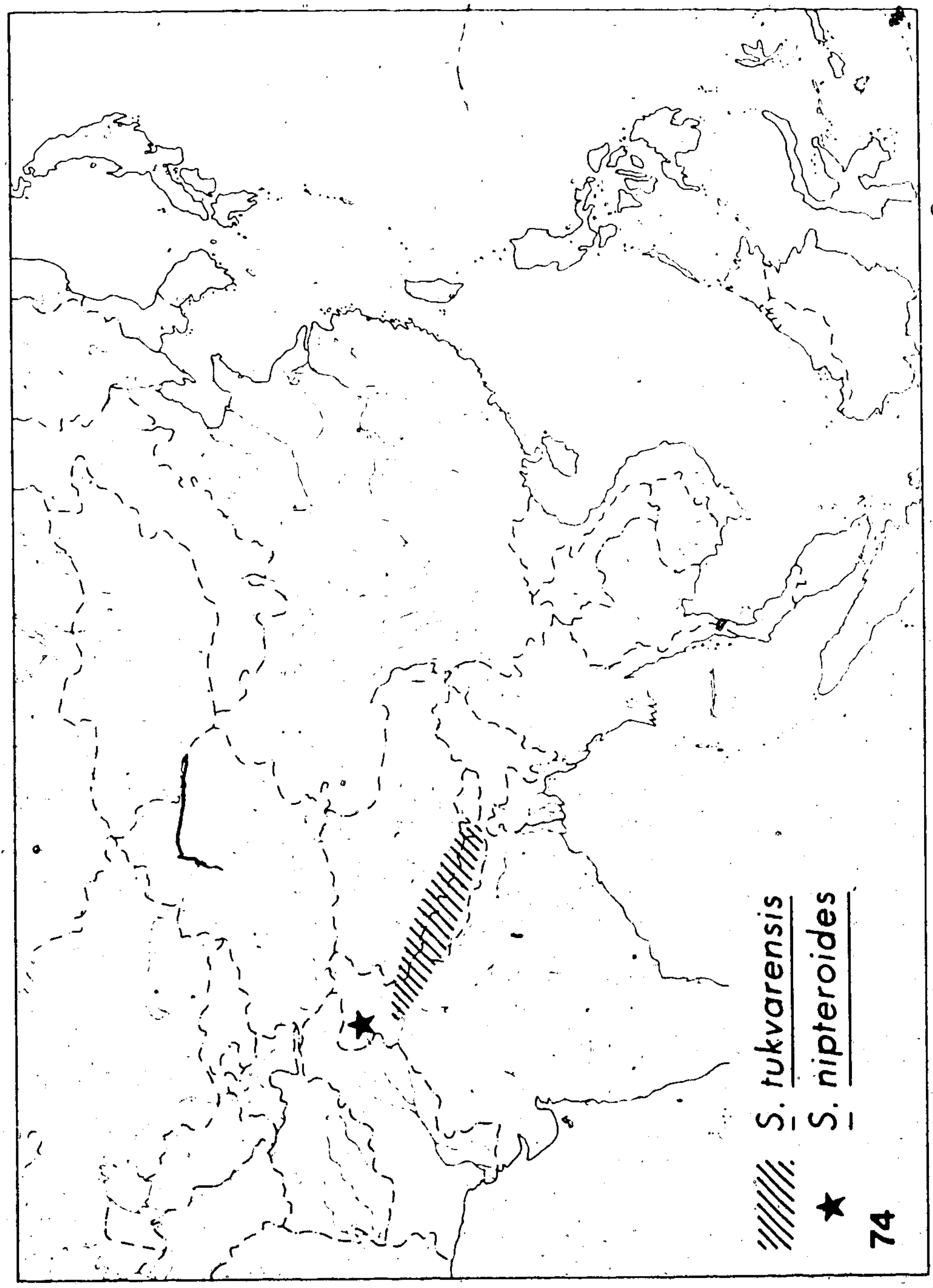
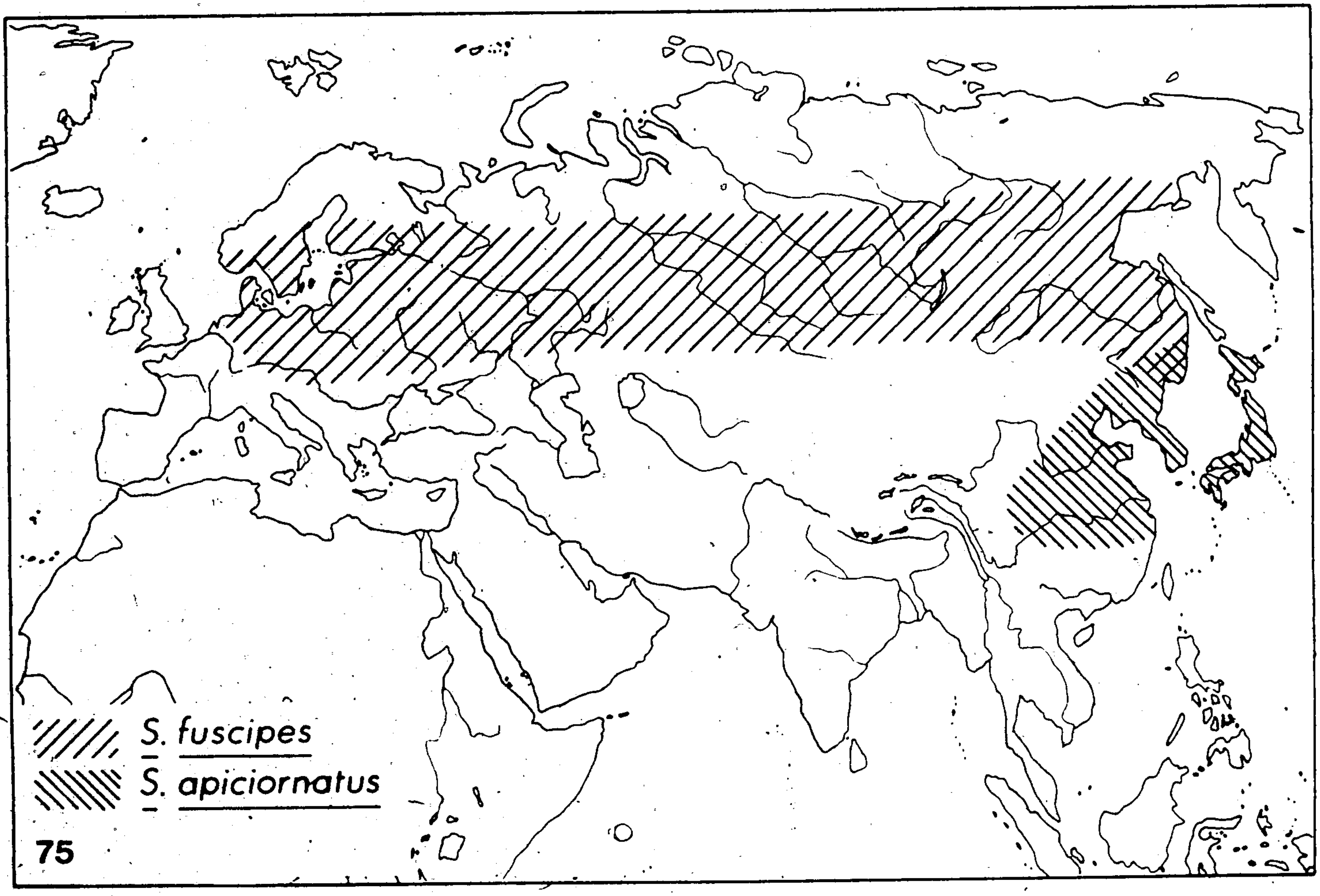
**Figure 74.** Geographical distribution of *S. tukvarensis* and *S. nipteroides*.



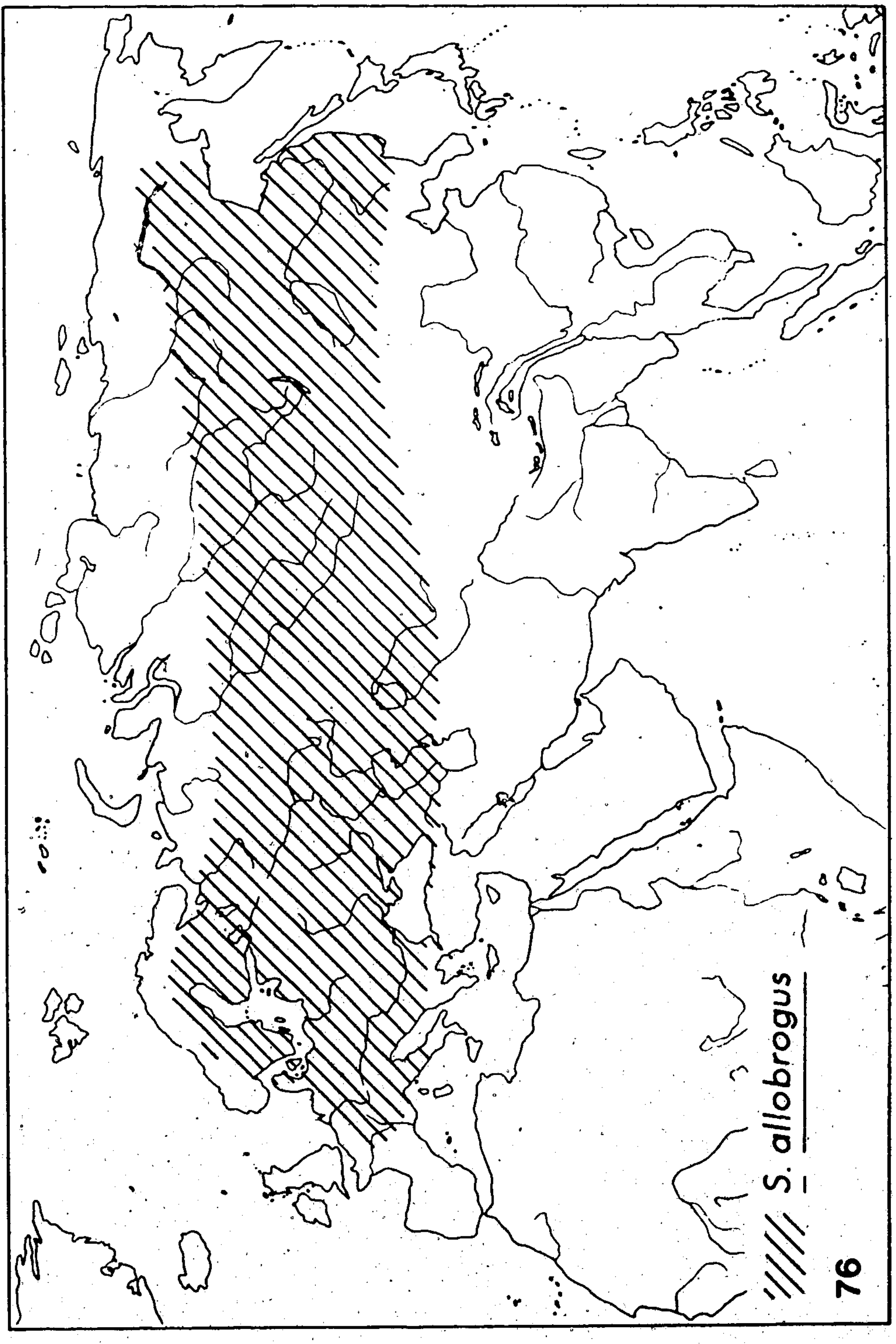
74

Figure 75. Geographical distribution of *S. fuscipes* and *S. apiciornatus*.



75

**Figure 76.** Geographical distribution of *S. allobrogus*.



76

Figure 77. Geographical distribution of *S. cristatus*.

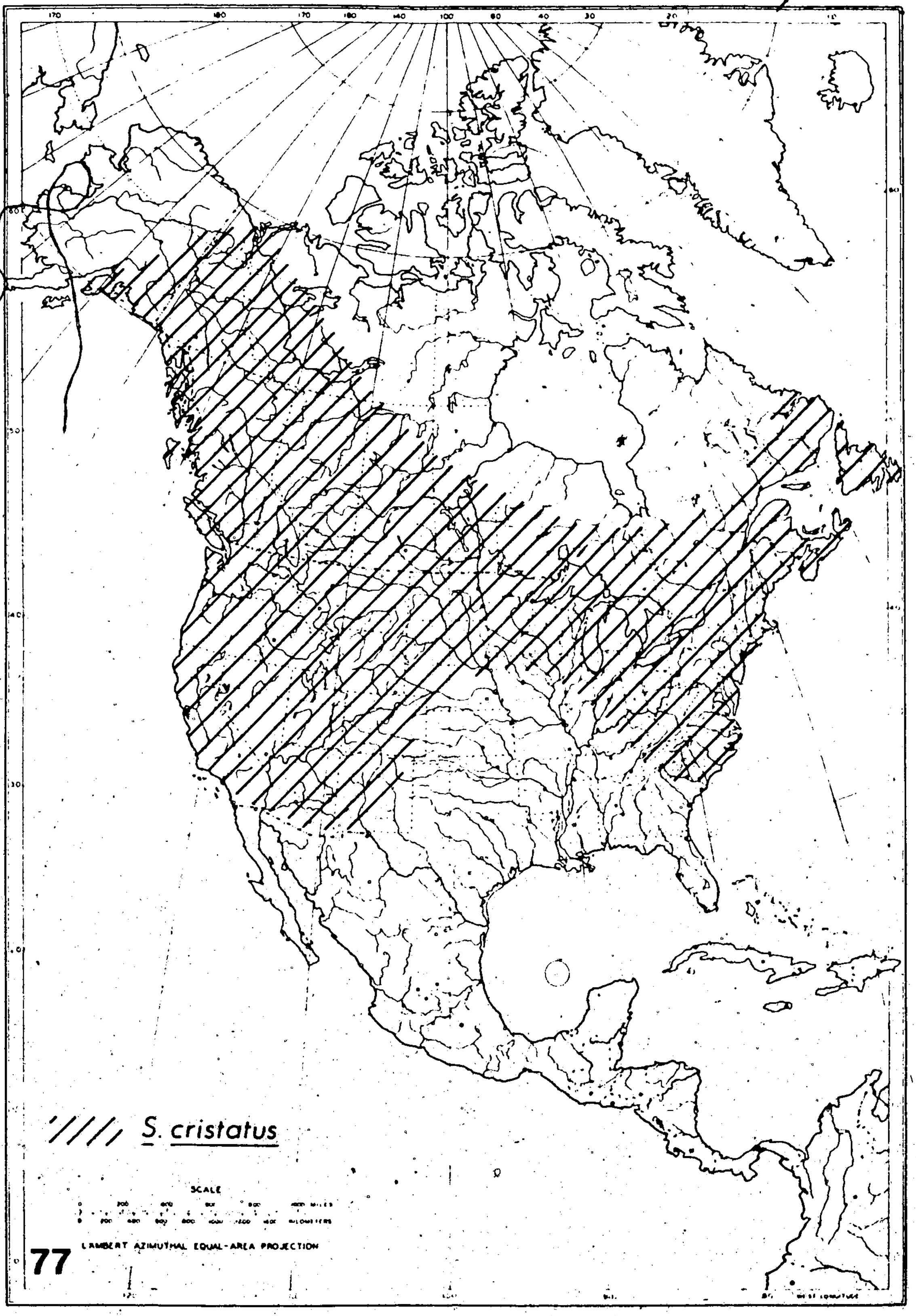
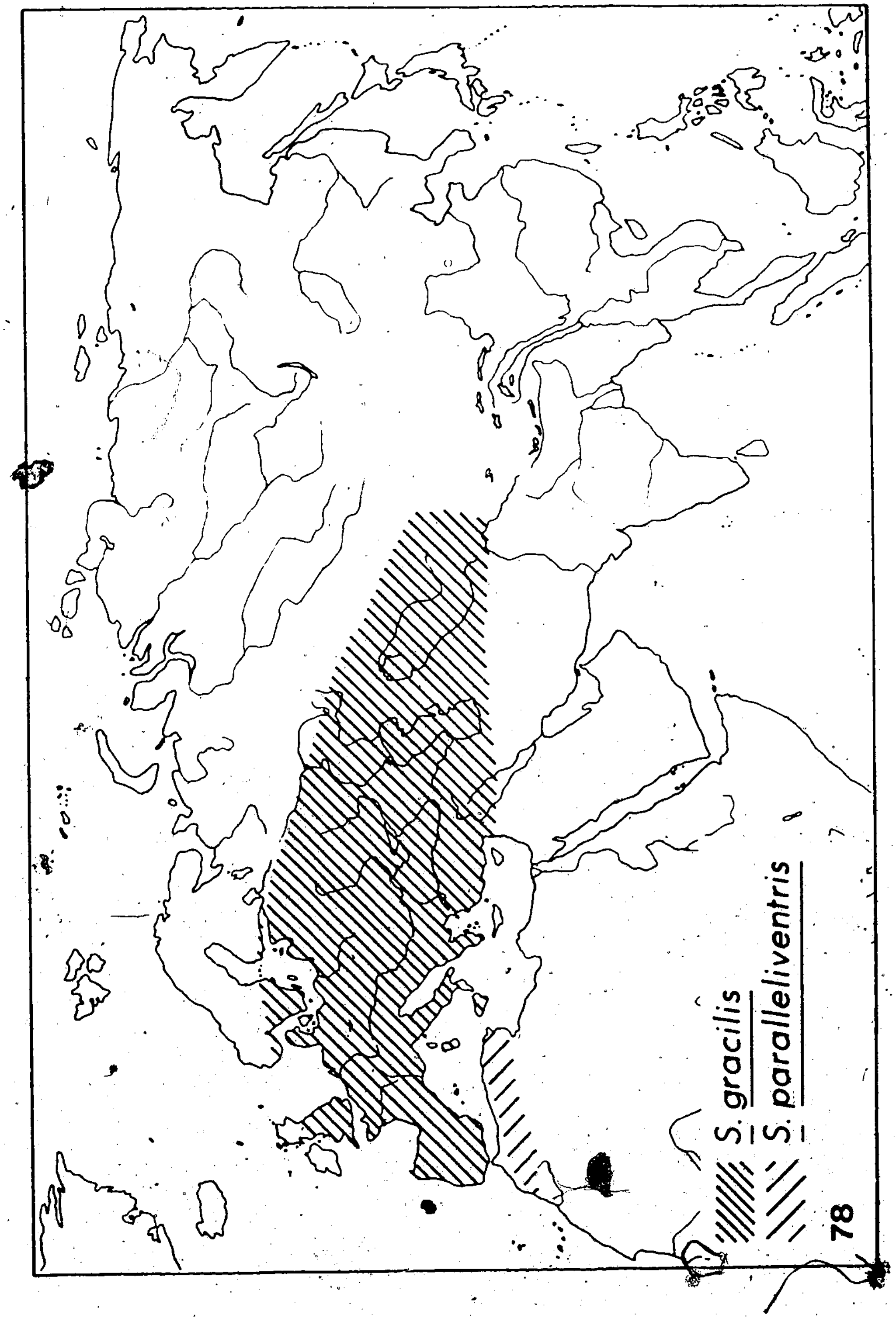
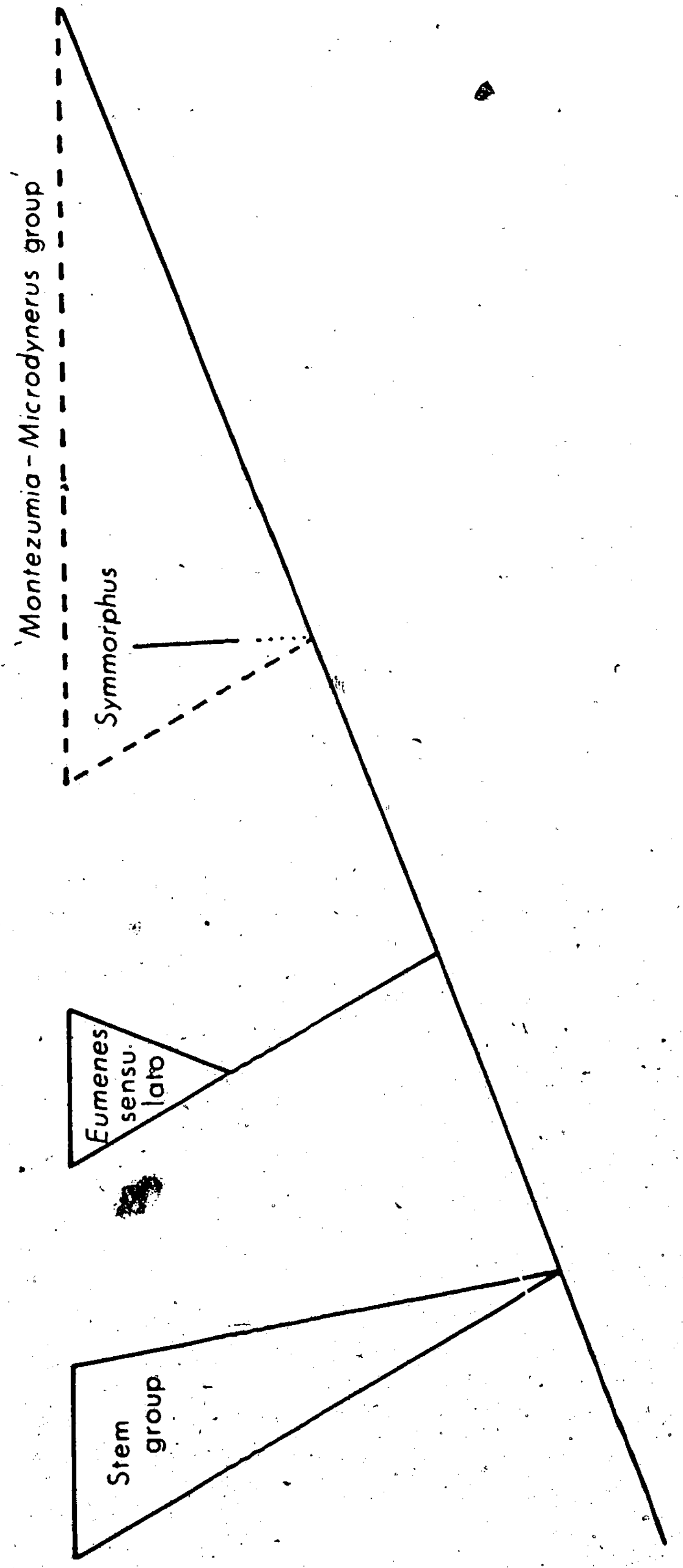

//// S. cristatus
SCALE
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
77

**Figure 78.** Geographical distribution of *S. gracilis* and *S. paralleliventris*.



78
S. gracilis
S. paralleliventris

**Figure 79**. Major lineages of Eumeninae according to Carpenter and Cumming (1985), showing proposed phylogenetic position of *Symmorphus*.

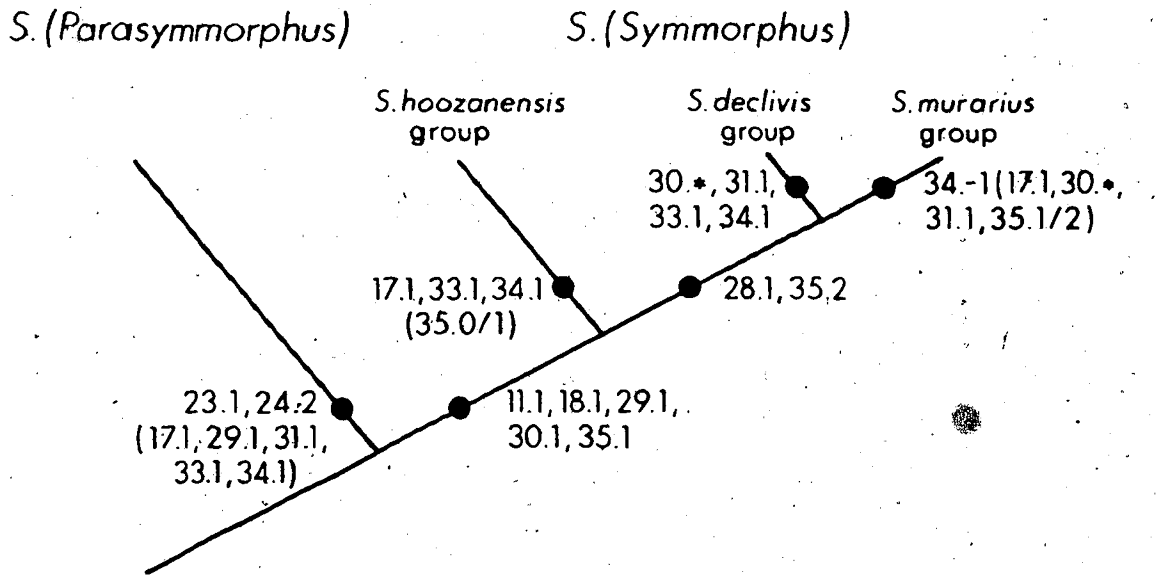

Montezumia–Microdynerus group
Symmorphus
Eumenes sensu. lato
Stem group

79

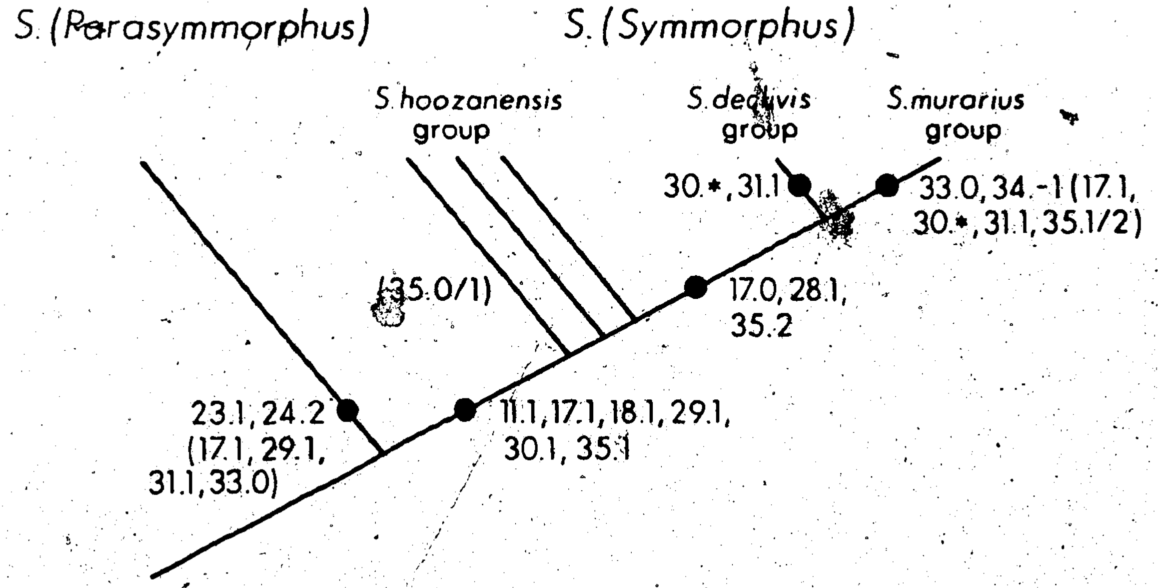
**Figures 80 to 81.** Alternative hypothesized cladistic relationships of subgenera and species groups of *Symmorphus*. Numbers below a clade denote apotypic states (from Tables 3 and 4). Apotypic states that have arisen in some but not all members of a taxon are placed in parentheses to indicate homoplasy.

**Figure 80.** Assuming states 33.0 and 34.0 as plesiotypic.

**Figure 81.** Assuming states 33.1 and 34.1 as plesiotypic.


S. (Parasymmorphus)
S. (Symmorphus)
S. hoozanensis group
S. declivis group
S. murarius group
30.*, 31.1, 33.1, 34.1
34.-1 (17.1, 30.*, 31.1, 35.1/2)
17.1, 33.1, 34.1 (35.0/1)
28.1, 35.2
23.1, 24.2 (17.1, 29.1, 31.1, 33.1, 34.1)
11.1, 18.1, 29.1, 30.1, 35.1

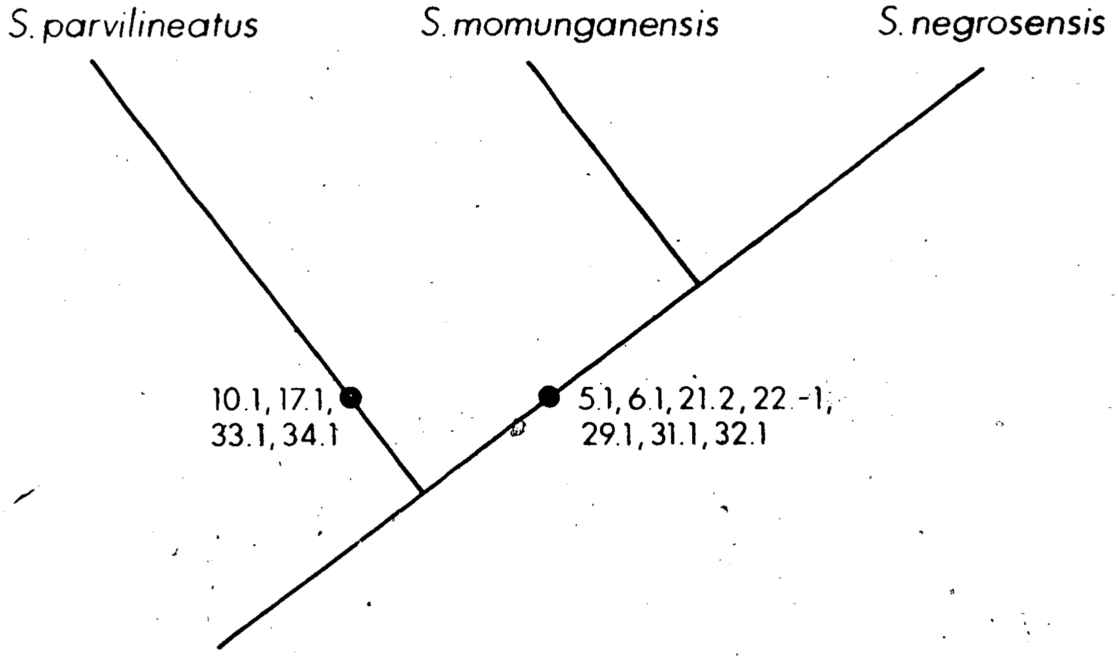
**80**


S. (Parasymmorphus)
S. (Symmorphus)
S. hoozanensis group
S. declivis group
S. murarius group
30.*, 31.1
33.0, 34.-1 (17.1, 30.*, 31.1, 35.1/2)
(35.0/1)
17.0, 28.1, 35.2
23.1, 24.2 (17.1, 29.1, 31.1, 33.0)
11.1, 17.1, 18.1, 29.1, 30.1, 35.1

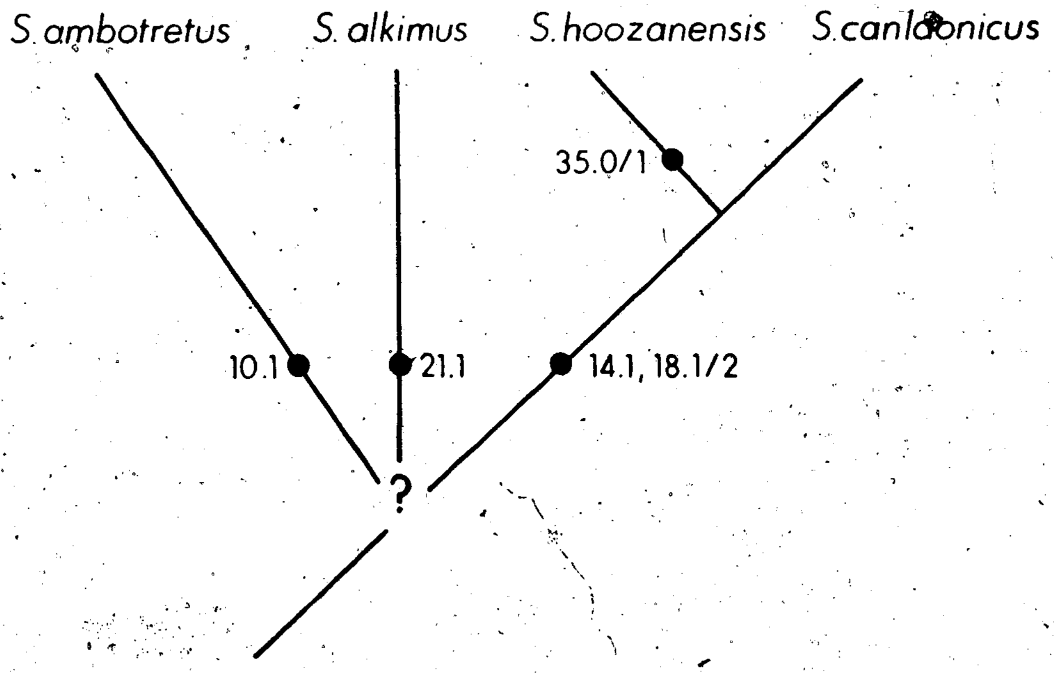
**81**

**Figure 82.** Hypothesized cladistic relationships of species of *S.* (*Parasymmorphus*). Numbers below a clade denote apotypic states (from Tables 3 and 4).

**Figure 83.** Hypothesized cladistic relationships of species of *S.* (*Symmorphus*) *hoozanensis* group. Numbers below a clade denote apotypic states (from Tables 3 and 4).

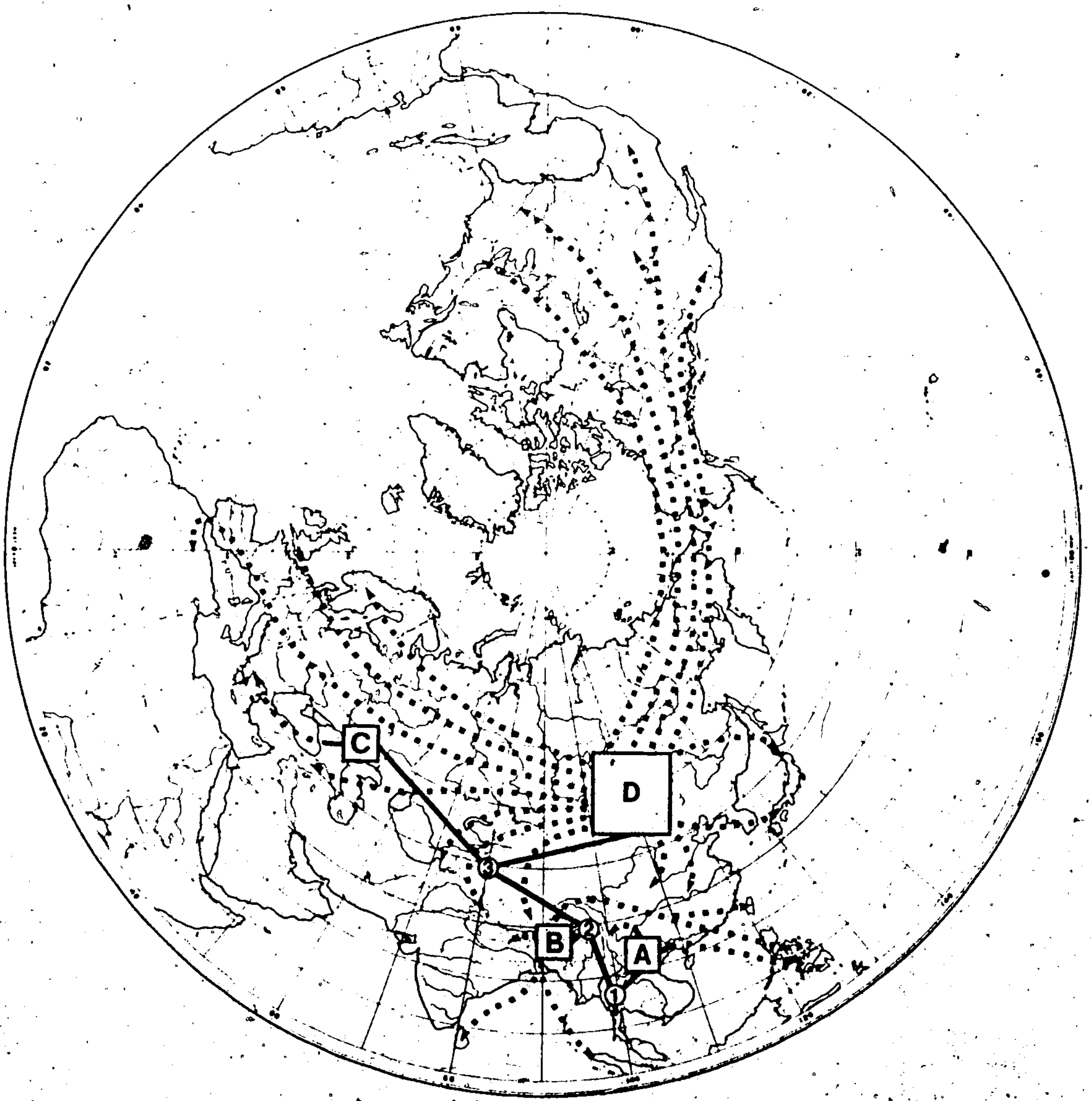

S. parvilineatus
S. momunganensis
S. negrosensis
10.1, 17.1,
33.1, 34.1
5.1, 6.1, 21.2, 22.-1,
29.1, 31.1, 32.1

**82**


S. ambotretus
S. alkimus
S. hoozanensis
S. canlaonicus
35.0/1
10.1
21.1
14.1, 18.1/2
?

**83**

**Figure 84.** Generalized historical zoogeography of *Symmorphus*. Solid lines indicate early Cenozoic events, whereas broken lines indicate later Cenozoic events without necessarily implying one-step dispersal routes (see text for details). 1) Divergence of the ancestral stock of *S. (Parasymmorphus)* (A) from that of *S. (Symmorphus)* (internode 1-2) at the beginning of the Cenozoic. 2) Divergence of the *S. hoozanensis* group lineage (B) from the *S. declivis* group + *S. murarius* group lineage (internode 2-3) during the early Paleocene. 3) Divergence of the ancestral stock of the *S. declivis* group (C) from that of the *S. murarius* group (D) in the early Eocene.



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