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THE UNIVERSITY OF ALBERTA

A TAXONOMIC REVISION OF *SCHIZOGENIUS* (COLEOPTERA: CARABIDAE: SCARITINI)

by

DONALD R. WHITEHEAD

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

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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 "A Taxonomic Revision of *Schizogenius* (Coleoptera: Carabidae: Scaritini)" submitted by Donald R. Whitehead in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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ABSTRACT

North and Middle American species of *Schizogenius* Putzeys are reviewed in detail, and South American species are treated provisionally. The genus is redefined, characterized, and illustrated. Two subgenera are *Genioschizus* new subgenus, with three species groups, and *Schizogenius s. str.*, with 21 species groups. Keys are given to: subgenera; described species groups, species, and subspecies of *Genioschizus*; same of North and Middle American *Schizogenius s. str.*; and species groups and most described species of South American *Schizogenius s. str.*

I describe as new the following 27 taxa: *S. crenulatus chiapatecus*, *S. sculptilis*, *S. impuncticollis*, *S. suturalis*, *S. jacarensis*, *S. bicolor*, *S. cearaensis*, *S. negrei*, *S. costipennis*, *S. reichardti*, *S. ocellatus*, *S. lindrothi*, *S. brevisetosus*, *B. seticollis vandykei*, *S. plurisetosus*, *S. kulti*, *S. dilatus*, *S. tibialis*, *S. ozarkensis*, *S. planuloides*, *S. neovalidus*, *S. chiricahuanus*, *S. pacificus*, *S. emdeni*, *S. scopaeus*, *S. falli*, and *S. ochthocephalus*. Synonymies proposed for the first time are: *S. peninsularis* Van Dyke (= *S. auripennis* Bates), *S. angusticollis* Putzeys (= *S. arechavaletae* Putzeys), *S. validus* Fall (= *S. longipennis* Putzeys), and *S. championi* Kult (= *S. pygmaeus* Van Dyke).

Given for each species are, as appropriate: synonymic list, diagnostic combination, description, discussion of variation, etymological derivation, geographic distribution list, collecting notes, taxonomic notes, and illustrations of important structural characteristics. Geographic distributions are mapped for all North and Middle American species. Descriptions of most North and Middle American species are augmented by a table of descriptive statistics. Results of detailed statistical analyses of geographic variation for members of some North and Middle American species groups are tabulated, mapped, and discussed.

A phylogeny is reconstructed for the genus, and carefully integrated with historical zoogeography. No geographic evidence is used to reconstruct the phylogeny of major groups and lineages; phylogenies derived from contrasting phyletic and phenetic techniques are favorably compared. To derive the phylogeny of members of the *truquii* lineage, which includes most North and Middle American species of *Schizogenius*, use of zoogeographic evidence is essential; simple cladistic techniques are not used because character states of too many characteristics are reversible. An average time between dichotomies in the reconstructed phylogeny of *Schizogenius* is about 3,000,000 years. This interval is used to integrate *Schizogenius* phylogeny and zoogeography. On the same basis, phylogenies and zoogeographies of *Brachinus* and *Evarthrus* are compatible. Zoogeographies of *Brachinus, Evarthrus*, and *Schizogenius* are compared for North and Middle American faunas.

Ancestral *Schizogenius* evolved in South America about Middle Eocene. Ancestors of the *ferrugineus* group, the *truquii* lineage, and the *crenulatus* group entered North America in Late Eocene, Middle Oligocene, and Middle Miocene. The ancestor of the *truquii* lineage ultimately evolved into eight species groups, and their evolutionary zoogeographies are discussed in detail. Since Early Pleistocene, members of the *tenuis*, *optimus*, and *lindrothi* groups have crossed the Panamanian land bridge to Middle America, and members of the *depressus* group have spread southward into South America.

ACKNOWLEDGEMENTS

Numerous individuals have contributed much toward this study, and I wish to extend my sincerest appreciation to all of them.

This investigation was suggested by, and constantly encouraged by, G. E. Ball of the University of Alberta. In addition to acting as supervisor, he obtained financial support for my studies (including support from National Science Foundation grant GB-3312 and National Research Council grant A-1399). From him I have learned much, both in the laboratory and in the field. He provided me with an opportunity to join him as field assistant during a year-long collecting trip to Mexico, for which I am most grateful.

Serving as members of my committee, D. A. McB. Craig, B. S. Heming, and J. G. Packer of the University of Alberta, and R. L. Wenzel of the Field Museum of Natural History, read and criticized this manuscript and provided numerous useful suggestions.

I am grateful to my wife, Jo, for her patience in living the life of a graduate student's wife for so long; for typing the manuscript, and commenting upon it; and for providing constant moral support.

Many individuals and institutions provided material on loan, as listed in section 2.1. I thank them all heartily, particularly those who made special efforts to secure specimens for my work. I also wish to thank D. K. Duncan and F. H. Parker of Globe, Arizona, for donation of specimens. P. J. Darlington and P. J. Spangler were courteous and helpful hosts during visits to the Museum of Comparative Zoology and the United States National Museum, respectively.

I am particularly indebted to numerous colleagues during my student years at the University of Alberta; the following stand out: J. Awram and A. P. Nimmo, for companionship in the field as well as continued friendship; B. B. Chiolino, T. L. Erwin, R. Freitag, H. Goulet, D. J. Larson, R. E. Leech, and D. H. Kavanaugh, all for their willingness at all times to partake in discussions.

If I have overlooked some person, or persons, I here offer both apologies and thanks.

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AUTOBIOGRAPHY

Born in Orange, New Jersey, on August 14, 1938, I spent my early years in Morris Plains, New Jersey. My formal education began there, and continued through high school in Morristown. In 1956, I became a student at Rutgers University with a major in agricultural research, and was awarded the degree of Bachelor of Science in 1960. During those years, my interest in entomology, which began to develop several years earlier, was encouraged and stimulated especially by Professor John B. Schmitt. I was even then interested chiefly in Coleoptera taxonomy, and gradually focused my attention on the family Carabidae. While at Rutgers, I made a preliminary survey of the insect fauna of the William L. Hutcheson Memorial Forest, an ecological research property of the University. I also identified insects for Trubek Laboratories in their research on insect attractants.

Upon graduation, I received a commission as Second Lieutenant in the U. S. Army, and was stationed as a medical entomologist for the U. S. Army Environmental Hygiene Agency at Edgewood, Maryland. While there, I was assigned to various entomological projects of interest to the Surgeon General, under the general supervision of Lieutenant Colonel Frank G. Favorite, Jr. The project of greatest interest to me was a study of the flight and attack behavior of tabanid flies, particularly of various local species of *Chrysops*.

In the summer of 1963, before entering the University of Alberta as a graduate student, I made some collections of carabid beetles and myriapods from various parts of Mexico, and developed an abiding interest in the carabid fauna of that country. At the University of Alberta, I concentrated on the carabid tribe Scaritini, and for a doctoral thesis began a taxonomic revision of the genus *Schizogenius* under the direction of Professor George E. Ball. For a year during 1965-1966, I joined Professor Ball in a major collecting expedition to Mexico. My first published papers, on the taxonomy of *Halocoryza* and *Schizogenius*, appeared during this period. These were followed by a paper coauthored with Professor Ball on collecting in Mexico, and by additional papers on the taxonomy of *Halocoryza* and *Dyschirius*.

In the spring of 1968, I married Gloria Jo Turner. We spent that summer in Europe, where I studied the important carabid collections at the British Museum (Natural History) in London and the Museum National de Histoire Naturelle in Paris. My studies there were of various Mexican agonine genera, especially of *Colpodes*, a sideline project of great interest to me. After completion of this thesis, I hope to complete various projects in the Scaritini and Agonini, in the higher classification of the Carabidae, and in the taxonomy of certain genera of Staphylinidae and Tenebrionidae.

1.0 INTRODUCTION

Small American beetles of the tribe Scaritini have received little careful attention. This is unfortunate since as a result no other aspects of their biologies have been studied, but fortunate in that comparatively few taxonomic errors have been introduced into the literature. Lindroth (1961) wrote a fine revision of the Canadian and Alaskan members of this fascinating group of beetles. His treatment of *Schizogenius*, the subject of my investigations, is excellent for the limited Canadian fauna but is not adequate to identify specimens from most regions in the United States. The genus, after all, is mainly Neotropical in distribution, and in fact a good taxonomy for it can be based on nothing less than an entire continental fauna. Except for Lindroth's (1961) key to described species from America north of Mexico, the most recent full revisions of *Schizogenius* were done by Putzeys (1866) for Mexico and southward, and by LeConte (1879) for America north of Mexico.

How much is known about these beetles? In the nearly 150 years since Thomas Say named the first species in 1823, little more than descriptive morphological work has been done. Immature stages remain completely unknown, and aside from collector's notes on habitat we have no information on adult biology. The earliest names for species now placed in *Schizogenius* were proposed by Say (1823), Castelnau (1835), and Haldeman (1843). Putzeys (1846) introduced the generic name *Schizogenius*, and in this and subsequent important papers (1863, 1866, 1878) he named numerous species. Meanwhile, LeConte (1848, 1852, 1857, 1863) studied Nearctic species, and in 1879 summarized his knowledge about them in a key and synonymic list. Bates (1881, 1891) treated the species of the Mexican and Middle American faunas as known to him. Darlington (1934, 1939), Fall (1901), Kirsch (1873), Steinheil (1869), and Van Dyke (1925, 1949) each introduced one or more new names to the literature. Kult (1950) produced the first major report on the Neotropical fauna since the end of the nineteenth century, and Lindroth (1961) did likewise for the Nearctic fauna. Since I began my studies on the genus I have named two South American *Schizogenius* species as new (1966a), and transferred Darlington's *S. arenarius* to *Halocoryza*, a closely related genus which I revised and characterized (1966b, 1969).

In this study I treat in detail the taxonomy and distribution of *Schizogenius* in North and Middle America, and provide the basis for a similar study of the South American fauna. I define "North America" as America north of Guatemala, "Middle America" as America from Guatemala to Costa Rica plus the West Indies, and "South America" as South America proper plus Panama. I hope that my work will not only make possible the identification of specimens, but that it will stimulate more detailed investigations into the many problems in evolutionary biology that render members of this genus so interesting. Thus, I have attempted to unravel some of the myriad puzzles in speciation in North and Middle American *Schizogenius*, and have pointed out others that particularly demand attention.

2.0 MATERIALS AND METHODS

2.1 Materials

This revision is based on the study of 9098 adult specimens of North and Middle American *Schizogenius*, plus 929 adults from South America. I have collected these insects along streams in much of the United States and Mexico, and other collections were made especially for this study by G. E. Ball, T. L. Erwin, D. J. Larson, and H. B. Leech. Other specimens were loaned to me by various museums and private collectors; the following abbreviations represent these collections and their respective curators.

AMNH	American Museum of Natural History, New York, New York 10024; P. Vaurie.
ANSP	Academy of Natural Sciences, Philadelphia, Pennsylvania 19103; H. R. Roberts.
BMNH	British Museum (Natural History), London, England; P. Hammond, R. D. Pope.
CAS	California Academy of Sciences, San Francisco, California 94118; H. B. Leech.
CNC	Canadian National Collection of Insects, Entomology Research Institute, Ottawa, Ontario; E. C. Becker, W. J. Brown.
CNHM	Chicago Natural History Museum, Chicago, Illinois 60605; H. Dybas.
CPBo	C. Bolivar y Pieltain, Instituto Politecnico Nacional, Mexico, D. F.

CUNY	Cornell University, Ithaca, New York 14850; H. Dietrich, L. L. Pechuman.
DHKa	D. H. Kavanaugh, University of Alberta, Edmonton 7, Alberta.
DJLa	D. J. Larson, University of Calgary, Calgary, Alberta.
DRWh	D. R. Whitehead, University of Alberta, Edmonton 7, Alberta.
FDAG	Florida Department of Agriculture, Gainesville, Florida 32601; R. E. Woodruff.
HGou	H. Goulet, University of Alberta, Edmonton 7, Alberta.
INHS	Illinois State Natural History Survey, Urbana, Illinois 61803; L. K. Gloyd.
IRSB	Institut Royal des Sciences Naturelles de Belgique, 31, Rue Vautier, Bruxelles 4, Belgium; R. Damoiseau.
JHen	J. Hendrichs S., Apartado Postal 11-774, Mexico 11, D. F.
JNeg	J. Negre, 9, Boulevard de Lesseps, Versailles, France.
KHSt	K. H. Stephan, 3038 East Eastland, Tucson, Arizona 85716.
KSUM	Kansas State University, Manhattan, Kansas 66502; H. D. Blocker.
LACM	Los Angeles County Museum, Exposition Park, Los Angeles, California 90007; C. L. Hogue.
LBSC	Long Beach State College, Long Beach, California 90804; E. L. Sleeper.
MCZ	Museum of Comparative Zoology, Cambridge, Massachusetts 02138; P. J. Darlington, Jr., J. F. Lawrence.
MGFT	Museum G. Frey, Entomologisches Institut, Tutzing bei Munchen, Germany; M. von Falkenhayn.
MHNG	Museum d'Histoire Naturelle, Geneva, Switzerland; C. Besuchet.
MNHP	Museum National d'Histoire Naturelle, Paris, France; A. Bons, J. Negre.

MSUL	Michigan State University, East Lansing, Michigan 48823; T. F. Hlavac.
MSUM	Montana State University, Missoula, Montana 59801; N. Anderson.
MZSP	Museu de Zoologia da Universidade de Sao Paulo, Caixa Postal 7172, Sao Paulo, Brazil; H. Reichardt.
OSUC	Ohio State University, Columbus, Ohio; C. A. Triplehorn.
PSUU	Pennsylvania State University, University Park, Pennsylvania 16802; W. W. Boyle, S. W. Frost.
RFre	R. Freitag, Lakehead University, Thunder Bay, Ontario.
RTBe	R. T. Bell, University of Vermont, Burlington, Vermont 05401.
RUNB	Rutgers University, New Brunswick, New Jersey 08903; J. B. Schmitt.
SDNH	San Diego Natural History Museum, San Diego, California 92112; C. F. Harbison.
TCBa	T. C. Barr, University of Kentucky, Lexington, Kentucky 40506.
TLEr	T. L. Erwin, United States National Museum, Washington, D. C. 20560.
UAFA	University of Arkansas, Fayetteville, Arkansas 72701; R. T. Allen.
UASM	University of Alberta, Strickland Museum, Edmonton 7, Alberta; G. E. Ball.
UATA	University of Arizona, Tucson, Arizona 85721; F. G. Werner.
UCB	University of California, Berkeley, California 94720; J. A. Powell.
UCD	University of California, Davis, California 95616; R. O. Schuster.
UCR	University of California, Riverside, California 92502; S. Frommer.
UKSM	University of Kansas, Snow Museum, Lawrence, Kansas 66045; G. W. Byers.

UMCG University of Miami, Coral Gables, Florida; H. F. Strohecker.

USNM United States National Museum, Washington, D. C. 20560; P. J. Spangler.

UWLW University of Wyoming, Laramie, Wyoming 82070; N. L. Marston.

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

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

2.2 Methods and techniques

2.21 Dissecting techniques

Representative female specimens of subgenera and some species groups were relaxed in boiling water, then dissected with fine forceps. Their mouthparts, wings, and ovipositors were mounted in Hoyer's medium on slides, studied with the aid of a compound microscope, and drawn. As I failed to find characteristics useful in species recognition, these dissections were not done routinely at species level. The disarticulated specimens were irretrievably damaged, and so were discarded at the end of the study.

Male genitalia were dissected from the abdominal apices of relaxed specimens. After a general examination for peculiarities in form, the usual procedure was to make whole mounts, including parameres, in Hoyer's medium on slides. Proper positioning was obtained by spreading the drop of mounting fluid to a thin layer before placing the cover slip. Two or three days after mounting, each preparation had cleared sufficiently for study, and no additional clearing techniques were used. The internal sac was everted in at least one specimen of nearly every North and Middle American species, specimens permitting, by hooking and pulling the apex of the virga with a fine pin. I did not attempt this for most South American species, because in older material, particularly specimens collected in other than ethyl acetate, incidence of damage was prohibitive. Nor was this procedure used routinely for members of the *depressus* group, because of their generally small sizes. After the genitalia were studied and drawn, they were removed from the slides, glued to cards, and pinned with the specimens.

2.22 Measurements and statistics

2.221 Mensurable and meristic data

Certain routine measurements used in species descriptions and in variation analyses were made with a Leitz steroscopic microscope at a magnification of 50 diameters, using a micrometer eyepiece with a scale interval of 0.025 mm. These measurements and their abbreviations are:

DP, maximum depth of thorax from intercoxal process of prosternum to basal carina of pronotum;

LE, length of left elytron along suture from basal tubercle to apex;

LH, length of head from base of eye to anterolateral angle of clypeus;

LP, length of pronotum along midline;

PS, minimum distance from apex of left paramedian longitudinal sulcus to base of pronotum;

Ta, length of hind tarsus, claws excluded;

Ti, length of hind tibia;

TL, total length, combining LH, LP, and LE;

WE, maximum width across closed elytra;

WF, minimum width of head between eyes;

WH, maximum width of head across eyes;

WP, maximum width of pronotum, hind angles excluded.

Most of these measurements can be made accurately, but fixed reference points are not available for intercoxal process in DP, apex of paramedian sulcus in PS, or base of tibia in Ti, and thus these measurements are less accurate. Least accurate is the Ta measurement, made from base of article one to apex of article five regardless of expansion or contraction between articles.

Some of these measurements were used to obtain ratios which help express body proportions. These ratios are: DP/LP, relative depth or convexity of thorax; LE/WE, form of elytra; LP/WE, relative size of pronotum; LP/WP, form of pronotum; PS/LP, relative length of paramedian pronotal sulcus; Ta/Ti, relative length of hind tarsus; and WF/WH, relative eye size. The range of variation in any given sample depends in part on the accuracy of measurements used to form ratios; for example, Ta/Ti is quite inaccurate and thus too variable for use in infraspecific comparisons. Except for LE/WE, a ratio used only for species and species groups for which it had been used before (Kult, 1950), these proportions are intended to represent different, independent aspects of body form.

In those species having more than three or four setae on the elytral disc, counts were made of numbers of setae on intervals three, five, and seven of the left elytron. These counts were totalled when used for statistical analysis. Similar counts were made of numbers of marginal pronotal setae, in the few forms having more than the standard two pairs.

I used two sets of statistics to handle these data. Descriptive statistics as discussed in section 2.222 are used mainly to enhance species descriptions, but may also be used to compare closely related species or to compare species groups. The second set of descriptive statistics as discussed in section 2.223 are used to describe variation within species, to detect probable gene flow patterns, and to aid in determining possible reproductive isolation between related, allopatric forms. Although I am not sure that variation in numbers of elytral setae exactly follows a normal distribution, especially when numbers are small, I treated these data in the same way as I did the mensurable data. Sokal and Rohlf (1969) suggest, as a rule of thumb, that the number of unit steps in a range of variables should range from about 30 to 300. Such a broad range in the proportion variables would require greater accuracy in the original measurements than I found practical. Nor do numbers of setae per elytral disc, at least in most species, vary to this amount. But, since I use statistics to provide some evidence about relationships rather than about similarities, I believe the descriptive statistics based on these data are adequate.

2.222 Descriptive statistics

Except for the poorly known and unusually variable *S. tibialis*, I give descriptive statistics for one sample of each described North and Middle American species; I have not done so for South American species because of inadequate material. Mensurable and meristic data so treated include, where appropriate, TL, LE, WH, WP, WE, setae on intervals three, five, and seven of the left elytron and their total, WF/WH, LP/WP, DP/LP, LP/WE, LE/WE, Ta/Ti, and PS/LP. When at least eight specimens made up a sample, I give range of variation, mean, 1.5 standard deviations and two standard errors (Hubbs and Hubbs, 1953), and coefficient of variability. I use 1.5 rather than one standard deviation, since it is more critical as an analytical tool (Mayr, *et al.*, 1953). When fewer than eight specimens were used in a sample, I give only the range and the mean. I do not use coefficient of difference, a statistic suggested by Mayr (1969) for subspeciation analysis, since my criteria for subspecies differ from his; see section 2.24.

Ideally, each sample included at least 20 males, all collected at one time and place, preferably at or near the type locality. These conditions were often not entirely satisfied, usually because of inadequate numbers. In those species belonging to species groups which do not have reliable external characteristics to distinguish sexes, sex was ignored. For some species, samples of adequate size could be made only by combining specimens collected over a more or less extensive area. When too few specimens were available for adequate statistical treatment, the sample comprised all specimens on hand regardless of sex or provenance.

These statistics complement species characterizations, and provide data for comparisons between closely related species or between species groups. They are not intended for comparisons between less closely related species. Thus, the statistical treatment is as uniform as possible for species within a species group, but sample compositions or characteristics studied may differ for different species groups. I am aware that these statistics describe characteristics of only a sample of a species, and less approximately describe characteristics of the species. If sufficient material was available, and if one set of descriptive statistics clearly was insufficient to reasonably describe variation, I complemented this set of descriptive statistics with procedures discussed in section 2.223.

2.223 Analysis of geographic variation

Where problems in species recognition were evident, I carefully studied variation among population samples before making taxonomic decisions. I chose for analysis characteristics which could be easily and accurately measured, and which promised to tell the most about geographic variation. These were LE, WF/WH, LP/WP, total number of setae on disc of left elytron, and, for the *pluripunctatus* group, PS/LP and LP/WE. For each sample and each characteristic, I determined range, mean, 1.5 standard deviations, two standard errors, and coefficient of variability. If two samples differ from one another by non-overlap of two standard errors from the means, I term them "statistically significantly different;" this is equivalent to the t-test at 0.05% probability. I use the term "taxonomically significantly different" if two samples differ from one another by non-overlap of 1.5 standard deviations from the means, to imply that 90% or more specimens from one sample can be distinguished from 90% or more from the other sample (Mayr *et al.*, 1953).

Samples were composed of equal numbers of females and males, despite probably increasing sample variance and thereby decreasing statistical sensitivity, in order to increase the numbers of samples suitable in size for useful comparisons. Ideally, each sample included at least ten of each sex, and samples having fewer than five of each were not analyzed. To insure that samples represented biological populations, I tried to form each sample from specimens collected at one time and place. If this could not be done, then date of collection was ignored. When still no adequate sample could be made, I drew from a wider geographic area. These latter samples probably represent composite biological populations, but are approximations which can be modified after additional collections are made. Henceforth, I use the word "population" to mean the statistical population from which a sample was drawn, unless otherwise specified. Sample composition is assumed to be random, since there is no reason to suspect deliberate bias during collection.

In order to achieve the best possible geographic coverage, I tried to select samples systematically; but because samples were limited by numbers and distributions of available specimens, this geographic coverage is less than ideal. At best, samples form a loose network over the geographic area covered, and proximate samples may not represent truly proximate biological populations. Thus, statistical data among proximate samples only approximately suggest biological relationships, and should be reinterpreted if geographically intermediate samples become available.

Understanding relationships between taxa requires knowledge of similarities, but within a species, or between closely related allopatric phena, similarity alone may not be a useful yardstick of relationship (Mayr, 1969). Statistical analysis of single characteristics yields limited direct information about relationships. If statistics are used to obtain such direct information, they should represent the total phenotype and be studied by various procedures of multivariate analysis or numerical taxonomy (e.g., Sokal and Sneath, 1963). In an analysis of geographic variation, however, each characteristic should first be considered independently, since characteristics within a species may vary independently. This is clinal variation, or the geographic variation of single characteristics (e.g., Mayr, 1969). Only after characteristics have been studied separately may they be profitably studied in combination, as for example by hybrid index techniques (e.g., Freitag, 1965). I have limited my statistical studies of geographic variation to clinal analyses, since for purposes of this revision more sophisticated procedures seemed unnecessary.

Statistically significant differences in one or more characteristics between population samples of a species, or between closely related allopatric phena, are evidence of evolutionary divergence between them. Indeed, if evolution is a dynamic continuing process, some evolutionary divergence between any two biological populations of a species should take place, given sufficient time. Its extent would depend on geographic relationships of the populations, duration and completeness of their isolation, and various environmental factors. Speciation occurs when two populations or groups of populations have diverged sufficiently to acquire reproductive isolation, and when they have lost reproductive links through other populations.

Statistically or taxonomically significant differences in one or more characteristics between samples of geographically distant populations provide no information about presence, absence, or amount of gene flow between them. They do give information about amount of divergence or similarity, but not about biological relationships, and without additional data from intermediate population samples they yield little useful evidence either for or against conspecificity. Furthermore, since any two proximate samples may not represent contiguous biological populations, the biological significance of whatever statistical difference, or indeed or any difference, between them cannot readily be interpreted. More meaningful comparisons may be made of two samples via one or more intermediate samples. From them, one may predict the relative extent of gene flow between populations represented by these samples. The intent of this discussion is to emphasize that the terms "statistically significant" and "taxonomically significant" indicate amount of difference or similarity, not any precise relationship. These points are illustrated in, for example, my analysis of *S. pygmaeus* and *S. scopaeus* in sections 3.535 and 3.536.

I use statistics to study clinal relationships among populations within species and between closely related allopatric species or phena, in order to determine probable biological relationships of samples rather than similarities or differences. These clinal studies yield evidence about possible gene flow, and consequently about possible reproductive isolation. From them, one can reasonably predict whether or not populations are conspecific, given sufficient data. Mayr (1969) states that isolated allopatric populations may be either species or subspecies, and that a taxonomic decision may be arbitrary; he suggests that such isolates are best treated as subspecies. However, I think information on clinal variation is relevant in such decisions. If the nearest populations in two isolated groups of populations are the most similar, or at least show no evidence of divergence, then I would expect that some gene exchange does exist and that the populations are conspecific. If these two populations are the most different in one or more characteristics, or even if only one of them is divergent, then I think that gene flow is unlikely and that the two groups of populations are not conspecific. Within the *pluripunctatus* group, section 3.48, an example of the former situation is the taxon *S. seticollis*, with two subspecies; and as an example of the second, I regard the taxa *S. plurisetosus* and *S. multisetosus* as separate species. If intermediate samples diverge in one or more characteristics, then the more distant samples, regardless how similar, may not be conspecific; see for example my treatment of the taxa *S. pygmaeus* and *S. scopaeus* in sections 3.535 and 3.536. And if the intermediate samples converge, then the more distant samples probably are conspecific, regardless how dissimilar; see my disposition of the names *S. pygmaeus* and *S. championi* in section 3.535.

In a statistical study of character clines, I think the most useful statistic is the sample mean, compared with means of proximate samples.

Statistics of dispersion from the mean are more useful to estimate the relative significance of observed differences between means than to estimate absolute differences. They suggest whether differences between means probably are or are not the result of coincidence. If two samples differ significantly in a particular characteristic, but an intermediate sample differs significantly from neither, I conclude not only that the first two populations have diverged but also that gene flow still exists between them. I think this pattern is unlikely to result from coincidence.

2.23 Illustrations

Line drawings were made on paper squared to a one cm grid, with the aid of an ocular grid mounted in a Leitz stereoscopic dissecting microscope. I used much care in preparing these drawings, since I used them to make direct comparisons of details of form and structure, and to supplant verbal description. Homologous structures are drawn consistently to the same scale to facilitate comparisons. Male genitalia, endophalli, and other small organs mounted on slides were drawn from an optical magnification of 150 diameters, and their details checked at still higher magnifications with a compound microscope. Partial and entire habitus drawings were made from a magnification of 50 diameters, and fine detail and shading added as needed.

Distribution maps are given for all North and Middle American species; I do not give such maps for South American species since most are known from too few localities to even begin to picture their distributions.

Special maps were prepared to illustrate clinal relationships, where studied, and also to illustrate broad zoogeographic patterns.

2.24 Criteria for species-group and genus-group taxa

For deciding interrelationships of specimens and populations at species level, I follow a slightly qualified version of the biological species definition proposed by Mayr (1963, 1969): species are populations or groups of populations through which gene flow actually or potentially exists, but which are reproductively isolated from all other populations. The biological species, if bisexual, is the only taxon which can be said to have nonarbitrary boundaries at any given time and place; it is nonarbitrary as to what is included and as to what is excluded (Simpson, 1961). However, in contemporary, bisexual organisms, nonarbitrariness may be difficult to demonstrate for geographically distant populations, since information about gene flow or potential reproductive isolation may not be available. For example, consider a series of populations the most distant of which are similar to one another and may not be reproductively isolated, while the most proximate, especially when parapatric or sympatric, are dissimilar and reproductively isolated. The entire aggregate of populations may fit the biological species definition, but the most potent available taxonomic evidence is the reproductive isolation of the near populations. The biological species definition cannot here be strictly applied, for lack of evidence, and I think the best taxonomic solution is to recognize two biological species where there may really be only one. But, while sympatry is a test for reproductive isolation between two populations, it may not always indicate specific distinctness. If, for example, the two sympatric populations were shown to be end points in a circle of races, then I would regard them as members of a single species.

Beyond the question of species definition is that of practical species recognition. For *Schizogenius*, the only data presently available are from adult morphology and distribution; there is no direct information about reproductive isolation, at least between allopatric populations, and indeed the limits of populations are unknown. In carabid beetles, the structures of greatest use in species recognition, because of diversity in form, are often in the male genitalia. In *Schizogenius*, major differences in male genitalia among related species are exceptional, and so I could not rely upon finding them to distinguish species. In the few species groups where major differences were found, however, and assuming no contrary evidence, I accept them as suitable criteria for species recognition. When species are sympatric, there is usually little difficulty in their recognition. If two forms differ constantly in one or more ways, and if there is no geographic or biologic evidence to the contrary, I assume the differences are maintained through reproductive isolation and treat the two forms as separate species. Generally, differences between sympatric species are numerous and well marked. When similar differences distinguish allopatric forms, and again if there is no contrary evidence, I consider the allopatric forms to represent distinct species. When allopatric forms differ less markedly, I use analytical methods described in section 2.223 to determine if reproductive isolation is likely, specimens permitting. When two allopatric forms cannot be linked in some reasonable geographic way because adjacent or intermediate samples are divergent in one or more characteristics, I regard them as separate species. If these samples do not diverge, and particularly if they actually converge, then I regard the allopatric forms they represent as conspecific.

I use the subspecies category only for taxa of uncertain status, and then only for the sake of completeness. All or nearly all individuals of a subspecies are morphologically distinguishable from those of an allopatric form, yet no judgment may yet be made as to biological status in terms of reproductive isolation. That is, there is a substantial statistical or morphological gap between the two forms, but one which could easily be bridged by collections made in intermediate areas if the two forms are truly conspecific. If, on the other hand, I have strong evidence of gene flow between allopatric forms, or if I have the direct evidence of hybridization between them, I recognize only one geographically variable taxon, the species. Aside from this use of the subspecies category as an expression of uncertainty, I share Erwin's (1970) view that the naming of subspecies is undesirable.

Unlike species-group taxa, genus-group taxa are groupings which are arbitrarily limited as to inclusiveness (Simpson, 1961). Most taxonomists agree that the subgenus or genus should contain an aggregate of related species separated from similar aggregates by a gap. It is not agreed how large this gap should be, nor is it agreed how inclusive should be the aggregates so separated. In the study of single genera, I think the existing concept of the genus should be accepted unless it is poorly defined or clearly unreasonable. I have elsewhere (1966b) segregated and defined the genus *Halocoryza*. I see no reason to otherwise modify Putzeys' (1846, 1863, 1866) concept of *Schizogenius*.

A supraspecific taxon should be strictly monophyletic, according to Hennig (1966). However, especially when no fossil evidence is available, I doubt that monophyly can be definitely demonstrated for all groupings; and other objections to this strict requirement for monophyly have been expressed by Mayr (1969). I have already (1966b) suggested that *Halocoryza* and *Schizogenius* share a common ancestry. I think that *Schizogenius* itself really is a monophyletic aggregate of closely related forms. However, *Halocoryza* may be either paraphyletic or monophyletic, and if my interpretations of its origin and relationships were correct it is indeed paraphyletic. If so, the requirement for monophyly indicates: 1, a single genus comprising *Halocoryza* + *Schizogenius*; 2, the Old World genus *Halocoryza* and the New World genus *Schizogenius*; or 3, three genera, the Old World *Halocoryza*, New World "*Halocoryza*," and *Schizogenius*. I chose none of these, since my separation of *Halocoryza* and *Schizogenius* better reflects known biological and zoogeographic peculiarities. Also, the relationships I suggested are based more on conviction than on demonstrable fact; it is quite possible that the two genera, as I define them, really are monophyletic assemblages.

Lindroth (1969) notes that recognition of subgenera may lead to chaos, and he uses informal "species groups." I agree that one should not formally recognize numerous closely related subgenera, but believe that use of the category may be justified for larger genera if done sparingly and carefully, and in accord with Simpson's (1961) suggestions about the ranking of taxa. I use the subgenus category for major monophyletic lineages which are approximately equally divergent from one another, yet are subordinate in my concept of the genus. I use the informal species group category for minor monophyletic lineages within subgenera.

2.25 Taxonomic methods

Specimens of North and Middle American *Schizogenius* were first sorted into presumptively related or conspecific complexes based on external morphological similarity. These complexes were further sorted by geographic locality, and the original sorting then refined. A preliminary survey of the male genitalia within each complex was then made, and the complexes refined further, as necessary. Relationships and status of specimens within each complex were then decided, based on criteria given for species and subspecies in section 2.24. If sufficient specimens were available, and if there was a problem in deciding whether forms were conspecific or not, I used methods of analytical statistics described in section 2.223. I examined at least six male genitalia for each species, specimens permitting, and as many more as necessary to reach appropriate conclusions about variation. Naming of specimens was based on knowledge of type specimens of all previously described taxa, and lectotypes were designated as required. The diacritical mark "(!)" is used to indicate that I examined the type specimen.

Similar methods could not be applied throughout to the South

American specimens studied, because of insufficient numbers. More reliance was placed on absolute superficial or genitalic similarity, and none on statistical methods, but criteria for species recognition remained the same. No subspecies were recognized. When taxonomic decisions could not be made, specimens were left undescribed or unassigned to species. I studied type material of some, but not all, described South American species, and may therefore have made some errors in association. I think this fault is outweighed by the need to provide the basis for future study of the South American fauna, and also to aid in understanding the North and Middle American faunas.

Simpson (1961) gave a clear definition of zoological classification: it is the ordering of animals into groups based on their relationships. Accordingly, it should reflect the evolutionary history of animals. Mayr (1969) wrote that the major purpose of zoological classification is to provide a system for maximum information storage and retrieval, and that the most efficient classification for that purpose is one based on evolutionary relationships. I believe that the classification should allow one to make and test predictions about zoogeographic, biochemical, chromosomal, larval, or other relationships not already directly embodied in the classification. For this purpose, a classification based on hypotheses about evolutionary relationships is the most efficient, since only it can theoretically contain and yield more information than was used in its creation. The difference between a classification based on suspected or real relationships and one based only on similarities is that the former is structured around evolutionary theory, while the latter is a mechanical structure with no intended theoretical basis. This difference may be not or scarcely evident in the end product, but I think it important. I have tried to provide for *Schizogenius* a classification with, I hope, some predictive value, and I hope it will be tested in future investigations.

Mayr (1969) summarized methods used in zoological classification. I have used various of them in various combinations, depending on the particular problem at hand. I obtained much useful information about relationships of components of some species complexes by using methods of analytical statistics outlined in section 2.223. These methods did not, however, give useful information about less closely related forms. Perhaps some of the various techniques of multivariate analysis would be useful to detect these more distant relationships, but I remain unconvinced of either their validity or utility (Mayr, 1969). Similarly, I have not used other numerical or deliberately phenetic methods, except some methods of numerical cladistics (Camin and Sokal, 1965). I did use some of the weighted character methods suggested by Mayr (1969), together with some of the more rigidly cladistic approaches preferred by Hennig (1966). I give a more detailed discussion of phylogenetic methods in sections 4.1 and 4.2 and discuss relationships between classification and phylogeny in section 4.13.

2.26 Taxonomic literature and synonymic lists

Pertinent taxonomic works are listed for all previously described taxa in *Schizogenius* in synonymic lists for those taxa. Most such works are among those cited in section 1.0. These synonymic lists do not pretend to completeness. In particular, most faunal and catalogue listings are excluded.

I made no effort to verify locality records cited in faunal works, and unless such records are particularly important and probably correct, references to those works are excluded. Many old records are doubtless erroneous; for example, some reports of *S. lineolatus* from eastern North America are doubtless based on specimens of *S. sulcifrons*. Important faunal works that I normally omitted from synonymic lists include those by Blatchley (1910), Brimley (1938), Fattig (1949), Leonard (1926), and Smith (1910).

Catalogue listings are excluded, since they neither contribute new taxonomic information nor contain useful summaries of then available taxonomic information other than literature references. Such catalogues are those by Blackwelder (1944), Csiki (1927), Gemminger and Harold (1868), Leng (1920), and Leng and Mutchler (1933).

3.0 TAXONOMY

3.1 Genus *Schizogenius* Putzeys

Schizogenius Putzeys 1846:650. *Type species.* - *Schizogenius strigicollis* Putzeys 1846:650 (subsequent designation by Lindroth, 1961:164). LeConte 1857:82. Putzeys 1863:24. Putzeys 1866:222. LeConte 1879: 34. Kult 1950:139. Lindroth 1961:164.

Diagnostic combination. - Clypeus tridentate apically; frons with four or five pairs of longitudinally directed carinae between eyes; lacinia plurisetose on inner and outer margins; gula not more than 0.3 width of mentum; pygidium with numerous longitudinally directed crenulate carinae near middle; stylus and coxite of ovipositor fused, plurisetose.

Description. - Small to medium size, LE 1.65 to 5.00 mm. Body pedunculate, elongate, depressed to cylindrical. Color various, maculate or not, not to strongly aeneous or metallic. Integument shiny or dull; microsculpture varied in extent, isodiametric, often useful in species recognition.

Head. Large, prognathous. Labrum Fig. 1-3, biemarginate to deeply emarginate; dorsal surface with seven setae in front, median and two outer ones longest; lateral margins each with five to about fifteen pairs of frayed or bifid setae, anterior pairs curved forward and inward over mandibles. Clypeus with two strong paramedian teeth; median tooth prominent in most species; paramedian carinae varied, oblique or arcuate, joined at apex with median tooth or not; median field triangular or hemicircular, basal width varied; clypeus with one pair of setae basad and laterad to carinae. Clypeal suture obsolete to sharply engraved. Frontal lobes prominent. Frons with four or five pairs of longitudinally directed carinae between eyes, neither perfectly equidistant not equally raised, appearance of frons not evenly convex; median sulcus broader than outer paramedian sulci, with or without median carina; carina five variable, obsolete or not; carina six obsolete except on frontal lobes, not raised above dorsal margin of eye. Anterior supraorbital seta set in front of carina five; posterior seta set between bases of frontal carinae four and five. Eyes varied in size, prominence, and size and number of facets. Neck punctate at least on sides, orbit extended laterad along posterior margin of eye. Antennal articles five to ten slightly transverse to quite elongate, moniliform to filiform; scape with one subapical dorsal seta; pedicel with one ventral seta, or bisetose or plurisetose in some species; articles three to four plurisetose or pubescent; articles five to eleven pubescent, without glabrous areas. Mandibles Fig. 5-7, stout and broadly curved along lateral margin; inner ventral margin of right mandible with small tooth near middle; scrobe oblique. Maxilla Fig. 9-11, terminal article of palpus swollen basally; lacinia with apex acute and abruptly bent, setose on outer and inner margins. Labium Fig. 13-15, penultimate article of palpus bisetose. Mentum Fig. 17-20, deeply emarginate at middle, with one anterior pair of paramedian setae; median tooth obsolete to acute; epilobes truncate or with antero-lateral angles acutely produced; ventral surface with broad, abruptly depressed concave area, limited behind by arcuate carina; base of mentum with one pair of large, pouch-like sensory pits, and one pair of paralateral setae. Submentum with one paramedian and one postero-lateral pair of setae, plurisetose in *S. strigicollis* Putzeys. Gula narrow, at narrowest part 0.05-0.30 width of mentum.

Thorax. Pronotum slightly to moderately transverse; median longitudinal sulcus not bordered by carinae; paramedian longitudinal sulci well developed in most species, hooked basally; paralateral sulci present in some species; lateral grooves shallow, bordered by distinct carinae in some species; anterior and posterior pairs of marginal setae present, additional marginal setae present in some species; basal carina moderately to strongly elevated above margin; disc flattened to moderately convex. Prothoracic pleura smooth, without longitudinal ridge, rugose or punctate in some species. Prosternum strongly compressed between front coxae; posterior process broadened and convex, without setae or carinae. Metepisternum slender, elongate. Anterior coxal cavities closed-separated-unbridged; middle and hind coxal cavities disjunct-confluent (see Bell, 1967).

Elytra. Lateral channel varied in form, slightly narrowed at apex, or flared and with one or more deep subapical pits (Fig. 22); umbilicate series of punctures unbroken. Elytron with whip-like seta at base of interval three; disc in most species with two or more setigerous punctures on interval three, in many species with variable numbers on intervals five and seven. Intervals one to six flat to convex, in some species with short apical carinae, in a few species entirely carinate; interval seven carinate or not; interval eight carinate at apex, in most species not joined at apex by other intervals. Striae punctate at least basally, faintly so in a few species; striae evident to apex, in most species deeply impressed, outer and inner striae equally engraved.

Hind wings. Macropterous and probably functional in all North and Middle American species, brachypterous in at least one South American species. Venation (Fig. 31-34) of usual carabid type except wedge cell absent and oblongum cell hooked in front.

Legs. Front tibia anisochaetous, with four evident external teeth; subapical spurs varied in size and form, not grossly unequal; ventral-basal margin with three or four setae. Middle and hind tibiae with apical spurs slender, inconspicuous. Anterior and middle tarsi of males of many species slightly dilated and more densely pubescent ventrally than in females, but without distinctive adhesive pads. Hind tarsi narrow and nearly glabrous. Tarsi moderately to markedly elongate, hind tarsus more than 0.55 length of hind tibia; article one of hind tarsus 2.0 to 4.0 times as long as article two. Paronychia obsolete to nearly as long as tarsal claws.

Abdomen. Sternum three with one pair of strong, oblique paramedian carinae, in many species strongly curved outward at apices. Sterna four to six each with one pair of paramedian ambulatory setae. Sternum seven with or without one pair of paramedian ambulatory setae, sexually dimorphic or not, and two pairs of approximately equidistant apical marginal setae. Sterna four to seven without basal transverse impressions. Pygidium (Fig. 23-25) with two or more pairs of paramedian setae, one pair of large setae near pygidial glands, variable numbers of microsetae, and conspicuous crenulate carinae along midline; margin of pygidium entire in males, but serrate or crenulate in some or all females of many species.

Male genitalia. Parameres subequal, slightly asymmetric, each with one to three large apical setae. Median lobe arcuate to angulate, in most species nearly symmetric, not constricted near base, base not lobate; apical third compressed, varied in form, in many species strongly deflected. Internal sac doubly invaginated; basal stylets of varied form; no flagellum; apical brush or virga without large spines; dorsal cap sclerite present; basal collar spines present in some species (see Whitehead, 1966a). Abdominal segment nine of normal carabid type, ring sclerite complete.

Female genitalia and ovipositor. Internal genitalia without sclerotized structures, not studied in detail. Ovipositor (Fig. 27-29) with stylus and coxite fused, plurisetose at middle; setae of posterior margin of valvifer normally in two groups; paraprocts absent; proctiger articulated with upper margin of valvifers.

Immature stages. Unknown; see Vinson (1956) for description of the presumably similar larva of *Halocoryza*.

Etymology. - Greek, *schizo* = split, plus *genio* = chin or mentum; in reference to form of mentum.

Distribution. - Members of this genus are known from continental North, Middle, and South America, from southern Canada to central Argentina; one species is endemic to Cuba.

3.11 Separation of *Schizogenius* and *Halocoryza*

In my review of *Halocoryza* (Whitehead, 1966b), I stated that members of the genus *Schizogenius* were best distinguished by uni- or bisetose antennal pedicels and striate pygidia. However, at least one South

American species has plurisetose antennal pedicels, probably secondarily so. Also, American *Halocoryza* species may have striate pygidia, but the striations are inconspicuous and weakly developed (Fig. 26). These striae are actually rows of tubercles, file-like ridges possibly used for stridulation; in this work I call them "crenulate carinae."

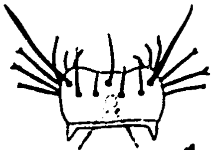
Several other differences listed in that paper are apparently without exception. The lacinia of *Schizogenius* is setose only on the outer margin. The gula of *Schizogenius* is much narrower than that of *Halocoryza* (Fig. 21). Another important difference, not recognized previously, is that in *Halocoryza* the fused stylus and coxite of the ovipositor has one large seta (Fig. 30). I found no characters in the labrum (Fig. 4), mandibles (Fig. 8), labium (Fig. 16), or wing useful to distinguish *Schizogenius* from *Halocoryza*, but in some forms of *H. arenaria* the apical part of the wing is reduced.

I continue to treat *Halocoryza* as a distinct genus, though I recognize that once a generic revision of the world Scaritini is completed its status may be reduced, especially if other generic concepts in the tribe remain as broad as they now are.

3.12 Key to subgenera of *Schizogenius*

I here recognize two subgenera, *Genioschizus* new subgenus and *Schizogenius s. str.*, both represented in North, Middle, and South America. *Genioschizus* is a small, mainly South American subgenus, composed of three closely related species groups. *Schizogenius s. str.* is much larger and more varied, and particularly in North America is

Fig. 1-4. Labrum, dorsal aspect. 1. *Schizogenius crenulatus* LeConte. 2. *S. optimus* Bates. 3. *S. sallei* Putzeys. 4. *Halocoryza acapulcana* Whitehead. Fig. 5-8. Mandibles, dorsal aspect. 5. *S. crenulatus* LeConte. 6. *S. optimus* Bates. 7. *S. sallei* Putzeys. 8. *H. acapulcana* Whitehead. Fig. 9-12. Left maxilla, ventral aspect. 9. *S. crenulatus* LeConte. 10. *S. optimus* Bates. 11. *S. sallei* Putzeys. 12. *H. acapulcana* Whitehead. Fig. 13-16. Labium, ventral aspect. 13. *S. crenulatus* LeConte. 14. *S. optimus* Bates. 15. *S. sallei* Putzeys. 16. *H. acapulcana* Whitehead.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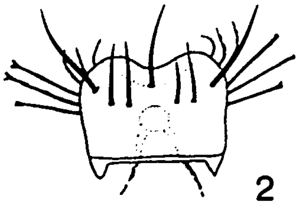
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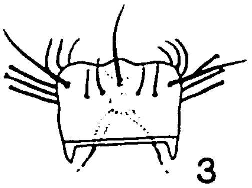
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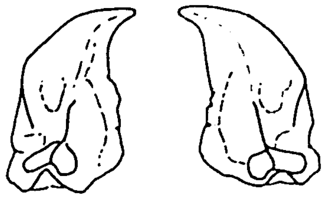
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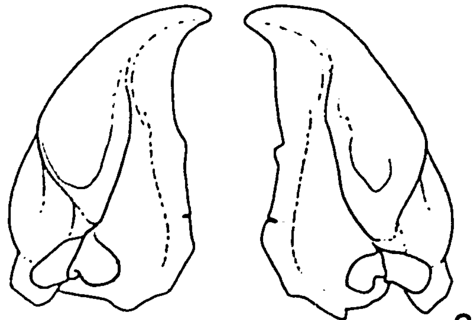
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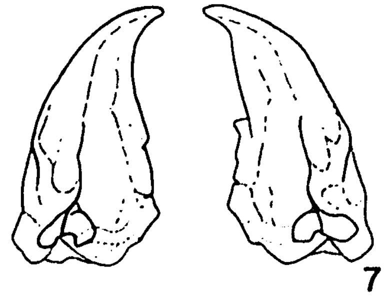
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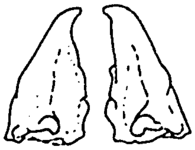
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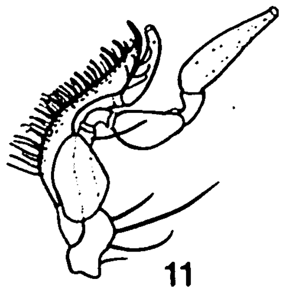
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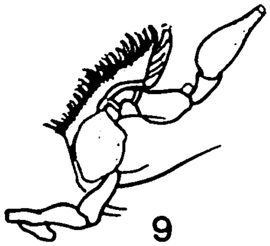
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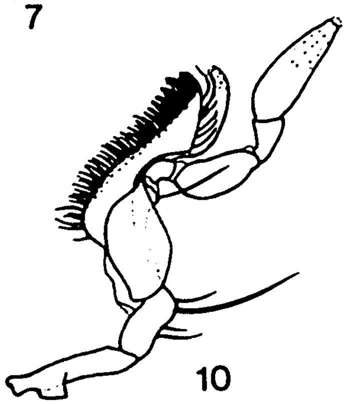
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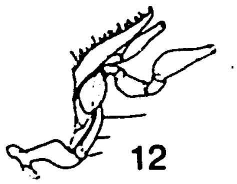
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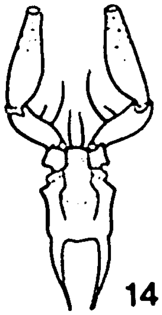
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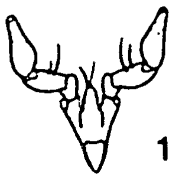
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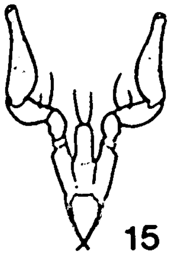
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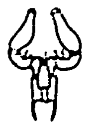
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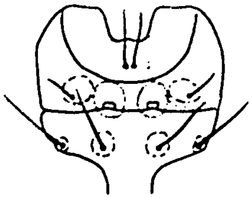
Fig. 17-21. Mentum, ventral aspect. 17. *S. crenulatus* LeConte. 18. *S. tenuis* Bates. 19. *S. optimus* Bates. 20. *S. sallei* Putzeys. 21. *H. acapulcana* Whitehead. Fig. 22. Elytral apex, postero-lateral aspect, *S. crenulatus* LeConte. Fig. 23-26. Female pygidium, dorsal aspect. 23. *S. crenulatus* LeConte. 24. *S. optimus* Bates. 25. *S. sallei* Putzeys. 26. *H. arenaria* Darlington. Fig. 27-30. Ovipositor, lateral aspect. 27. *S. crenulatus* LeConte. 28. *S. optimus* Bates. 29. *S. sallei* Putzeys. 30. *H. arenaria* Darlington.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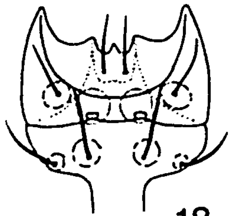
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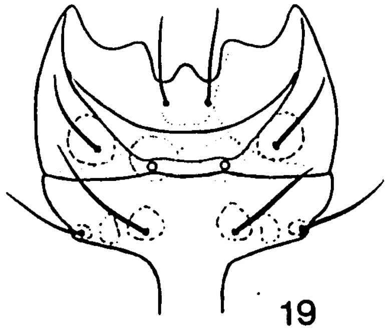
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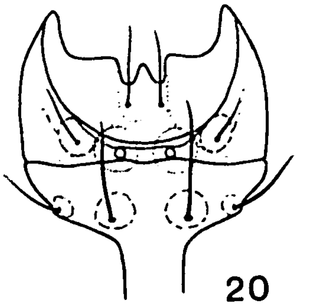
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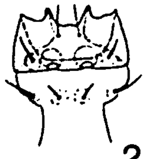
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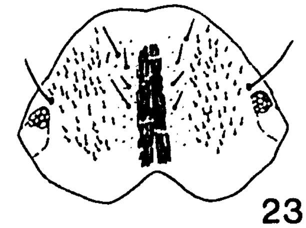
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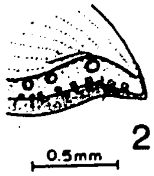

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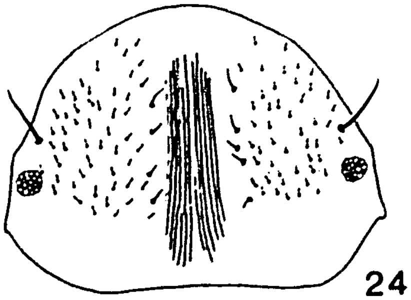
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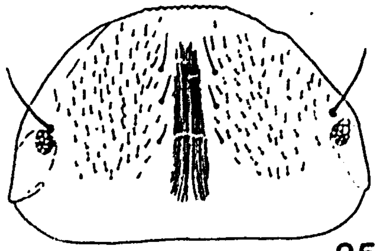
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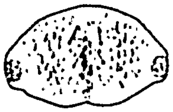
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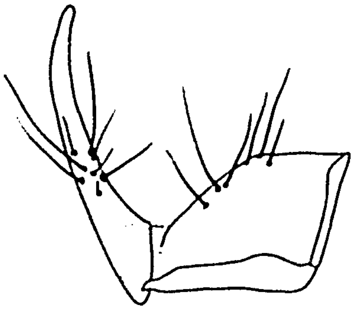
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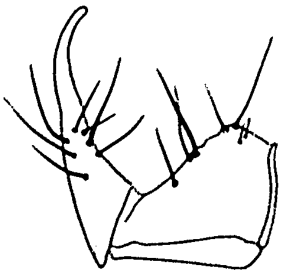
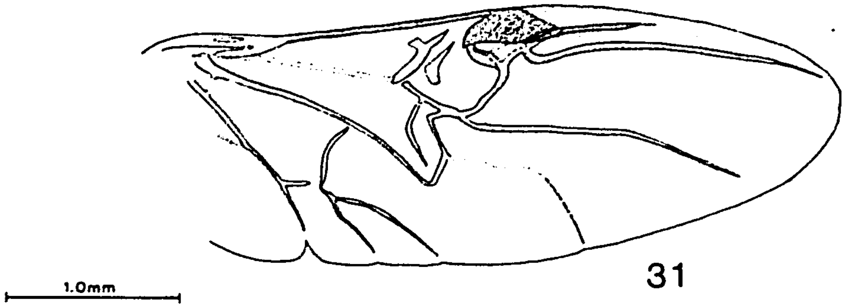

29


27

0.2mm


30

Fig. 31-34. Hind wing. 31. *S. crenulatus* LeConte. 32. *S. tenuis* Bates. 33. *S. optimus* Bates. 34. *S. sallei* Putzeys.



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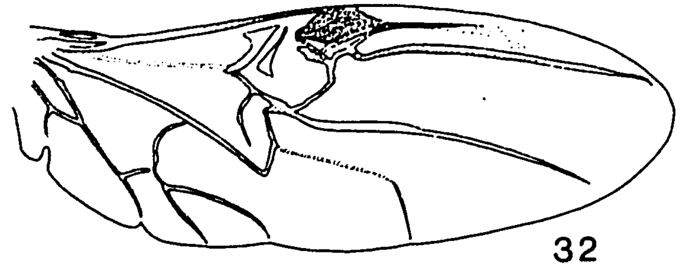

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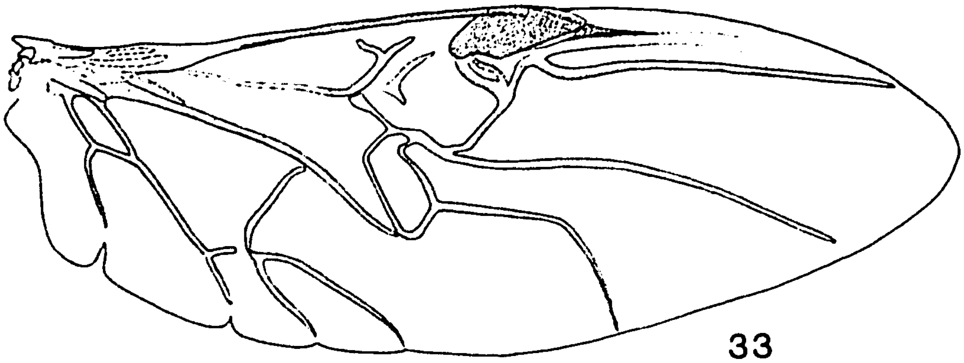

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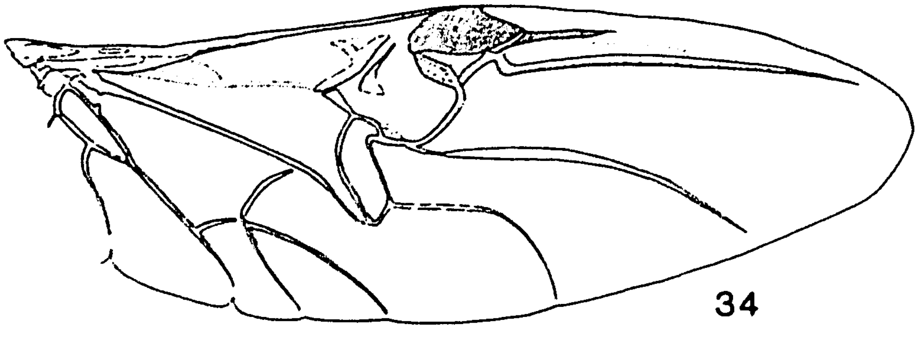


34

the dominant subgenus.

1. Lateral channel of elytron flared near apex, with one or more deep subapical pits . . . . *Genioschizus*, new subgenus, p. 34

1' Lateral channel of elytron narrowed near apex, without deep subapical pits . . . . *Schizogenius s. str.*, p.71

3.2 Subgenus *Genioschizus* new subgenus

Type species. - *Schizogenius crenulatus* LeConte 1849:197, here designated.

Diagnostic combination. - Lateral channel of elytron flared near apex and with one or more deep subapical pits. Also: paramedian clypeal carinae tuberculate, not joined to median clypeal tooth; clypeal suture not sharply engraved; antennae moniliform; paralateral longitudinal sulci present on pronotum or not; front tarsi slightly dilated in males only; paramedian ambulatory setae on sternum seven in both sexes; and pygidium not serrate or crenulate in either sex.

Description. - Small beetles, LE 1.65-2.75 mm. Body cylindrical. Color testaceous to piceous, aeneous or not, elytra sellate or not. Integument shiny; microsculpture reduced on or absent from median frontal sulcus, prothoracic pleura, and middle of abdominal sterna, present in small patches in coxal depressions of sternum three.

Head. Labrum (Fig. 1) slightly emarginate or biemarginate apically, margined laterally with five or six pairs of setae. Clypeus with median tooth reduced; paramedian carinae short, ended before median tooth, either oblique and tuberculate or arcuate and with apices nearly joined in an arc; median field triangular or hemicircular, at base more than 1.5 greatest width of median frontal sulcus. Clypeal suture obsolete. Frontal carinae one to four irregular, nearly parallel, confused basally or not, carinae one and four more strongly raised, carina five reduced or obsolete; median sulcus wider than at least outer paramedian sulci, not limited in front by transverse carina, with no trace of median carina, sides parallel or slightly divergent behind. Eyes prominent (WF/WH, 0.49-0.63), multifaceted, facets uniform or inner facets enlarged. Antennal articles five to ten square to slightly elongate, moniliform; pedicel unisetose; articles three to eleven pubescent. Mandibles (Fig. 5) stout. Mentum (Fig. 17-18) deeply emarginate at middle; median tooth either small and sharp or obsolete; antero-lateral angles of epilobes either broadly rounded or acutely produced; anterior paramedian setae close together. Submentum without accessory setae. Gula narrow, its narrowest part 0.15-0.20 width of mentum.

Thorax. Pronotum in most species slightly transverse (LP/WP, 0.91-1.01); paramedian sulci well developed; paralateral sulci present or absent; lateral grooves not bordered by distinct carinae; accessory marginal setae absent; hind angles reduced or nearly obsolete. Prothoracic pleura impunctate.

Elytra. Lateral channel broad and deep at apex, with one to three or four large pits near apex above umbilicate series (Fig. 22). Disc with two to four setae on interval three, zero to two basally on interval five, and none on interval seven. Interval eight strongly carinate, especially near apex; interval seven carinate at least in basal half; intervals two to seven subequal in width, convex, sharply carinate at extreme apices or not; interval eight joined by combined apices of intervals five and seven or not; interval seven normally joined by apex of interval five and either ended before apex of interval three or joined to it. Striae deeply engraved and, particularly near base of elytron, coarsely punctate.

Hind wings. Fully developed and probably functional in all species. Venation, Fig. 31-32.

Legs. Front and middle tarsi at most slightly more dilated and densely pubescent ventrally in male than in female; hind tarsus narrow, moderately elongate (Ta/Ti, 0.59-0.75); article one of hind tarsus 2.0-2.5 times as long as article two. Paronychia conspicuous, about as long as tarsal claws. Front tibia narrowed evenly to base where much narrower than at level of subapical spur; distal tooth nearly straight, stout, and blunt; apical and subapical spurs subequal, slender and acute; posterior ventral margin with three setae proximad to spur.

Abdomen. Sternum seven with paired paramedian ambulatory setae in both sexes. Paramedian carinae of sternum three not rounded at apices. Margin of pygidium entire in both sexes.

Male genitalia. Median lobe arcuate, symmetric. Endophallus without distinct basal collar spines; membrane around virga reduced; basal stylets various, useful in species recognition.

Female ovipositor. Number and position of setae variable, of no value in species recognition (Fig. 27).

Etymology. - *Genioschizus* is an anagram of *Schizogenius*, and bears the same meaning: Greek, *genio* = mentum; *schizo* = split.

Distribution. - Members of this subgenus range from southern Arizona and New Mexico in the north, southward at least to northern Argentina and Brazil. None are known from the West Indies. I examined 326 specimens of this subgenus.

Taxonomic notes. - Members of this subgenus are here placed in three quite easily distinguished and apparently natural groups, but some species are difficult to distinguish. The *crenulatus* group contains a single polytypic species found from southwestern United States to southern Mexico. The *quinquesulcatus* group, known only from South America, includes three recognized species. The *tenuis* group includes one species distributed from Mexico to Colombia, one species endemic to southern Mexico, and three additional species described from Colombia. I examined five additional specimens of the *tenuis* group frcm Argentina, Bolivia, Brazil, and Peru; these specimens probably represent at least two undescribed species, but I prefer not to treat them formally until additional material is available for study. I tentatively assign to the *tenuis* group a species described from Brazil, *S. maculatus* Kult, but I have seen neither the type nor any other specimens which match its description.

3.21 Key to described species groups, species, and subspecies of the subgenus *Genioschizus*

1. Pronotum with two pairs of paramedian longitudinal sulci. . . 2
1' Pronotum with one pair of paramedian longitudinal sulci (*tenuis* group) 6
2.(1). Epilobes of mentum truncate, their antero-lateral angles broadly rounded; median tooth of mentum obsolete. North America

(*crenulatus* group) 3

2' Epilobes of mentum angulate, their antero-lateral angles acutely produced; median tooth of mentum sharp, prominent. South America (*quinquesulcatus* group). 4

3.(2). Abdominal sterna without coarse lateral microsculpture; base of interval five normally asetose. Arizona and California to Sinaloa and Nayarit. . . . .
. . . . *S. crenulatus crenulatus* LeConte, p. 40

3' Abdominal sterna with coarse lateral microsculpture; base of interval five normally with one or two setae. Jalisco to Chiapas . . . *S. crenulatus chiapatecus* new subspecies, p. 45

4.(2'). Elytra uniformly dark. Brazil, Ecuador. . . . .
. . . . *S. quinquesulcatus* Putzeys, p. 47

4' Elytra pale, with dark sutural macula 5

5.(4'). Sides of pronotum broadly rounded (Fig. 37). Colombia, Argentina . . . . *S. szekessyi* Kult, p. 51

5' Sides of pronotum not strongly rounded (Fig. 38). Brazil. . .
. . . . *S. janae* Kult, p. 52

6.(1'). Base of interval five asetose; elytra with sutural macula. Brazil. . . . . *S. maculatus* Kult, p. 68

6' Base of interval five with one seta. Colombia and northward (specimens from south of Colombia not keyed) 7

7.(6'). Interval six of elytron conspicuously narrowed and carinate in apical third; abdominal sterna normally with coarse lateral microsculpture. Chiapas and Tabasco. . . . .
. . . . *S. sculptilis* new species, p. 54

7' Interval six of elytron not narrowed in apical third, finely carinate only at extreme apex if at all; abdominal sterna four to six usually without continuous, coarse lateral microsculpture 8

8.(7'). Median longitudinal sulcus of frons not narrowed toward apex; median lobe of male genitalia with apex sharply deflexed (Fig. 53). Colombia. . . . . *S. impressicollis* Putzeys, p. 64

8' Median longitudinal sulcus of frons narrowed toward apex; median lobe of male genitalia with apex not sharply deflexed 9

9.(8'). Head with neck nearly or quite impunctate along midline. Colombia. . . . . *S. impuncticollis* new species, p. 65

9' Head with neck distinctly punctate along midline. 10

10.(9'). Disc of elytron with distinct sutural macula. Colombia . . . . *S. suturalis* new species, p. 67

10' Disc of elytron without sutural macula; eyes with inner facets larger than outer facets. Mexico to Colombia. . . . . *S. tenuis* Bates, p. 58

3.22 The *crenulatus* group

Diagnostic combination. - Clypeal carinae strongly arcuate; mentum with median tooth obsolete, epilobes truncate; pronotum with short but evident paralateral longitudinal sulci; elytron with three or four conspicuous pits near apex of lateral channel; interval five with or without basal setae; intervals two to seven not carinate apically; interval eight free to apex; and parameres normally uni- or bisetose.

The mentum, with epilobes truncate, is diagnostic within the genus. The group differs from other North and Middle American members of the subgenus by ecarinate apices of elytral intervals two to seven.

Distribution. - This group includes one species, *S. crenulatus* LeConte, with two subspecies distributed from extreme southwestern United States to Chiapas. Other groups of the subgenus have more tropical distributions, though one species of the *tenuis* group ranges nearly as far northward. I studied 62 specimens of the *crenulatus* group.

3.221 *Schizogenius crenulatus* LeConte

Diagnostic combination. - Specimens of *S. crenulatus* differ from other *Schizogenius* by truncate mentum epilobes. I recognize two subspecies, distinguished by extent of microsculpture on abdominal sterna.

3.2211 *Schizogenius crenulatus crenulatus* new combination

Schizogenius crenulatus LeConte 1852:197. *Type locality* "California," here restricted to the Colorado River opposite Yuma, Yuma County, Arizona; type in MCZ, specimen labelled MCZ 5480 here designated lectotype (!). LeConte 1857:82. Putzeys 1863:24. Putzeys 1866: 223. LeConte 1879:34. Lindroth 1961:165.

Diagnostic combination. - From specimens of the other subspecies, specimens of this form are distinguished by reduced microsculpture on sides of abdominal sterna. Also, they are often paler, and most lack basal setae on elytral interval five.

Description. - Color rufopiceous, legs paler, palpi, antennae, and tarsi testaceous; without strong aeneous luster, elytra not sellate or maculate.

Integument. Fine but conspicuous microsculpture on genae, gula, mouthparts, front tibiae and apical half of anterior surfaces of front femora, middle legs except trochanters, hind tibiae and posterior surfaces of hind femora, elytral epipleura at base and on apical two thirds, and in coxal depressions of sternum three; paramedian frontal sulci obscurely microsculptured.

Head. Sculpture and form of clypeus and frons as in Fig. 35. Eyes prominent, subglobose, coarsely and uniformly faceted. Neck densely and coarsely punctate. Genae strongly punctate, finely rugose in front. Mentum (Fig. 17) epilobes truncate, median tooth obsolete. Antennae short, moniliform, article five 1.0-1.1 times as long as wide.

Pronotum. Form and sculpture as in Fig. 35. Paramedian sulci faintly punctate, shallow apically, deep and broadly hooked basally, basal tips abruptly limited; paralateral sulci usually deep, coarsely punctate, no more than half length of paramedian sulci; anterior transverse impression finely to coarsely punctate; base transversely rugose.

Elytra. Three discal setigerous punctures on interval three adjacent to second stria; interval five asetose or in some specimens with one basal seta. Intervals one to six convex; interval seven carinate in basal two-thirds; interval eight carinate throughout, sharply so in apical third. Interval eight fused with interval one at apex, otherwise free; intervals three and five joined to apex of interval seven in most specimens. Lateral channel with three or four large pits near apex.

Male genitalia. Median lobe (Fig. 44) variable, some specimens as in *chiapatecus* (Fig. 45), apical portion suddenly deflexed; basal stylets, Fig. 58-59; virga (Fig. 57) without distinguishing spines or scales. Seven specimens studied.

Measurements and proportions. See Table 1.

Variation. - One specimen from Blythe, California, has a basal seta on the fifth interval of the left elytron, but in all other specimens interval five is asetose on both elytra. Paralateral pronotal sulci are in some specimens quite weakly impressed. Paramedian clypeal carinae are in some specimens short and widely separated at apices. There is no pronounced external sexual dimorphism, though males are often distinguished by slightly broader front tarsi. Among specimens studied, extremes in size were found in two females from Rio San Lorenzo in Sinaloa (LE, 1.89-2.61 mm). Variation in selected characteristics in specimens from the Colorado River drainage basin of Arizona and California is given in Table 1.

Etymology. - Latin, *crenulatus* = minutely toothed, in reference to the minutely toothed elytral apices.

Distribution. - Specimens of *S. crenulatus crenulatus* have been collected at low elevations in the lower reaches of the Colorado River and environs in southern California and Arizona, south to southern Sinaloa and northern Nayarit (Fig. 74). I studied 56 specimens from the following localities.

UNITED STATES

No locality (1; ANSP). ARIZONA (7; CAS, INHS, USNM): Gila Co., Salt River (2; ANSP, MCZ); Maricopa Co., Phoenix (1; CUNY); Pima Co. (1;

Table 1. Descriptive statistics for *S. crenulatus*, based on 28 specimens of undetermined sex from Arizona and California.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.52-4.25	3.962	0.272	0.068	4.57
LE	2.16-2.60	2.426	0.172	0.043	4.47
WH	0.69-0.83	0.776	0.048	0.012	4.08
WP	0.94-1.16	1.075	0.081	0.021	5.05
WE	1.10-1.35	1.246	0.089	0.022	4.74
B. Proportions.					
WF/WH	0.54-0.59	0.569	0.023	0.006	2.78
LP/WP	0.94-1.01	0.975	0.025	0.006	1.70
DP/LP	0.80-0.86	0.831	0.025	0.006	2.00
LP/WE	0.81-0.87	0.842	0.022	0.006	1.73
Ta/Ti	0.63-0.73	0.691	0.038	0.010	3.69
PS/LP	0.62-0.69	0.651	0.025	0.006	2.55

USNM); Yuma Co. (10; CAS, USNM), Yuma (9; CAS, MCZ, USNM). CALIFORNIA: Riverside Co., Blythe (2; CAS).

MEXICO

NAYARIT: Jesus Maria (2; UCB). SINALOA: 30.6 mi. s. Culiacan (18; DRWh, UASM), 21 mi. e. Villa Union (2; CNC), 26 mi. ne. Villa Union 1000' (1; LBSC).

Collecting notes. - The most recently collected specimens seen from the United States are those from Blythe and Phoenix, taken in 1917. Perhaps, because of environmental changes resulting from manipulation of the Colorado River system, *S. crenulatus* may now be extinct or nearing extinction in the southwestern United States. All Mexican specimens, however, were collected more recently.

According to label data, adults of *S. crenulatus* are probably active throughout the year. Several specimens were taken at lights, so no doubt wings are functional. I have no field experience with adults of this subspecies, but suspect they normally live in sandy river banks rather than gravel bars. G. E. Ball, T. L. Erwin, and R. E. Leech collected 19 specimens near Culiacan, Sinaloa, under litter on moist sand along the Rio San Lorenzo.

Taxonomic notes. - I treat the old name *S. crenulatus* as a new combination, *S. crenulatus crenulatus*, because I recognize, as a new subspecies, *S. crenulatus chiapatecus*. Available specimens of the two forms are well distinguished morphologically, and hence I think that recognition of separate subspecies is well justified. Proximate localities of these allopatric forms are not greatly distant, but I can neither reject nor defend a proposition of reproductive isolation.

3.2212 *Schizogenius crenulatus chiapatecus* new subspecies

Type material. - Holotype, female, labelled "MEXICO. Chiapas. 3.2 mi. n. Arriaga 400' Rte. 195 III.2.1966" and "George E. Ball, D. R. Whitehead collectors" (MCZ). Four females and one male from various localities in Chiapas, Guerrero, Jalisco, and Oaxaca are paratypes (FDAG, MCZ, UASM).

Diagnostic combination. - Sterna four to six with continuous microsculpture on each side. All specimens seen have one or two basal setigerous punctures on interval five on at least one elytron.

Description. - As in *S. crenulatus crenulatus* except as follows. Color darker in most specimens with faint aeneous luster, strongest in Chiapas specimens; antennae, maxillae, labial palpi, and tarsi dark testaceous.

Integument. Conspicuous microsculpture on sternum two, sternum three except median field, sterna four to six at sides, and sternum seven along margin.

Pronotum. Anterior transverse impression more finely punctate; base of pronotum often more strongly rugose, basal tips of paramedian sulci not sharply limited.

Elytra. Interval five normally with one or two basal setae.

Male genitalia. Median lobe, Fig. 45; basal stylets, Fig. 60; virga as in *S. crenulatus crenulatus*. One specimen studied.

Measurements and proportions. Holotype: TL, 4.36 mm; LE, 2.72 mm; WH, 0.85 mm; WP, 1.14 mm; WE, 1.38 mm; WF/WH, 0.55; LP/WP, 0.98; DP/LP, 0.84; LP/WE, 0.81; Ta/Ti, 0.72; PS/LP, 0.67. Holotype plus paratypes:

TL, 3.80-4.09-4.31 mm; LE, 2.35-2.54-2.67 mm; WH, 0.75-0.80-0.85 mm; WP, 1.02-1.11-1.18 mm; WE, 1.17-1.29-1.36 mm; WF/WH, 0.55-0.57-0.58; LP/WP, 0.94-0.96-0.98; DP/LP, 0.82-0.85-0.86; LP/WE, 0.81-0.82-0.84; Ta/Ti, 0.65-0.70-0.75; PS/LP, 0.63-0.68-0.70.

Variation. - Variations in numbers of discal setae on elytra include: absence of middle seta of interval three of left elytron in Chiapas paratype; absence of seta of interval five of left elytron in Oaxaca male; and presence of two setae near base of fifth interval on both elytra in Acapulco specimen. Otherwise I found no noteworthy variation.

Etymology. - The name *chiapatecus* is given in reference to the type locality, in Chiapas.

Distribution. - The six known specimens of *S. crenulatus chiapatecus* were collected at low elevations from Jalisco south to Chiapas (Fig. 74).

MEXICO

CHIAPAS: 3.2 mi. n. Arriaga (2; MCZ, UASM). GUERRERO: Acapulco (1; MCZ). JALISCO: Pitillal (1; UASM). OAXACA: Rio Jaltepec (2; FDAG).

Collecting notes. - Specimens of this subspecies have been collected in January, March, May, and August. The Chiapas specimens were taken in coarse sand along a small stream. Other specimens were collected at lights, and probably arrived by flight.

Taxonomic notes. - Since the Chiapas locality is the most distant from the known range of *S. crenulatus crenulatus*, I chose one of the two females from there as holotype. I found no diagnostic characteristics in the male genitalia. *S. crenulatus chiapatecus* may be a biologically distinct species, but evidence from morphological characteristics reported here is inconclusive. That the possibility exists, however, is sufficient reason to distinguish this form taxonomically. As all known specimens of this subspecies are distinguishable from all known specimens of the other, the names refer to distinctive taxa which may eventually prove to be reproductively isolated.

3.23 The *quinquesulcatus* group

Diagnostic combination. - Head with clypeal carinae straight to moderately arcuate; mentum with median tooth small and sharp, epilobes acutely produced at antero-lateral angles; pronotum with short but evident paralateral longitudinal sulci; elytron with at least two conspicuous pits near apex of lateral channel; interval five with basal seta; intervals two to seven finely carinate at extreme apices; interval eight free to apex; and parameres normally unisetose.

The acutely produced epilobes of the mentum and the deep paralateral sulci of the pronotum are, in combination, diagnostic of the group within the genus.

Distribution. - I here recognize three species, all closely related, from nearly throughout continental South America. I studied 20 specimens of the group from northern Colombia south to northern Argentina.

3.231 *Schizogenius quinquesulcatus* Putzeys

Schizogenius quinquesulcatus Putzeys 1863:26. *Type locality* "Amazone," Brazil; type female in IRSB (!). Putzeys 1866:232.

Schizogenius exaratus Putzeys 1863:27. *Type locality* Nova Friburgo, Brazil;

type female in IRSB (!). Putzeys 1866:232, established synonymy.

Diagnostic combination. - Within the *quinquesulcatus* group, specimens of this species are distinguished by having dark, non-sellate elytra.

Description. - Color dark piceous; femora rufous or infuscated, legs and antennae otherwise ferrugineous; palpi testaceous; elytra with slight aeneous luster, not sellate or maculate, apex pale or not.

Integument. Fine microsculpture on genae, gula, mouthparts, front tibiae and anterior surfaces of front femora, middle legs except trochanters, hind tibiae and posterior surfaces of hind femora, elytral epipleura on base and apical two-thirds, sides of sterna two to six, and apex of sternum seven; paramedian frontal sulci obscurely microsculptured.

Head. Sculpture and form of clypeus and frons as in Fig. 36; paramedian clypeal carinae straight to arcuate, apices widely separated, median field triangular or hemicircular; inner paramedian frontal carinae nearly parallel. Eyes prominent, subglobose, coarsely and uniformly faceted. Neck densely, finely to coarsely punctate. Genae strongly punctate, finely rugose in front. Mentum with epilobes acutely produced, median tooth conspicuous but short and sharp. Antennae short, moniliform, article eight 1.0-1.2 times as long as wide.

Pronotum. Form and sculpture as in Fig. 36; sides broadly rounded; paralateral longitudinal sulci and anterior transverse impression punctate; base transversely rugose.

Elytra. Three discal setigerous punctures on interval three, near or adjacent to stria two; interval five with one seta near base. Striae deep and sharply engraved throughout, evidently punctate except near apex of elytron, coarsely punctate in basal half. Intervals one to six broad, convex, narrowed and finely carinate at apices; interval six not carinate basally; interval seven carinate throughout; interval eight carinate in apical half. Interval eight free to apex; intervals seven, five, and usually three joined at apices. Lateral channel with two large conspicuous pits near apex.

Male genitalia. Median lobe, Fig. 46-47; basal stylets, Fig. 61-63; virga without distinguishing spines or scales. Three specimens studied.

Measurements and proportions. Ranges of variation in measurements and proportions among eight specimens studied are: TL, 3.24-3.95 mm; LE, 1.99-2.50 mm; WH, 0.65-0.76 mm; WP, 0.92-1.07 mm; WE, 1.00-1.28 mm; WF/WH, 0.57-0.62; LP/WP, 0.88-0.91; DP/LP, 0.84-0.91; LP/WE, 0.74-0.82; LE/WE, 1.94-1.99; Ta/Ti, 0.67-0.79; PS/LP, 0.64-0.73.

Variation. - The specimen from Ecuador differs from Brazilian specimens by more coarsely punctate neck, longer antennae, and shorter paramedian pronotal sulci, but is otherwise not distinctive. The form of the paramedian clypeal carinae varies, but this variation is probably not important.

Etymology. - For *quinquesulcatus*, Latin, *quinque* = five, plus *sulcatus* = grooved, in reference to the five longitudinal grooves on the pronotum. For *exaratus*, Latin, *ex* = out, plus *aratus* = plow, in reference to the fossorial habitus.

Distribution. - I studied 14 specimens of this species from Atlantic and Pacific drainage systems from the following continental South American localities.

BRAZIL

"Amazones" (1; IRSB, Type of *quinquesulcatus*). CEARA: Fortaleza (1; IRSB). RIO DE JANEIRO: Nova Friburgo (1; IRSB, type of *exaratus*).

SANTA CATARINA (2; IRSB): Nova Teutonia (6; DRWh, MCZ). SAO PAULO: Piracicaba (2; OSUC, UASM).

ECUADOR

EL ORO: 9 mi. s. Santa Rosa (1; CAS).

Collecting notes. - Specimens of this species have been collected in January, February, April, August, September, October, and November, and individuals may therefore be active throughout the year.

Taxonomic notes. - The names *quinquesulcatus* and *exaratus* were both originally proposed for unique specimens. The specimen listed here as type of *S. quinquesulcatus* is certainly so, but label data on the *S. exaratus* specimen ("S. exaratus. P," handwritten on green paper, and "Dup. 8/8 47 Bres.," handwritten on white paper) are equivocal. Neither specimen matches its original description in detail, but since Putzeys often erred in his descriptions I think this may be ignored. My reasons for suggesting that the *S. exaratus* specimen is indeed the type are the following. Putzeys gave no indication that the type was deposited elsewhere than in his collection, and no other specimen in IRSB can be the type. The specimen was collected well before the date of the original description, and thus was likely available to Putzeys since he corresponded with Dupont. Most important, the specimen is the only one labelled as *S. exaratus* in Putzeys' own hand, something he probably would not have done with subsequent material as his discovery of a third specimen of the species prompted him to propose the synonymy of the two names. Quite possibly the third specimen mentioned by Putzeys (1866) is the Ceara specimen.

I believe all of the Brazilian specimens are conspecific, despite variation in form of clypeal carinae; this variation forms no evident geographic pattern. The Ecuadorian specimen may well not be conspecific, but I am unable to decide without additional material.

3.232 *Schizogenius szekessyi* Kult

Schizogenius szekessyi Kult 1950:144. *Type locality* Aracataca, Colombia; type in Budapest Museum, not studied.

Diagnostic combination. - From specimens of *S. janae,* the only other described member of the *quinquesulcatus* group having pale elytra with a dark sutural macula, specimens of this form are distinguished by broadly rounded pronotal sides.

Description. - As in *S. quinquesulcatus* except: body paler, rufopiceous; elytron rufotestaceous, with dark sutural macula extended outward to interval three or four; head and pronotum, Fig. 37, clypeal carinae straight and neck coarsely punctate in all specimens studied; male median lobe (Fig. 48) and basal stylets (Fig. 64-65) as illustrated; three specimens studied.

Measurements and proportions. Ranges of variation in measurements and proportions among the five specimens studied are: TL, 3.52-3.78 mm; LE, 2.20-2.35 mm; WH, 0.65-0.79 mm; WP, 0.96-1.08 mm; WE, 1.14-1.24 mm; WF/WH, 0.55-0.58; LP/WP, 0.89-0.92; DP/LP, 0.85-0.87; LP/WE, 0.76-0.78; LE/WE, 1.90-2.00; Ta/Ti, 0.65-0.73; PS/LP, 0.63-0.73.

Variation. - The specimen from Argentina differs from Colombian specimens by having a somewhat smaller sutural macula and relatively narrower elytra, but I think these differences are trivial. This specimen has only two setae on interval three of the left elytron.

Etymology. - This species was named in honor of the Hungarian entomologist, Dr. W. Szekessy.

Distribution. - I have assigned the name *S. szekessyi* to four topotypic specimens from Colombia, and one additional specimen from Argentina.

ARGENTINA

SALTA: Oran (1; MCZ).

COLOMBIA

MAGDALENA: Aracataca (4; DRWh, MCZ).

Collecting notes. - Colombian specimens were collected from January to May, and the Argentinian specimen was taken in September; thus, individuals are probably active as adults throughout the year.

Taxonomic notes. - I have not studied type material of this species, but think there is no question of identity since topotypic material agrees with the original description. I see no reason to treat the specimen from Argentina as other than conspecific.

3.233 *Schizogenius janae* Kult

Schizogenius janae Kult 1950:145. *Type locality* Brazil; type in Kult Collection, not studied.

Diagnostic combination. - The sides of the pronotum are less broadly rounded in specimens of *S. janae* than in those of *S. szekessyi*, the only other member of the *quinquesulcatus* group having a sutural macula on the elytra; differences in form of median lobe of male genitalia may also be useful in species recognition. However, as these features may be subject to variation, it is quite possible that all specimens with the sutural macula are conspecific, and thus that the names *S. janae* and *S. szekessyi* are synonyms.

Description. - As in *S. quinquesulcatus* except as follows. Color of body paler, rufopiceous; elytra rufotestaceous, each with a dark sutural macula extended outward to interval three or four. Head and pronotum, Fig. 38; pronotal sides weakly rounded, clypeal carinae straight, and neck coarsely punctate. Male median lobe (Fig. 49) and basal stylets (Fig. 66) as illustrated; one specimen studied.

Measurements and proportions. TL, 3.25 mm; LE, 2.00 mm; WH, 0.68 mm; WP, 0.92 mm; WE, 1.02 mm; WF/WH, 0.59; LP/WP, 0.91, DP/LP, 0.80; LP/WE, 0.82; LE/WE, 1.96; Ta/Ti, 0.68; PS/LP, 0.72.

Etymology. - This species was dedicated by Kult to his wife.

Distribution. - I studied one specimen of this species from Brazil.

BRAZIL

MATO GROSSO: Jacare (1; MGFT).

Collecting notes. - The Brazilian specimen reported here was collected in September.

Taxonomic notes. - I have not studied the type, but think this specimen represents *S. janae* because it agrees well with the original description and comes from a suitable locality. In particular, the specimen is smaller and paler than specimens of *S. szekessyi*, and the form of the pronotum is correct. Other characters given in the original description are unreliable.

I think it highly probable that the names *S. janae* and *S. szekessyi* are synonyms, despite differences illustrated for form of pronotum and male median lobe. More specimens are needed from throughout the range to determine extent of individual and geographic variation.

3.24 The *tenuis* group

Diagnostic combination. - Head with clypeal carinae normally arcuate; mentum with median tooth prominent, epilobes acutely produced; pronotum without paralateral sulci; elytron with one to three conspicuous subapical pits in lateral channel; interval five with or without basal seta; intervals two to seven carinate apically; interval eight free to apex or not; and parameres in most species bi- or trisetose.

The lack of paralateral longitudinal sulci from the pronotum is unique within the subgenus.

Distribution. - Specimens of this group have been collected from northern Mexico to northern Argentina. I here recognize one species known only from Mexico, another from Mexico to Colombia, and three others from Colombia. Five unplaced specimens from widely separated localities elsewhere in South America probably represent at least two additional, undescribed, species. I tentatively place as a member of this group a species described by Kult from Brazil, *S. maculatus*. I examined 244 specimens of the *tenuis* group.

3.241 *Schizogenius sculptilis* new species

Type material. - Holotype, male, and allotype, female, labelled "MEXICO. Chiapas San Quintin 700' 91°20'-16°24' stream margins II. 5-20. 1966" and "George E. Ball D. R. Whitehead collectors" (MCZ). Twenty additional specimens from two localities in Chiapas and Tabasco are paratypes (BMNH, CAS, CNC, DRWh, IRSB, UASM, USNM).

Diagnostic combination. - Most reliably distinguished from *S. tenuis* by narrowed, carinate apices of elytral interval six, and by characteristic form of basal stylets of median lobe. On most specimens, the abdomen is microsculptured laterally, while in most Middle American specimens of *S. tenuis* the abdomen lacks extensive microsculpture.

Description. - Color dark piceous, legs, palpi, and antennae paler; no definite aeneous luster; elytra not sellate or maculate, apices normally not pale.

Integument. As described for *S. tenuis* except on abdomen; sides of sterna four to six and margin of sternum seven strongly microsculptured in most specimens.

Head. Fig. 39. Generally as described for *S. tenuis*. Frontal carina one broad, carinae two to four narrow, carina five short but well developed. Inner facets of eyes much larger than marginal facets. Mentum with median tooth minute.

Pronotum. Fig. 39. Generally as described for *S. tenuis* except disc flatter, paramedian sulci longer, and anterior transverse impression coarsely punctate.

Elytra. Discal setae and striae as in *S. tenuis*. Intervals one to five broad, convex, carinate at extreme apices; interval six narrowed, carinate in apical third; interval seven carinate throughout; interval eight carinate in apical half. Apex of interval eight fused with interval one, nearly fused with interval two, otherwise free; intervals three, five, and seven often more or less fused at apex. Lateral channel with one small but conspicuous subapical pit.

Male genitalia. Median lobe (Fig. 50) arcuate, apical part not suddenly deflexed; basal stylets (Fig. 67) characteristic; virga without distinguishing spines or scales. Four specimens studied.

Measurements and proportions. See Table 2. Holotype: TL, 3.83 mm; LE, 2.30 mm; WH, 0.78 mm; WP, 1.08 mm; WE, 1.21 mm; WF/WH, 0.59; LP/WP, 0.96; DP/LP, 0.82; LP/WE, 0.86; Ta/Ti, 0.73; PS/LP, 0.71. Allotype: TL, 3.82 mm; LE, 2.30 mm; WH, 0.78 mm; WP, 1.11 mm; WE, 1.24 mm; WF/WH, 0.60; LP/WP, 0.93; DP/LP, 0.81; LP/WE, 0.83; Ta/Ti, 0.63; PS/LP, 0.74.

Variation. - Two specimens from Chiapas and one from Tabasco have reduced abdominal microsculpture. Another Chiapas specimen has an extra seta on interval three of the left elytron, and one Tabasco specimen has pale elytral apices. Aside from slightly broader front tarsi in males, there is no evident secondary sexual differentiation.

Etymology. -Latin, *sculptilis* = carved, in reference to form of apices of elytral intervals

Distribution. - Specimens of this species have been collected at two localities (Fig. 75) in lowland rain forests of Chiapas and Tabasco. I studied 22 specimens from the following localities.

MEXICO

CHIAPAS: San Quintin (20; BMNH, CAS, CNC, IRSB, MCZ, UASM, USNM).

TABASCO: 59.4 mi. se. Villahermosa (2; DRWh).

Collecting notes. - Adults of *S. sculptilis* are probably active throughout the year, since specimens were collected in February and June. No specimens were seen to fly, and none were taken at lights, but like other North and Middle American *Schizogenius*, adults of *S. sculptilis*

Table 2. Descriptive statistics for *S. sculptilis*, based on 22 unsexed specimens from Chiapas and Tabasco.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.33-3.98	3.658	0.271	0.077	4.93
LE	1.94-2.44	2.210	0.184	0.052	5.56
WH	0.70-0.81	0.749	0.048	0.014	4.27
WP	0.93-1.12	1.036	0.078	0.022	5.02
WE	1.09-1.26	1.176	0.075	0.021	4.28
B. Proportions.					
WF/WH	0.57-0.63	0.592	0.028	0.008	3.15
LP/WP	0.91-0.99	0.945	0.027	0.008	1.91
DP/LP	0.80-0.89	0.830	0.037	0.011	3.00
LP/WE	0.81-0.86	0.834	0.021	0.006	1.67
Ta/Ti	0.59-0.73	0.666	0.053	0.015	5.32
PS/LP	0.68-0.74	0.715	0.029	0.008	2.67

probably are capable of flight. Among North and Middle American members of *Schizogenius*, habits of this species are unusual in that the preferred habitat is in sand, along shaded forest streams. Three specimens were taken under leaf litter on sand along the Rio Jatate, but all other San Quintin specimens were collected in deep forest in a sand-gravel substrate along stream margins. Specimens of *S. tenuis* also found at San Quintin were collected on sandy, sunlit shores of the Rios Jatate and Perlas.

Taxonomic notes. - In addition to characters mentioned in the diagnostic combination, specimens of *S. sculptilis* generally differ from specimens of *S. tenuis* by: uniformly dark elytra; second and eighth elytral intervals united at apex; and subapical pit in lateral channel smaller. Ecological and morphological differences, and sympatry at least in Chiapas, indicate reproductive isolation. *S. sculptilis* agrees with *S. tenuis*, and differs from other South American species, by having enlarged inner eye facets, a peculiarity suggesting possible close relationship with *S. tenuis*. But *S. tenuis* is otherwise more similar to other South American species, and I suspect the relationship between *S. sculptilis* and *S. tenuis* is remote.

3.242 *Schizogenius tenuis* Bates

Schizogenius tenuis Bates 1881:38. *Type locality* Paso Antonio, Guatemala; type in BMNH, specimen labelled as holotype here designated lectotype (!).

Diagnostic combination. - Specimens of this species differ from those of *S. sculptilis*, the only other member of the *tenuis* group known from

Middle America, most conspicuously by differences in elytral structure: interval six not carinate except finely at extreme apex, and subapical pits of lateral channel larger. Also, the basal stylets of the median lobe are strikingly different. Specimens of *S. tenuis* differ from other South American specimens of the group seen by me by the combination of: neck punctate medially; elytra not sellate or maculate; and eyes normally with inner facets enlarged.

Description. - Color dark piceous, legs, palpi, antennae, and usually elytral apices paler; elytra with slight aeneous luster, not sellate.

Integument. Fine but conspicuous microsculpture on paramedian sulci of frons, genae, gula, mouthparts, sides and base of pronotum, front tibiae and anterior surfaces of front femora, middle legs except trochanters, hind tibiae and posterior surfaces of hind femora, elytral epipleura on base and apical two-thirds, and coxal depressions of sternum three. Abdomen without extensive microsculpture on sides of sterna four to six or margin of sternum seven.

Head. Fig. 40. Clypeus with apices of paramedian carinae fused to form an arc, or nearly so; median field hemicircular, width at base more than 2.0 apical width of median field of frons. Frons with median longitudinal sulcus narrowed in front. Eyes prominent, subglobose, coarsely faceted, inner facets usually larger than marginal facets. Neck densely and coarsely punctate. Genae strongly punctate, finely rugose in front. Mentum (Fig. 18) with epilobes acutely produced, median tooth conspicuous but short and sharp. Antennae short, moniliform, article five 1.0-1.1 times as long as wide.

Pronotum. Fig. 40. Disc convex, slightly transverse, greatest width near middle; paramedian sulci short, faintly punctate, deep and abrupt apically, deep and broadly hooked basally, basal tips normally confused laterad with basal rugosity; paralateral sulci absent; anterior transverse impression impunctate to finely punctate.

Elytra. Three discal setigerous punctures on interval three, first adjacent to second stria, others in middle of interval; interval five with one seta at base. Intervals one to six broad, convex, carinate at most at extreme apices, interval six not carinate basad of posterior discal seta; interval seven carinate throughout; interval eight carinate in apical half. Apex of interval eight often fused with apices of intervals three, five, and seven, as well as with interval one. Lateral channel with at least one large subapical pit, some specimens with one or more additional smaller pits, or with two or three large pits.

Male genitalia. Median lobe (Fig. 51) arcuate, apical part not suddenly deflexed; basal stylets, Fig. 68; endophallus without distinguishing spines or scales on virga. Thirteen specimens studied.

Measurements and proportions. See Table 3.

Variation. - I found no important geographic variation in size or body proportions, and because of paucity of material did no statistical analysis of variation. The smallest specimen studied (LE, 1.86 mm) is from Paso Antonio, Guatemala, and the largest (LE, 2.50 mm) is from Villahermosa, Tabasco. Variation in discal setae on elytra includes reduction, with the middle seta of interval three lacking from both elytra in one specimen from San Luis Potosi, and addition, with four setae on interval three of one or both elytra in several specimens. All specimens have at least one large subapical pit in the lateral channel

Table 3. Descriptive statistics for *S. tenuis*, based on 22 unsexed specimens from San Quintin, Chiapas.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.38-3.98	3.645	0.263	0.075	4.82
LE	2.09-2.49	2.255	0.169	0.048	5.00
WH	0.68-0.92	0.747	0.055	0.016	4.89
WP	0.88-1.05	0.957	0.072	0.021	5.05
WE	1.04-1.25	1.135	0.084	0.024	4.93
B. Proportions.					
WF/WH	0.49-0.57	0.544	0.031	0.009	3.78
LP/WP	0.95-1.00	0.968	0.015	0.004	1.06
DP/LP	0.80-0.87	0.828	0.032	0.009	2.58
LP/WE	0.79-0.85	0.818	0.027	0.008	2.16
Ta/Ti	0.60-0.75	0.675	0.070	0.020	6.87
PS/LP	0.62-0.68	0.655	0.027	0.008	2.73

of the elytron. Many have one or more additional, but much smaller, pits as well. Small specimens, especially from the Paso Antonio and El Coyul samples, tend to have unusually large secondary pits, and a strongly marked tendency for the apices of elytral intervals three, five, and seven to converge on interval eight. I don't think these differences have any geographic significance. In some Colombian specimens, and less noticeably in some Costa Rican specimens, the inner eye facets are not as distinctly enlarged as in specimens from more northern areas, but the transition is gradual.

Etymology. - Latin, *tenuis* = thin, in reference to body form.

Distribution. - The known distribution of *S. tenuis* (Fig. 76) extends from northern Mexico to Colombia, from low elevations to as high as 4000' in Puebla. I studied 204 specimens from the following localities.

MEXICO

CHIAPAS: San Quintin (23; UASM). DURANGO: Ventanas (1; BMNH). JALISCO: 18 km. n. Puerto Vallarta (25; UASM). NAYARIT: Acaponeta (1; CAS), Jesus Maria (5; UCB), Rio Santiago Ferry (2; CAS), 5 mi. s. Rio Santiago Ferry (4; CAS). OAXACA: 17.7 mi. w. El Camaron (2; DRWh), 29.4 mi. e. El Coyul (3; AMNH, CNC), 11.1 mi. n. Matias Romero (34; MGFT, UASM), Valle Nacional (5; UASM). PUEBLA: Tepexco (7; UASM). SAN LUIS POTOSI: Tamazunchale (3; CNHM, DRWh). SINALOA: 30.6 mi. s. Culiacan (2; IRSB). SONORA: 10 mi. w. Alamos (1; AMNH). TABASCO: Teapa (3; BMNH), Villahermosa (2; MCZ). VERACRUZ: 20 mi. nw. Huatusco (1; FDAG).

GUATEMALA

ESCUINTLA: Paso Antonio (2; BMNH). IZABAL: Los Amates (2; MCZ).

HONDURAS

CORTES: La Lima (25; FDAG).

COSTA RICA

GUANACASTE: Las Canas (2; UASM). LIMON: Los Diamantes (18; FDAG), Reventazon (9; USNM). PUNTARENAS: Palmar Sur (2; UAFA).

PANAMA

CANAL ZONE: San Pablo (1; USNM). CHIRIQUI: Tole (6; IRSB, MCZ).

COLOMBIA

MAGDALENA: Aracataca (2; MCZ), Rio Frio (10; MCZ). TOLIMA: Coyaima (1; CAS).

Collecting notes. - I have seen specimens of *S. tenuis* collected nearly throughout the year, except during the latter part of the dry season from early April to mid-June. Numerous specimens were taken at black lights, which probably indicates flight.

I collected numbers of this species only at Matias Romero and San Quintin. Specimens of several species were collected along the Rio Malatengo in gravel bars, but the *S. tenuis* were found alone, in sand. All but three of the San Quintin specimens were found along the Rio Jatate in sandy banks; the others were collected on the Rio Perlas a short distance away, perhaps also in sand. One specimen from Tamazunchale, two from Culiacan, and three from El Coyul were also taken in silt or fine sand; other specimens were hand collected by G. E. Ball or me at El Camaron and Valle Nacional, but whether in sand or not is unrecorded. *S. tenuis* thus probably agrees with other species of the subgenus by living in a sandy habitat, but, unlike those of *S. sculptilis*, specimens are more likely to be found along open rivers.

Taxonomic notes. - In Mexico, this species is sympatric with both *S. crenulatus*, at Jesus Maria and Culiacan, and *S. sculptilis*, at San Quintin. In Colombia, it is sympatric with at least two other members of the *tenuis* group; specimens of *S. tenuis, S. impuncticollis*, and *S. suturalis* were taken at Aracataca by P. J. Darlington.

Possibly related but probably distinct are a female from Tucuman, Argentina (JNeg), and a male (Fig. 52, 69) from Santa Isabel do Araguaia, Brazil (CAS). In addition to differences in the male genitalia as illustrated, the eyes are uniformly faceted and the elytral apices are pale in sharp contrast to the rest of the elytron.

3.243 *Schizogenius impressicollis* Putzeys

Schizogenius impressicollis Putzeys 1846:653. *Type locality* Colombia; lectotype here designated, a male in the Institut Royal des Sciences Naturelles de Belgique, so labelled. Putzeys 1863:24. Putzeys 1866:223.

Diagnostic combination. - Within the *tenuis* group, basal stylets (Fig. 70), form of median lobe (Fig. 53), and form of median frontal sulcus (Fig. 41), of the lectotype are distinctive. Also, lateral lobes of male genitalia are broad and trisetose apically, rather than bisetose as in other members of the group. The elytra probably are not sellate, the eyes are uniformly faceted, and the neck is sparsely punctate along the midline. Since I examined only one old, discolored specimen, I prefer not to give a detailed description.

Distribution. - The specific locality at which the type specimens were collected in Colombia is unknown, and I have seen no additional specimens.

Etymology. - Latin, *impressus* = impressed, plus *collum* = neck in reference to the sulcate pronotum.

Taxonomic notes. - In the original description of this species, Putzeys wrongly stated it to have three or four setae on intervals three, five, and seven; this was an error he repeated in several other species descriptions.

3.244 *Schizogenius impuncticollis* new species

Type material. - Holotype, male, labelled "Aracataca, Mgd. Colombia III 2 29 Darlington" (MCZ). Allotype female, label data same as in holotype except III 3 29 (MCZ). Two additional specimens from the same locality are paratypes (MCZ).

Diagnostic combination. - Specimens of this species are readily distinguished from other members of the *tenuis* group by having in combination: neck nearly or quite impunctate along midline; basal transverse impression of pronotum unusually deep; body strongly aeneous or metallic; and elytral apices contrastingly pale.

Description. - Color rufopiceous, strong aeneous or metallic green luster; front femora rufous; antennae, palpi, elytral apices, and legs except front femora testaceous.

Integument as described for *S. tenuis*.

Head and pronotum. Fig. 42. Generally as described for *S. tenuis*, except eyes uniformly faceted, neck not or hardly punctate along midline, anterior transverse impression strongly punctate, and basal transverse impression unusually deep.

Elytra. As in *S. tenuis* except more strongly bicolored.

Male genitalia. Median lobe, Fig. 54; basal stylets, Fig. 71; virga without distinguishing spines or scales. Three specimens studied.

Measurements and proportions. Holotype: TL, 3.35 mm; LE, 2.05 mm; WH, 0.69 mm; WP, 0.90 mm; WE, 1.09 mm; WF/WH, 0.62; LP/WP, 0.98; DP/LP, 0.77; LP/WE, 0.81; Ta/Ti, 0.70; PS/LP, 0.69. Holotype plus paratypes: TL, 3.23-3.36-3.49 mm; LE, 1.99-2.06-2.15 mm; WH, 0.65-0.68-0.70 mm; WP, 0.88-0.90-0.92 mm; WE, 1.05-1.10-1.16 mm; WF/WH, 0.59-0.60-0.62; LP/WP, 0.93-0.96-0.98; DP/LP, 0.77-0.79-0.82; LP/WE, 0.76-0.78-0.81; Ta/Ti, 0.66-0.70-0.72; PS/LP, 0.67-0.68-0.70.

Etymology. - Latin, *im* = not, plus *punctus* = punctate, plus *collum* = neck, in allusion to one diagnostic characteristic of specimens of this species, lack of punctures along midline of neck.

Distribution. - Only the type specimens from Aracataca, in northern Colombia, are known.

Collecting notes. - Specimens of this species were collected in March. As wings are fully developed, adults probably can fly.

Taxonomic notes. - The range of this species overlaps that of at least *S. tenuis* and *S. suturalis* among other members of the *tenuis* group. Also, specimens of this species differ sufficiently from those of the other described members of the group that they undoubtedly represent a distinct species.

A female from Yoay, Bolivia (CAS), a male from Yurac, Peru (CAS), and an unsexed specimen from El Cidral, Bolivia (MCZ) agree with the

Colombian specimens in having the neck impunctate. These specimens differ in coloration, being much less strongly metallic and having less strongly bicolored elytra, and they don't have the basal transverse impression of the pronotum so strongly deepened. The female (LE, 2.43 mm) is markedly larger than specimens from Colombia, and the male differs in form of median lobe (Fig. 55) and basal stylets (Fig. 72). For these reasons I doubt that these specimens represent *S. impuncticollis*. Final judgment as to their relationships must await study of additional material.

3.245 *Schizogenius suturalis* new species

Type material. - Holotype, male, and allotype, female, labelled "Aracataca, Mgd. Colombia III 2 29 Darlington" (MCZ). Five additional specimens from the same locality are paratypes (DRWh, MCZ, UASM).

Diagnostic combination. - Specimens of this species differ from others in the *tenuis* group by having, in combination, sellate elytra and one seta near base of interval five.

Description. - Color rufopiceous, with strong aeneous or metallic green luster; front femora rufous; elytra rufotestaceous, central macula aeneopiceous; antennae, palpi, and legs except front femora testaceous.

Integument. As described for *S. tenuis*.

Head and pronotum. Fig. 43. Generally as described for *S. tenuis* except eyes uniformly faceted.

Elytra. Except for coloration, as described for *S. tenuis*.

Male genitalia. Median lobe, Fig. 56; basal stylets, Fig. 73; virga without distinguishing spines or scales. Two specimens studied.

Measurements and proportions. Holotype: TL, 3.56 mm; LE, 2.18 mm; WH, 0.70 mm; WP, 0.94 mm; WE, 1.15 mm; WF/WH, 0.57; LP/WP, 0.97; DP/LP, 0.81; LP/WE, 0.79; Ta/Ti, 0.62; PS/LP, 0.60. Holotype plus paratypes: TL, 3.19-3.58-3.77 mm; LE, 1.96-2.21-2.35 mm; WH, 0.65-0.70-0.75 mm; WP, 0.83-0.95-1.02 mm; WE, 1.01-1.15-1.23 mm; WF/WH, 0.55-0.57-0.61; LP/WP, 0.94-0.95-0.97; DP/LP, 0.81-0.82-0.84; LP/WE, 0.77-0.79-0.81; Ta/Ti, 0.62-0.67-0.71; PS/LP, 0.57-0.62-0.66.

Variation. - One paratype has an extra seta on left margin of pronotum, and another has four setae on interval three of right elytron.

Etymology. - Latin, *sutura* = seam, in reference to the sutural macula.

Distribution. - The only known specimens are from Aracataca, in northern Colombia.

Collecting notes. - Specimens of this species were collected in March and May. Wings are fully developed, so individuals probably fly.

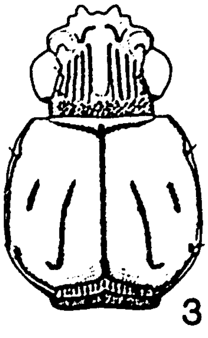
Taxonomic notes. - *S. suturalis, S. tenuis*, and *S. impuncticollis* are sympatric in Colombia, so are undoubtedly specifically distinct. The only other described species included in the *tenuis* group which has the sutural macula is *S. maculatus* Kult. If that species really belongs in the group, and if the original description is correct, then it differs from *S. suturalis* by not having a basal seta on interval five.

3.246 *Schizogenius maculatus* Kult

Schizogenius maculatus Kult 1950:143. *Type locality* Para, Amazonas, Brazil; type in Kult collection, present location not known, not seen by me.

Diagnostic combination. - Assuming the original description is correct, and if this species really is a member of the *tenuis* group, specimens of it

Fig. 35-43. Head and pronotum, dorsal aspect. 35. *S. crenulatus crenulatus* LeConte, Culiacan, Sinaloa. 36. *S. quinquesulcatus* Putzeys, Nova Teutonia, Brazil. 37. *S. szekessyi* Kult, Aracataca, Colombia. 38. *S. janae* Kult, Jacare, Brazil. 39. *S. sculptilis* new species, San Quintin, Chiapas. 40. *S. tenuis* Bates, Matias Romero, Oaxaca. 41. *S. impressicollis* Putzeys, Colombia. 42. *S. impuncticollis* new species, Aracataca, Colombia. 43. *S. suturalis* new species, Aracataca, Colombia. Fig. 44-55. Male median lobe, lateral aspect. 44. *S. crenulatus crenulatus* LeConte, Yuma, Arizona. 45. *S. crenulatus chiapatecus* new subspecies, Rio Jaltepec, Oaxaca. 46. *S. quinquesulcatus* Putzeys, Nova Teutonia, Brazil. 47. Same, Santa Rosa, Ecuador. 48. *S. szekessyi* Kult, Aracataca, Colombia. 49. *S. janae* Kult, Jacare, Brazil. 50. *S. sculptilis* new species, San Quintin, Chiapas. 51. *S. tenuis* Bates, Rio Santiago, Nayarit. 52. *S.* nr. *tenuis* Bates, Santa Isabel, Brazil. 53. *S. impressicollis* Putzeys, Colombia. 54. *S. impuncticollis* new species, Aracataca, Colombia. 55. *S.* nr. *impuncticollis* new species, Yurac, Peru.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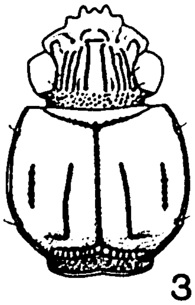
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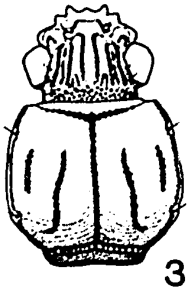
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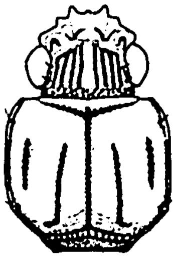
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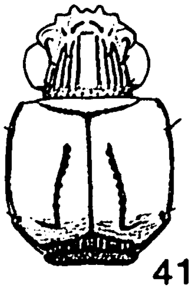
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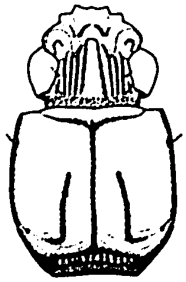
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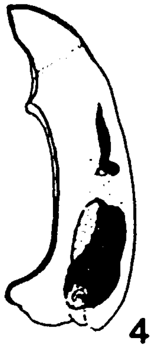
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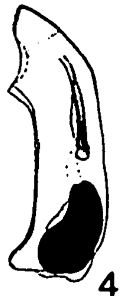
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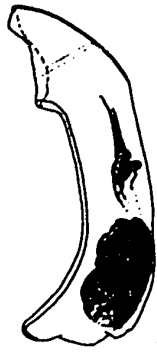
Fig. 56. Male median lobe, lateral aspect, *S. suturalis* new species, Aracataca, Colombia. Fig. 57. Male endophallus, *S. crenulatus crenulatus* LeConte, Culiacan, Sinaloa. Fig. 58-73. Basal stylets of male endophallus. 58, 59. *S. crenulatus crenulatus* LeConte, Culiacan, Sinaloa. 60. *S. crenulatus chiapatecus* new subspecies, Rio Jaltepec, Oaxaca. 61, 62. *S. quinquesulcatus* Putzeys, Nova Teutonia, Brazil. 63. Same, Santa Rosa, Ecuador. 64, 65. *S. szekessyi* Kult, Aracataca, Colombia. 66. *S. janae* Kult, Jacare, Brazil. 67. *S. sculptilis* new species, San Quintin, Chiapas. 68. *S. tenuis* Bates, Rio Santiago, Nayarit. 69. *S.* nr. *tenuis* Bates, Santa Isabel, Brazil. 70. *S. impressicollis* Putzeys, Colombia. 71. *S. impuncticollis* new species, Aracataca, Colombia. 72. *S.* nr. *impuncticollis* new species, Yurac, Peru. 73. *S. suturalis* new species, Aracataca, Colombia. Fig. 74-76. Known distributions. 74. *S. crenulatus crenulatus* LeConte, circles, and *S. crenulatus chiapatecus* new subspecies, triangles. 75. *S. sculptilis* new species. 76. *S. tenuis* Bates.



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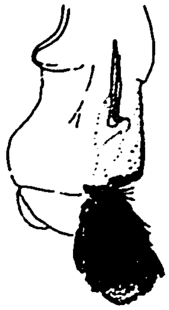

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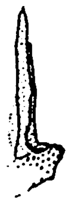

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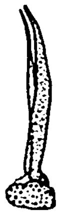

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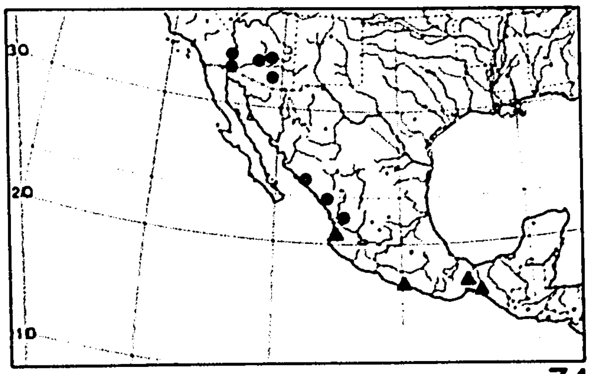

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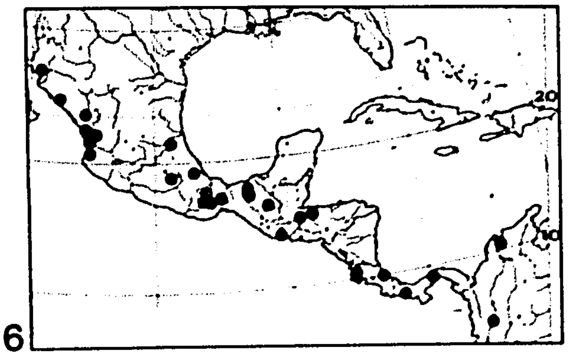

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should be readily recognized by not having a basal seta on elytral interval five. The only other described species in the group having a dark sutural macula is *S. suturalis*, which may differ further by having the striae coarsely punctate basally.

Taxonomic notes. - Since I have not studied specimens which I could identify with this name, I am unable to give further data on *S. maculatus*. My allocation to the *tenuis* group, and indeed to the subgenus *Genioschizus*, is tentative, since critical subgeneric characteristics were not mentioned in Kult's description. However, the only small species of *Schizogenius* with a sutural macula, reduced elytral setation, and moniliform antennae known to me are *Genioschizus*, and absence of paralateral pronotal sulci indicates placement in the *tenuis* group. Absence of basal setae from interval five of the elytron is not otherwise known in this group, but is characteristic of *S. crenulatus crenulatus* in the *crenulatus* group. I do not suspect Kult misinterpreted this characteristic, since he correctly described it in *S. szekessyi* and *S. janae*. The names *S. maculatus* and *S. suturalis* may be synonymous, but the information available to me indicates otherwise.

3.3 Subgenus *Schizogenius sensu stricto*

Type species. - *Schizogenius strigicollis* Putzeys 1846:650, subsequent designation by Lindroth, 1961:164.

Diagnostic combination. - Lateral channel of elytron not flared near apex, without deep subapical pits; and females, except of *S. pluripunctatus*, and species of *basalis* group ,normally without paramedian ambulatory setae on sternum seven. Also: paramedian clypeal carinae tuberculate or not; antennae moniliform to filiform; front tarsi markedly dilated or not in many species, more strongly so in males than females; male endophallus of many species with well developed basal collar spines; paralateral longitudinal sulci not present on pronotum; clypeal suture obsolete to sharply engraved; and pygidium serrate or crenulate in females of many species.

Description. - Size variable, LE 1.65-3.70 mm in North and Middle America, up to 5.00 mm in South America. Body cylindrical to strongly depressed. Color testaceous or ferrugineous to dark piceous, sometimes aeneous or metallic, elytra sometimes maculate or sellate in South America. Integument normally shiny, dorsum without extensive microsculpture except in some South American species; coxal depressions of sternum three often with small patches of particularly coarse microsculpture; microsculpture isodiametric or nearly so.

Head. Labrum (Fig.2-3) weakly emarginate or biemarginate apically, or in some South American species deeply emarginate; margined laterally with six or seven pairs of setae, to about fifteen pairs in *S. optimus*. Clypeus with median tooth prominent, nearly or quite as large as paramedian teeth, except in some South American species; paramedian carinae straight or arcuate, joined to median tooth or not; median field triangular or hemicircular, base of varied width. Clypeal suture obsolete to deeply engraved at middle. Frons with carinae one to four straight and nearly parallel, or arcuate in some South American species; carinae one and four more strongly elevated or not; carina five distinct or not; median sulcus wider than at least outer paramedian sulci, limited in front by a transverse carina or not, with median longitudinal carina in some species; sides of median sulcus parallel, divergent behind, or bowed outward at middle. Eyes flat to prominent, multifaceted, inner facets not enlarged in most species; eyes in *S. ocellatus* each reduced to an apparently single, bubble-like facet. Antennal articles five to ten moniliform to elongate; pedicel unisetose, or bisetose or plurisetose in some South American species; articles three and four pubescent, or plurisetose in some South American species; articles five to eleven pubescent. Mandibles (Fig. 6-7) elongate, prominent. Mentum (Fig. 19-20) deeply emarginate at middle, or shallowly in some South American species, median tooth large and sharp, or blunt in some South American species; antero-lateral angles of epilobes acutely produced; anterior paramedian setae widely spaced. Submentum without accessory setae, except in *S. strigicollis*. Gula narrow, its narrowest part 0.15-0.30 width of mentum, or less than 0.10 in some South American species.

Thorax. Pronotum convex to flat, transverse to elongate; paramedian longitudinal sulci usually present, paralateral sulci absent; lateral grooves narrow and deep, or broad and shallow in some South American species; lateral grooves not bordered internally by carinae, except in some South American species; accessory marginal setae present or absent; hind angles obsolete to prominent. Prothoracic pleura usually impunctate.

Elytra. Lateral channel narrow to broad at apex, shallow, not flared, without foveae or pits above umbilicate series. Disc without setae, with setae on interval three, intervals three and five, or on intervals three, five, and seven. Elytral intervals broad, flat to moderately convex, carinate in some South American species; interval eight and in some species intervals five and seven carinate at apex; interval eight free, interval seven in most species joined by apices of intervals three and five. Striae in most species deeply engraved, in most species distinctly punctate at least in basal half.

Hind wings. Fully developed except in *S. ocellatus*. Venation as in Fig. 33-34; oblongum cell broad, proximal transverse vein not broken.

Legs. Front and middle tarsi expanded and with relatively dense ventral pubescence in many species, particularly in males,or narrow in both sexes. Hind tarsi slender, short to elongate; article one of hind tarsus 2.5-4.0 times as long as article two. Paronychia varied from about half to quite as long as tarsal claws, or obsolete in some South American species. Front tibia narrowed evenly to base or not; distal tooth varied in form; spurs subequal, slender and acute; posterior ventral margin with three setae proximad to spur, or four in some South American species.

Abdomen. Sternum seven with paramedian ambulatory setae present in males of most species, absent from females except of *S. pluripunctatus* and of members of *basalis* group. Paramedian carinae of sternum three curved outward at apices or not. Margin of pygidium (Fig. 24-25) crenulate or not in females, not in males.

Male genitalia. Median lobe arcuate, nearly symmetric in most species, form of apex various. Endophallus with distinctive basal collar spines in many species; membrane around virga reduced or not; basal stylets various, distinctive in some species.

Female ovipositor. Number and position of setae variable, of no value in species recognition (Fig. 28-29).

Distribution. - Members of this subgenus range from southern Canada southward to central Argentina. One species is known from Cuba in the West Indies. I examined 9701 specimens of the subgenus *Schizogenius*.

Taxonomic notes. - The subgenus is most diverse in South America. Since this thesis treats only the North and Middle American fauna in detail, I deliberately mentioned characteristics peculiar to South American forms as such in the description. These characteristics are not repeated in species descriptions, except in species groups where appropriate.

3.31 Key to described species groups, species, and subspecies of the subgenus *Schizogenius* in North and Middle America

1. Pronotum with paramedian longitudinal sulci obsolete; clypeal suture obsolete; neither sex with paramedian ambulatory setae on sternum seven (*optimus* group). . . *S. optimus* Bates, p. 90

1' Pronotum with deep paramedian longitudinal sulci; clypeal suture sharply engraved; at least males with paramedian ambulatory setae on sternum seven 2

2. (1').Paramedian clypeal carinae tuberculate, not or hardly extended to median tooth; antennal articles four to ten moniliform (*ferrugineus* group) 3

2' Paramedian clypeal carinae extended to median tooth; antennal articles four to ten moderately to strongly elongated, filiform 4

3. (2). Abdomen strongly microsculptured; body without metallic luster . . . . *S. ferrugineus* Putzeys, p. 102

3' Abdomen not extensively microsculptured; body with distinct aeneous luster . . . . *S. auripennis* Bates, p. 108

4. (2'). Paramedian pronotal sulci extended forward nearly to anterior transverse impression; front tarsi slender in both sexes (*truquii* group). . . . . *S. truquii* Putzeys, p. 154

4' Paramedian pronotal sulci shorter; front tarsi slightly to strongly dilated, at least in males. 5

5. (4'). Interval seven with at most one seta, usually with none (*lindrothi* group) . . . . . *S. lindrothi* new species, p. 144

5' Interval seven of elytron with at least three discal setae 6

6. (5'). Discal setae of elytra average 1.2 or more times longer than maximum width of interval two; striae usually indistinctly punctate; body form cylindrical to subcylindrical; pronotum with or without accessory marginal setae (*pluripunctatus* group). 7

6' Discal setae of elytra average no more than 1.0 times longer than maximum width of interval two; striae usually distinctly punctate; body form various; pronotum without accessory marginal setae 12

7. (6). Pronotum with accessory marginal setae. 8

7' Pronotum without accessory marginal setae 10

8. (7). Front and middle tarsi strongly expanded in both sexes. California and Baja California. 9

8' Front and middle tarsi not strongly expanded. Northeastern Mexico . . . . *S. plurisetosus* new species, p. 175

9. (8). Disc of elytron with fewer than 60 setae. California . . . . *S. seticollis seticollis* Fall, p. 165

9' Disc of elytron with more than 60 setae. Southern Baja California. . . *S. seticollis yandykei* new subspecies, p. 172

10. (7'). Females with paramedian ambulatory setae; apex of median lobe weakly deflected; disc of elytron with 35 or more setae. Arizona and New Mexico south to Durango and northern Nayarit, north of Rio Grande de Santiago drainage basin . . . . *S. pluripunctatus* LeConte, p. 190

10' Females without paramedian ambulatory setae; apex of median lobe arcuate or sharply deflected. Not known from north of Rio Grande de Santiago drainage basin 11

11. (10'). Apex of median lobe sharply deflected; elytron normally with more than 40 discal setae, none seen with fewer than 37. San Luis Potosi south to Puebla and Oaxaca. . . . . *S. multisetosus* Bates, p.179

11' Apex of median lobe not angularly deflected; elytron normally with fewer than 35 setae, none seen with more than 41. Central Nayarit in west and Veracruz in east, south at least to Guatemala, near coasts or not . . *S. kulti* new species, p.195

12. (6'). Elytron with 35 or more short discal setae; abdomen not extensively microsculptured; body strongly depressed; color castaneous; eyes prominent (*brevisetosus* group) . . . . *S. brevisetosus* new species, p.159

12' Elytron with fewer than 35 discal setae, or abdomen extensively microsculptured 13

13. (12'). Abdomen with entire ventral surface microsculptured, or nearly so; paramedian frontal sulci not or hardly closed behind; body moderately to strongly depressed; not in West Indies (*tristriatus* group) 14

13' Abdomen not with entire ventral surface microsculptured, or paramedian frontal sulci strongly closed behind, or in West Indies 20

14. (13). Prothoracic pleura distinctly punctate; small, LE under 2.50 mm . . . . *S. amphibius* Haldeman, p.218

14' Prothoracic pleura not distinctly punctate; larger, LE over 2.50 mm. 15

15. (14'). Prothoracic pleura strongly microsculptured. . . . . *S. tibialis* new species, p.213

15' Prothoracic pleura not or weakly microsculptured 16

16. (15'). Range, United States; eyes flattened, WF/WH 0.65 or more; each elytron normally with 25 or more discal setae 17

16' Range, Mexico; eyes prominent, WF/WH 0.65 or less; each elytron normally with fewer than 25 discal setae 19

17. (16). Range, east of Mississippi River; median lobe, Fig. 175 . . . . *S. planulatus* LeConte, p224

17' Range, west of Mississippi River. 18

18. (17'). Range, north of Red River; median lobe, Fig. 176 . . . . *S. ozarkensis* new species, p. 227

18' Range, south of Red River; median lobe, Fig. 177 . . . . *S. planuloides* new species, p. 230

19. (16'). Elytra rufopiceous, apices reddish; front tibia not dilated proximally . . . . *S. tristriatus* Putzeys, p.208

19' Elytra castaneous, concolorous; front tibia distinctly expanded proximally. . . . . . . *S. dilatus* new species, p.211

20. (13'). Abdomen distinctly microsculptured along midline (*sallei* group). . . . . *S. sallei* Putzeys, p.203

20' Abdomen not distinctly microsculptured along midline, or if so then entire abdomen microsculptured. 21

21. (20'). Sternum three without small paralateral patch of distinct microsculpture on each side (*longipennis* group) 22

21' Sternum three with small paralateral patch of distinct microsculpture on each side 25

22. (21'). **Range**, Arizona and New Mexico; front femur piceous; frontal carina three in most specimens abbreviated behind; apex of median lobe (Fig. 197) deflected at nearly right angle . . . . *S. neovalidus* new species, p.251

22' If in Arizona and New Mexico, then front femur reddish; frontal carina three in most specimens not abbreviated behind; median lobe with apex less sharply deflected. 23

23. (22'). Elytra rufous to rufopiceous; endophallus (Fig. 204) with basal collar spines broad. Southern Arizona . . . . *S. chiricahuanus* new species, p.261

23' Elytra normally piceous 24

24. (23'). Endophallus (Fig. 203) with basal collar spines broad; virga small; most specimens smaller, stockier, and with tibiae paler. Western Mexico . . . . *S. pacificus* new species, p.264

24' Endophallus (Fig. 205) with basal collar spines narrow; virga large. Arizona and Tamaulipas south to Costa Rica . . . . *S. longipennis* Putzeys, p. 255

25. (21'). Pronotal hind angles sharply developed; elytra, except in specimens from Rio Grande drainage, piceous with aeneous tinge (in Rio Grande area, elytra castaneous with clearly paler apices). Rio Grande drainage and northward, east of Rocky Mountains (*lineolatus* group). .*S. lineolatus* Say, p. 237

25' Pronotal hind angles not sharply developed, or if so then elytra pale, unicolorous (*depressus* group). 26

26. (25'). Paramedian frontal sulci strongly closed behind by fused paramedian carinae; elytra testaceous to brunneous 27

26' Paramedian frontal sulci not or hardly closed behind, or elytra piceous 28

27. (26). Abdomen extensively microsculptured. Northern and central California. . . . . . . *S. ochthocephalus* new species, p. 323

27' Abdomen not extensively microsculptured. Not in northern and central California. . . . . *S. falli* new species, p. 312

28. (26'). Abdomen extensively microsculptured. Color piceous. West Indies. . . . . *S. arimao* Darlington, p. 272

28' Abdomen not extensively microsculptured. Not in West Indies 29

29. (28'). Elytra piceous, and range United States and Canada. 30

29' Elytra testaceous to brunneous, or range Mexico and southward 31

30. (29). Range, east of Mississippi River. . . . . *S. sulcifrons* Putzeys, p. 276

30' Range, Pacific coastal drainage systems . . . .
. . . . *S. litigiosus* Fall, p. 281

31. (29'). Pronotal hind angles normally prominent; color brunneous; larger, LE normally over 2.15 mm. . . . .
. . . . *S. depressus* LeConte, p. 327

31' Pronotal hind angles normally rounded; color various; size various, LE under or over 2.15 mm 32

32. (31'). Piceous; sternum three with paralateral patches of microsculpture reduced, indistinct; elytron with 12 to 14 discal setae. Guatemala to Costa Rica; median lobe, Fig. 223 . . .
. . . . *S. emdeni* new species, p. 274

32' Color various; sternum three with paralateral patches of microsculpture distinct; elytron with 14 or more discal setae
. . . . 33

33. (32'). Color testaceous to brunneous, not piceous; range, northeastern Mexico, and United States from Rio Grande River northward, east of Rocky Mountains; median lobe, Fig. 226, 227. .
. . . . *S. scopaeus* new species, p. 304

33' Color various; range, United States west of Rocky Mountains, and Mexico south to Colombia; in northeastern Mexico, color piceous; median lobe, Fig. 228, 229 . . . .
. . . . *S. pygmaeus* Van Dyke, p. 286

As I am unfamiliar with some named South American species of subgenus *Schizogenius* and cannot evaluate their characteristics from original descriptions, this key is provisional and incomplete. In particular, I have no useful concepts of forms named *S. canaliculatus* Putzeys, *S. gracilis*

Putzeys, *S. leprieuri* Castelnau, *S. sellatus* Putzeys, and *S. sulcatulus* Putzeys, and cannot place them to species group. From original descriptions, I associate the names *S. clivinoides* Putzeys and *S. interstriatus* Putzeys with species groups, but not with specimens. I tentatively associate the names *S. costiceps* Steinheil and *S. putzeysi* Kirsch with actual specimens. All other associations are more certain, since they are based either on type material or on specimens which are from at or near the type locality and which closely match good original descriptions. I did not key South American species belonging to the *darlingtoni*, *capitalis*, or *depressus* groups, since I am insufficiently familiar with them.

3.32 A partial key to South American species groups and species of the subgenus *Schizogenius*

1. Hind tarsi elongate, Ta/Ti 0.75 or more; paramedian frontal sulci not microsculptured; clypeal suture not strongly engraved; elytral disc asetose or with setae on interval three only 2

1' Hind tarsi shorter, Ta/Ti under 0.75; paramedian frontal sulci microsculptured in most species; clypeal suture weakly to strongly engraved 6

2. (1). Paramedian pronotal sulci well developed; interval three of elytron bi- or trisetose (*jacarensis* group). . . . .
. . . . *S. jacarensis* new species, p. 87

2' Combination of characters not as above (*optimus* group) . . . 3

3. (2'). Paramedian pronotal sulci obsolete or nearly so. 4

3' Paramedian pronotal sulci well developed; elytral disc asetose 5

4. (3). Elytra piceous, metallic; clypeal carinae straight, apices abbreviated; elytra ovate. . *S. dyschirioides* Putzeys, p. 94

4' Elytra brunneous, unmetallic; clypeal carinae arcuate, apices joined and extended by stem to median tooth; elytra elongate, not ovate . . . . *S. clivinoides* Putzeys, p. 97

5. (3'). Elytron with large sutural macula. . . . . *S. grossus* Whitehead, p. 97

5' Elytron not maculate. . . . . . *S. bicolor* new species, p. 98

6. (1'). Elytral disc with setae on intervals three, five, and seven; antennal articles five to ten nearly moniliform; paramedian clypeal carinae tuberculate, apices not extended to median tooth; clypeal field broad, at base more than 1.5 apical width of median frontal sulcus (*basalis* group). 7

6' Combination of characters not as above 10

7. (6). Pygidium not strongly crenulate in either sex; color ferrugineous, not or slightly aeneous . . . . *S. negrei* new species, p.117

7' Pygidium strongly crenulate in females; at least pronotum aeneopiceous to metallic. 8

8. (7'). Elytral striae not distinctly punctate in basal half; occiput densely punctate. . . . . *S. multipunctatus* Kult, p.116

8' Elytral striae distinctly punctate in basal half; occiput not densely punctate 9

9. (8'). Elytral disc with more than 40 setae; elytral length over 2.25 mm; pronotum piceous, metallic at sides and base only . . . . *S. basalis* Putzeys, p. 113

9' Elytral disc with fewer than 40 setae; elytral length under 2.25 mm; pronotum entirely metallic green . . . . *S. cearaensis* new species, p. 114

10 (6'). Paramedian pronotal sulci evident only at base; elytral intervals three, five, and seven asetose (*elongatus* group) 11

10' Paramedian pronotal sulci more elongated, developed well in front of base 12

11. (10). Metallic green; total length over 5 mm . . . . *S.* ***costiceps*** Steinheil, p. 120

11' Less strongly metallic; total length about 4 mm. . . . . *S. elongatus* Kult, p. 122

12. (10'). Elytral disc asetose, intervals carinate (*carinatus* group) 13

12' Elytral disc with setae at least on interval three. 14

13. (12). Body color piceous. . . . . . *S. carinatus* Whitehead, p. 124

13' Body color rufo-testaceous. . . . . *S. costipennis* new species, p. 125

14. (12'). Elytral disc with setae on interval three only. 15

14' Elytral disc with setae on interval five. 16

15. (14). Eye normal, multifaceted (*quadripunctatus* group). *S. quadripunctatus* Putzeys, p. 151

15' Eye ocellate, reduced to one bubble-like facet (*ocellatus* group). . . . . *S. ocellatus* new species, p. 137

16\. (14'). Elytral disc with setae on intervals three and five only. . .
. . . . 17

16' Elytral disc with setae on intervals three, five, and seven .
. . . . 21

17\. (16). Elytral interval five with setae in basal half only (*arechavaletae* group). 18

17' Elytral interval five with setae evenly distributed 19

18\. (17). Humeral angles of elytra prominent. . . . .
. . . . *S. reichardti* new species, p. 133

18' Humeral angles of elytra rounded. . . . .
. . . . *S. arechavaletae* Putzeys, p. 130

19\. (17'). Inner paramedian frontal carinae grossly enlarged; median frontal sulcus microsculptured, with or without median carina
. . . .(*darlingtoni* group), p. 139

19' Inner paramedian frontal carinae normal; median frontal sulcus not microsculptured, without median carina. 20

20\. (19'). Antennal articles five to ten short, nearly moniliform (*lindrothi* group) . . . . *S. banningeri* Kult, p.149

20' Antennal articles five to ten elongate, filiform . . . . . .
. . . . (*capitalis* group), p.141

21\. (16'). Submentum with numerous accessory setae; pronotum with lateral grooves bordered internally by distinct carinae (*strigicollis* group). . . . . . *S. strigicollis* Putzeys, p.128

21' Submentum with two standard pairs of setae only; pronotum without lateral carinae . . . . (*depressus* group), p.270

3.33 The *jacarensis* group

Diagnostic combination. - Members of this group may be distinguished by the following combination of characters: hind tarsi elongate, Ta/Ti over 0.75; clypeal suture weakly engraved; paramedian frontal sulci not microsculptured; elytral disc with two or three setae on interval three; paramedian pronotal sulci well developed; basal sensory bristles of terminal article of maxillary palpus arranged transversely; and apex of median lobe of male genitalia neither elongate nor strongly deflexed. Also: size large (LE over 2.75 mm); integument not extensively microsculptured; labrum strongly biemarginate, fringed laterally with six or seven pairs of setae; clypeal carinae straight and abbreviated; clypeal field at base more than 1.5 apical width of median frontal sulcus; clypeus with median tooth reduced; frontal carinae not arcuate; antennal articles five to ten moniliform, pedicel unisetose, articles three and four pubescent; mentum deeply emarginate, median tooth blunt; front and middle tarsi slender in both sexes; paronychia nearly obsolete; posterior ventral margin of front tibia with three setae near base; paramedian carinae of sternum three straight; paramedian ambulatory setae present on sternum seven of males only; pygidium not crenulate in either sex; and endophallus without enlarged basal collar spines.

Distribution. - This monobasic group is known only from three specimens from central Brazil.

3.331 *Schizogenius jacarensis* new species

Type material. - Holotype male and allotype female labelled "Jacare P. N. Xingu M. Grosso - Bras. XI.1961 leg. M. Alvarenga" (MGFT). A specimen from Goias state is a paratype (DRWh).

Diagnostic combination. - *S. jacarensis* is the only known member of the *jacarensis* group.

Description. - Body stout, subcylindrical, head proportionately large. Color rufocastaneous, elytra strongly aeneous or weakly metallic, not maculate; legs and mouthparts rufous; tarsi and antennae testaceous.

Integument. Fine microsculpture on genae, mouthparts, pronotal base, front tibiae and anterior surfaces of front femora, middle legs except trochanters, hind tibiae and posterior surfaces of hind femora, sterna two and three, sides of sterna four to six, and margin of sternum seven. Sternum three without patches of particularly coarse microsculpture in coxal depressions.

Head. Fig. 77. Labrum strongly biemarginate, fringed laterally with six or seven pairs of setae. Paramedian clypeal carinae straight, attenuate; median clypeal field triangular, width at base much more than 1.5 apical width of median field of frons; median clypeal tooth much shorter than paramedian teeth. Clypeal suture obsolete or nearly so. Frontal carinae weakly arcuate, median frontal sulcus narrowed from base to apex. Antennal articles five to ten moniliform, pedicel unisetose, articles three and four pubescent. Eye subglobose, uniformly faceted. Terminal article of maxillary palpus with basal sensory bristles arranged transversely. Mentum deeply emarginate, median tooth blunt.

Pronotum. Fig. 77. Sides bisetose, hind angles reduced; base not rugose; paramedian sulci sharply engraved; anterior transverse impression impunctate. Pronotum widest well in front of middle.

Legs. Front and middle tarsi slender in both sexes, without dense ventral pubescence; hind tarsus slender, elongate. Front tibia narrowed evenly to base; postero-ventral margin with three setae near base. Front femur not strongly constricted near apex. Paronychia much less than half length of tarsal claws.

Elytra. Disc with two or three setigerous punctures on interval three. Striae deep and sharply engraved, finely punctate in basal two-thirds. Intervals one to eight broad, convex, apices not carinate; intervals three, five, and seven joined at apices.

Abdomen. Paramedian carinae of sternum three straight. Sternum seven with paramedian ambulatory setae in males only. Pygidium with apical margin entire in both sexes.

Male genitalia. Median lobe, Fig. 81, apex neither elongate nor sharply deflexed; endophallus without distinctive spines. One specimen examined.

Measurements and proportions. Of holotype: TL, 5.36 mm; LE, 3.25 mm; WH, 1.42 mm; WP, 1.60 mm; WE, 1.68 mm; WF/WH, 0.75; LP/WP, 0.80; DP/LP, 1.02; LP/WE, 0.76; Ta/Ti, 0.81; PS/LP, 0.60. Of allotype: TL, 4.94 mm; LE, 3.07 mm; WH, 1.24 mm; WP, 1.43 mm; WE, 1.56 mm; WF/WH, 0.73; LP/WP, 0.82; DP/LP, 1.06; LP/WE, 0.75; Ta/Ti, 0.83; PS/LP, 0.58.

Variation. - Two specimens have three setae on interval three of the left elytron.

Etymology. - *S. jacarensis* is named after the type locality, Jacare

National Park.

Distribution. - I studied three specimens of this species, from the following localities.

BRAZIL

GOIAS: Santa Isabel do Morro (1; DRWh). MATO GROSSO: Jacare P. N. Xingu (2; MGFT).

Collecting notes. - Specimens of this species were collected in June and November.

Taxonomic notes. - This species probably represents an early side branch of the *optimus* group, since the weakly engraved clypeal suture, elongate hind tarsi, and unmicrosculptured paramedian frontal sulci are all characteristics shared with members of that group. Males do not have the elongated apex characteristic in genitalia of members of the *optimus* group, and the head is proportionately much larger, the eyes smaller, and the pronotum more transverse. As in all other members of *Schizogenius* except those of the *optimus* group, basal sensory bristles of terminal article of maxillary palpus in *S. jacarensis* are transversely arranged.

3.34 The *optimus* group

Diagnostic combination. - Members of this group are distinguished by the following combination of characters: hind tarsi elongate, Ta/Ti over 0.75; clypeal suture weakly engraved; paramedian frontal sulci not microsculptured; elytral disc asetose or with setae on interval three only; if interval three setose; then paramedian pronotal sulci obsolete or nearly so; basal sensory bristles of terminal article of maxillary palpus arranged longitudinally; and apex of median lobe of male genitalia elongate and strongly deflexed. Also: size medium to large (LE 2.75-5.00 mm); integument extensively microsculptured or not, testaceous to dark piceous, metallic or not, elytra maculate in one species; labrum weakly to strongly emarginate or biemarginate, fringed laterally with six or seven to about 15 pairs of setae; clypeal carinae straight and abbreviated, or fused in an arc and joined to median tooth by common stem; clypeal field at base more than 1.5 apical width of median frontal sulcus; clypeus with median tooth reduced or not; antennal articles five to ten moniliform, pedicel uni- or bisetose, articles three and four plurisetose to pubescent; mentum shallowly to deeply emarginate, median tooth blunt to sharp; gula 0.05-0.20 width of mentum; anterior and middle tarsi slender in both sexes; paronychia obsolete to about half length of tarsal claws; posterior ventral margin of front tibia with three to four setae near base; paramedian carinae of sternum three straight; paramedian ambulatory setae present on sternum seven of males only, or absent; pygidium not crenulate in either sex; and endophallus without enlarged basal collar spines.

Distribution. - One Middle American species extends from Chiapas south to Costa Rica. Four other species occur in Panama and much of continental South America. I studied 116 specimens of the *optimus* group.

3.341 *Schizogenius optimus* Bates

Schizogenius optimus Bates 1881:37. *Type locality* Rio Naranjo, Guatemala;

type in BMNH, specimen labelled lectotype by G. E. Ball here so designated (!).

Diagnostic combination. - This is the only Middle American species of *Schizogenius* having obsolete paramedian pronotal sulci. Specimens of *S. optimus* are distinguished from others in the *optimus* group by the following character combination: elytra piceous, metallic, not extensively microsculptured, not maculate; antennal pedicel unisetose; clypeal carinae arcuate, fused apically and joined by common stem to median tooth; elytral interval three asetose; and labrum not deeply emarginate, margined laterally with no more than seven pairs of setae.

Description. - Body stout, subcylindrical. Color piceous, elytra and pronotum strongly metallic, legs, mouthparts, and antennae testaceous.

Integument. Fine microsculpture on gena, mouthparts, pronotal base, front tibiae and anterior surfaces of front femora, middle legs except trochanters, hind tibiae and posterior surfaces of hind femora, sternum two, coxal depressions of sternum three, sides of sterna four to six, and margin of sternum seven. Sternum three without patches of particularly coarse microsculpture in coxal depressions.

Head. Fig. 78. Labrum strongly emarginate, fringed laterally with six or seven pairs of setae. Paramedian clypeal carinae arcuate, fused apically and extended by common stem to median tooth; median clypeal field hemicircular, width at base over 1.5 apical width of median field of frons; median clypeal tooth shorter than paramedian teeth. Clypeal suture obsolete to weakly engraved. Frontal carinae not arcuate, median frontal sulcus narrowed from base to apex. Antennal articles five to ten moniliform, pedicel unisetose, articles three and four pubescent.

Eyes subglobose, uniformly faceted. Terminal article of maxillary palpus with basal sensory bristles longitudinally arranged. Mentum deeply emarginate, median tooth sharp.

Pronotum. Fig. 78. Sides bisetose, hind angles reduced; base not rugose; paramedian sulci absent or barely evident at base; anterior transverse impression finely punctate.

Legs. Front and middle tarsi slender in both sexes, without dense ventral pubescence; hind tarsus slender, elongate. Front tibia narrowed evenly to base where much narrower than at base of antennal cleaner; posterior ventral margin of front tibia with three setae near base. Front femur not strongly constricted near apex. Paronychia short, about half length of tarsal claws.

Elytra. Disc without setigerous punctures, one seta at base of interval three. Striae deep and sharply engraved, finely punctate in basal two-thirds. Intervals one to eight broad, convex; intervals five, seven, and eight carinate apically; interval seven joined by apex of interval five, otherwise free.

Abdomen. Paramedian carinae of sternum three straight. Sternum seven without paramedian ambulatory setae in either sex. Pygidium with apical margin entire in both sexes.

Male genitalia. Median lobe (Fig. 82) with form of apex characteristic; endophallus (Fig. 85) with enlarged scales on dorsal side of virga. Four specimens examined.

Measurements and proportions. See Table 4.

Variation. - I found two males with one paramedian ambulatory seta on sternum seven.

Table 4. Descriptive statistics for *S. optimus*, based on 31 unsexed specimens from Pijijiapan, Chiapas.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	4.98-6.17	5.634	0.390	0.093	4.61
LE	3.00-3.70	3.387	0.238	0.057	4.69
WH	1.12-1.42	1.258	0.095	0.023	5.03
WP	1.43-1.88	1.668	0.128	0.031	5.11
WE	1.58-2.06	1.803	0.146	0.035	5.41
B. Proportions					
WF/WH	0.66-0.69	0.675	0.012	0.003	1.20
LP/WP	0.86-0.92	0.892	0.022	0.005	1.66
DP/LP	0.85-0.91	0.876	0.021	0.005	1.62
LP/WE	0.78-0.87	0.826	0.030	0.007	2.41
Ta/Ti	0.80-0.92	0.849	0.053	0.013	4.16

Etymology. - Latin, *optimus* = best, a reference to the large size of individuals of this species.

Distribution. - The known range of *S. optimus* extends from southern Chiapas to Costa Rica (Fig. 86). I studied 45 specimens from the following localities.

MEXICO

CHIAPAS: Pijijiapan (31; CAS, CNC, DRWh, IRSB, UASM).

GUATEMALA

GUATEMALA: Agua Caliente (2; MCZ). SAN MARCOS: Rio Naranjo (2; BMNH).

HONDURAS

COMAYAGUA: Rancho Chiquito (2; FDAG). EL PARAISO: El Paraiso (1; UCD).

COSTA RICA

No locality (1; USNM). LIMON: Rio Reventazon (2; BMNH, USNM).

PUNTARENAS: 3-7 mi. ne. Puerto Viejo (4; UAFA).

Collecting notes. - I found specimens of this species at Pijijiapan, Chiapas, in gravel along a river. They were concentrated near the edge of the water in a strip only a few feet in length, for no reason apparent to me; specimens of several other *Schizogenius* species were found along the same stream but were not so concentrated. Adult individuals of *S. optimus* are probably active throughout the year, and I have seen specimens collected in March, May, June, August, and October.

3.342 *Schizogenius dyschirioides* Putzeys

Schizogenius dyschirioides Putzeys 1863:28. *Type locality* "Amazone," Brazil; type specimens not seen, probably in the Chevrolat

Collection of the Hope Museum at Oxford, or in the Bates Collection in MNHP. Putzeys 1866:222.

Diagnostic combination. - Specimens of the *optimus* group with combination of metallic elytra, bisetose second antennal articles, bisetose elytral interval three, and obsolete paramedian pronotal sulci probably all represent this species.

Description. - Body form, color, and integument generally as described for *S. optimus*, except sides of sterna four to six more strongly and extensively microsculptured.

Head. Fig. 79. As described for *S. optimus* except clypeal carinae straight, neither fused apically nor extended to median tooth; and antennal pedicel bisetose.

Pronotum. Fig. 79; generally as described for *S. optimus*.

Legs. As in *S. optimus* except paronychia shorter, much less than half length of tarsal claws.

Elytra. As described for *S. optimus* except interval three bisetose, and intervals three, five, and seven joined at apices.

Abdomen. As in *S. optimus* except males with paramedian ambulatory setae on sternum seven.

Male genitalia. Median lobe, Fig. 83; endophallus not studied in detail, without conspicuously enlarged spines. Two specimens studied.

Measurements and proportions. Based on five specimens from Brazil, Colombia, and Panama. TL, 4.66-5.10-5.33 mm; LE, 2.85-3.10-3.23 mm; WH, 0.98-1.09-1.15 mm; WP, 1.32-1.48-1.56 mm; WE, 1.54-1.66-1.72 mm; WF/WH, 0.63-0.65-0.67; LP/WP, 0.87-0.90-0.92; DP/LP, 0.85-0.86-0.86; LP/WE, 0.79-0.80-0.82; Ta/Ti, 0.82-0.88-0.91.

Variation. - The Para specimen, a female, is much smaller than specimens from Colombia and Panama, and has an extra seta on interval three of left elytron.

Etymology. - Latin, *dyschirioides* = *Dyschirius*-like, a reference to the quite oval elytra.

Distribution. - I refer to this species 16 specimens from the following South American localities.

BRAZIL

PARA: Belem (1; USNM).

COLOMBIA

MAGDALENA: Rio Frio (13; MCZ), Sevilla (1; MCZ).

PANAMA

CANAL ZONE: San Pablo (1; USNM).

Collecting notes. - Specimens of *S. dyschirioides* were collected in March and May.

Taxonomic notes. - Though I have not seen type specimens of *S. dyschirioides*, there is little doubt that this association is correct. The specimens well match the original description, and the Para specimen may even by topotypic.

I suspect that presence of paramedian ambulatory setae on sternum seven in males is secondary; these setae are present in some specimens of *S. optimus*. The extra seta on the antennal pedicel clearly is a novelty. Other than these features, form of clypeal carinae, and presence of setae on elytral interval three, *S. dyschirioides* is not greatly different from *S. optimus*.

3.343 *Schizogenius clivinoides* Putzeys

Schizogenius clivinoides Putzeys 1866:229. *Type locality* "Pampas," Argentina; type not seen, possibly in the Chaudoir collection in MNHP.

Diagnostic combination. - From the description, specimens of this species should have the following combination of characteristics: paramedian pronotal sulci obsolete; color yellowish or brownish, unmetallic; elytral interval three bisetose; elytral striae punctate to apex; and paramedian frontal carinae arcuate, apices fused and extended to median tooth.

Taxonomic notes. - I have seen no specimens that conceivably could belong to this species. Specimens of it should be readily identified from my diagnosis, if the original description is accurate.

3.344 *Schizogenius grossus* Whitehead

Schizogenius grossus Whitehad 1966:3. *Type locality* Rio Madeira, Brazil; holotype male in USNM (!).

Diagnostic combination. - Specimens of this species are the only members of the *optimus* group with maculate elytra. They are the only members of the genus known to have four rather than three posteroventral setae near the base of the front tibia, and the only ones to have more than ten pairs of marginal setae on the labrum. Other characteristics are: color castaneous, unmetallic; integument extensively microsculptured; labrum weakly biemarginate; paramedian clypeal carinae straight, attenuate; antennal articles three and four plurisetose; paramedian pronotal sulci present; paronychia much less than half length of tarsal claws; elytral disc asetose, elytral striae shallow; and sternum seven with paramedian ambulatory setae in neither sex.

Description. - The original description and illustrations (Whitehead, 1966a) are adequate.

Etymology. - Latin, *grossus* = gross, a reference to the large size of these insects.

Distribution. - In addition to the type series from Bolivia and Brazil, I studied the following two specimens.

ARGENTINA

SALTA: Aguas Blancas (1; MZSP), San Martin (1; MZSP).

3.345 *Schizogenius bicolor* new species

Type material. - Holotype male and allotype female labelled "Jacare P. N. Xingu M. Grosso - Bras. XI.1961 leg. M. Alvarenga" (MGFT). An additional 40 specimens from two localities in the Brazilian state of Mato Grosso are paratypes (CAS, DRWh, IRSB, MCZ, MGFT, MZSP, UASM).

Diagnostic combination. - Specimens of this species have in combination: characters of *optimus* group; no setae on elytral disc; plurisetose antennal articles three and four; elytra paler than pronotum, not metallic, not maculate; and pronotum with strong paramedian sulci.

Description. - Body stout, subcylindrical. Color castaneous, elytra and appendages rufotestaceous, unmetallic, elytra not maculate.

Integument. As described for *S. optimus*, except elytra faintly microsculptured.

Head. Fig. 80. As in *S. optimus* except: paramedian carinae straight, attenuate; details of paramedian frontal sulci and carinae differ; antennal articles three and four plurisetose.

Pronotum. Fig. 80. Side margins indented at anterior marginal setae as in *S. grossus*. Paramedian longitudinal sulci well developed. Sides bisetose, hind angles reduced; base not rugose; anterior transverse impression with longitudinal rugae.

Legs. As in *S. optimus* except paronychia much less than half length of tarsal claws.

Elytra. As in *S. optimus* except more parallel sided; intervals three, five, and seven not carinate, joined at apices; and striae finely punctate in basal half.

Abdomen. As described for *S. optimus*.

Male genitalia. Median lobe, Fig. 84; endophallus not studied in detail. Two specimens studied.

Measurements and proportions. Of holotype: TL, 5.19 mm; LE, 3.19 mm; WH, 1.10 mm; WP, 1.50 mm; WE, 1.64 mm; WF/WH, 0.66; LP/WP, 0.93; DP/LP, 0.83; LP/WE, 0.85; Ta/Ti, 0.88; PS/LP, 0.60. Of allotype: TL, 5.48 mm; LE, 3.40 mm; WH, 1.17 mm; WP, 1.61 mm; WE, 1.72 mm; WF/WH, 0.66; LP/WP, 0.91; DP/LP, 0.87; LP/WE, 0.85; Ta/Ti, 0.91; PS/LP, 0.65.

Variation. - Six specimens from Piaui state are darker and less distinctly bicolored than specimens in the type series.

Etymology. - Latin, *bi* = two, plus *color* = color, in reference to the distinctive coloration of individuals of this species.

Fig. 77-80. Head and pronotum, dorsal aspect. 77. *S. jacarensis* new species, Jacare, Brazil. 78. *S. optimus* Bates, Pijijiapan, Chiapas. 79. *S. dyschirioides* Putzeys, Sevilla, Colombia. 80. *S. bicolor* new species, Jacare, Brazil. Fig. 81-84. Male median lobe, lateral aspect. 81. *S. jacarensis* new species, Jacare, Brazil. 82. *S. optimus* Bates, Pijijiapan, Chiapas. 83. *S. dyschirioides* Putzeys, Rio Frio, Colombia. 84. *S. bicolor* new species, Jacare, Brazil. Fig. 85. Male endophallus, *S. optimus* Bates, Pijijiapan, Chiapas. Fig. 86. Known distribution of *S. optimus* Bates.

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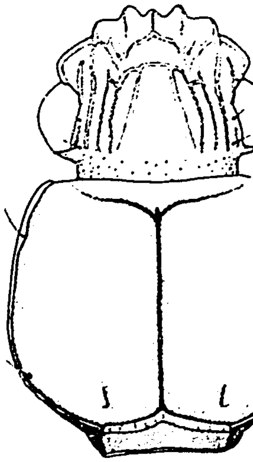

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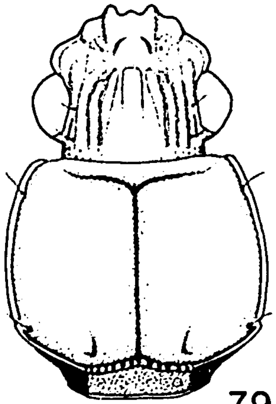

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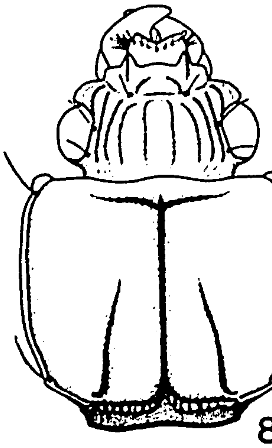

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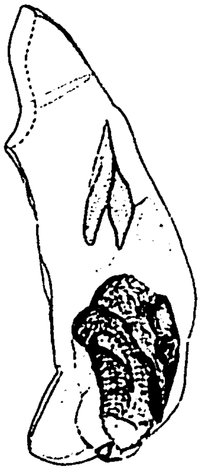

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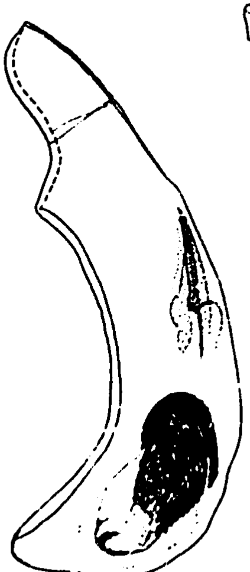

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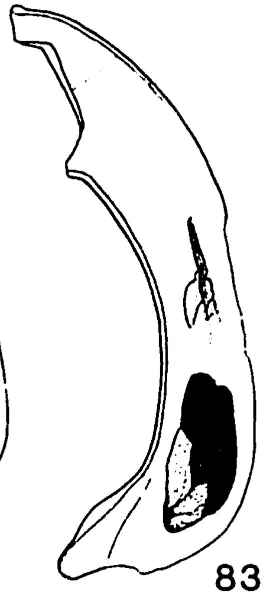

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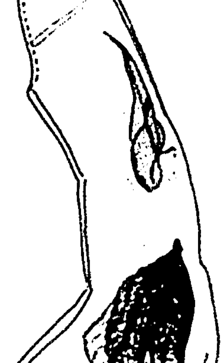

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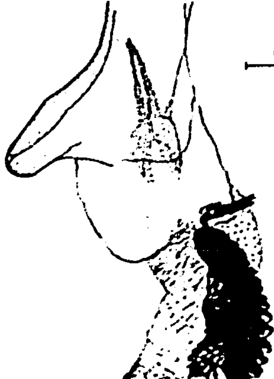

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Distribution. - Specimens of this species have been taken in the Brazilian states of Mato Grosso and Piaui. I studied 48 specimens from the following localities.

BRAZIL

MATO GROSSO: Barra de Tapirape (2; MZSP), Jacare P. N. Xingu (40; CAS, DRWh, IRSB, MCZ, MGFT, UASM). PIAUI: Terezina (6; MGFT).

Collecting notes. - Specimens of this species were collected in November and January.

Taxonomic notes. - This species is most closely related to *S. grossus* Whitehead, but is less specialized. Specimens are less extensively microsculptured, have more sharply engraved elytral striae, have a deeply emarginate mentum, have just three postero-ventral setae on the front tibia, and have only six or seven pairs of marginal setae on the labrum. But they are similar in habitus, distribution of discal setae, and non-pubescent third and fourth antennal articles.

3.35 The *ferrugineus* group

Diagnostic combination. - Within the subgenus, members of this group are characterized by the following combination of characters: paramedian clypeal carinae tuberculate, apices nearly or quite obsolete; clypeal field triangular, its base 1.0 to more than 1.5 times apical width of median frontal sulcus; clypeal suture sharply impressed; antennal articles five to ten moniliform; anterior tarsi slender in both sexes; elytral disc with setae on intervals three, five, and seven; paramedian carinae of sternum three straight; paramedian ambulatory setae present in males only; pygidium not crenulate in either sex; and endophallus without enlarged basal collar spines.

This group contains the only North and Middle American *Schizogenius* species whose members each have tuberculate clypeal carinae in combination with discal setae present on intervals three, five, and seven.

Distribution. - One species ranges throughout much of eastern North America, southwestward to Arizona. A second species overlaps the first in Arizona, and ranges southward in Pacific drainage systems to at least Costa Rica. I examined 623 specimens of the *ferrugineus* group.

Taxonomic notes. - The two species included in this group are similar in habitus but are not closely related. They may even not form a monophyletic group, as I have found no assuredly synapomorphic characteristics except perhaps loss of paramedian anal setae from sternum three of females, but I have no reason to treat them otherwise.

3.351 *Schizogenius ferrugineus* Putzeys

Schizogenius ferrugineus Putzeys 1846:653. *Type locality* Galveston, Texas; location of type unknown. LeConte 1857:82. Putzeys 1863:24. Putzeys 1866:223. LeConte 1879:34. Lindroth 1961:168.

Clivina sulcata LeConte 1848:214. *Type area* New York State; type in LeConte Collection, MCZ.

Schizogenius sulcatus, LeConte 1857:83, suggested synonymy.

Diagnostic combination. - Specimens of this species are readily distinguished from those of *S. auripennis*, the only other known species of the group, by ferrugineous coloration and extensively microsculptured abdomen.

Head. Fig. 87. Clypeal carinae tuberculate, not or weakly extended to median clypeal tooth; median clypeal field triangular, broad, width at base about 1.5 apical width of median field of frons. Clypeal suture sharply engraved. Eye prominent, subglobose, uniformly faceted. Neck densely but finely punctate. Gena rugose in front. Antennal articles four to ten moniliform.

Pronotum. Fig. 87. Sides bisetose, hind angles reduced, base not rugose. Paramedian sulci long, impunctate, shallow and indistinct apically, deep and strongly hooked basally. Anterior transverse impression impunctate or finely punctate.

Legs. Front and middle tarsi slender, without dense ventral pubescence; hind tarsus slender, short. Paronychia inconspicuous, about half length of tarsal claws. Front tibia evenly narrowed to base where much narrower than at base of antennal cleaner. Front femur not strongly constricted near apex.

Elytra. Five to seven setigerous punctures each on intervals three and five, and three to five on interval seven. Striae deep and sharply engraved, finely punctate in basal two thirds. Intervals one to seven broad and convex, interval eight carinate at apex; intervals three and five broadly joined apically with interval seven.

Abdomen. Sternum three with paramedian carinae straight at apices. Sternum seven with paramedian ambulatory setae in male only. Pygidium with apical margin entire in both sexes.

Male genitalia. Median lobe, Fig. 93; endophallus, Fig. 98, without enlarged basal collar spines. Six specimens examined.

Measurements and proportions. See Table 5.

Variation. - Among specimens studied, the largest female (LE,

Table 5. Descriptive statistics for *S. ferrugineus*, based on 20 males from Round Mountain, Texas.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.13-3.76	3.434	0.297	0.089	5.77
LE	1.89-2.27	2.072	0.180	0.054	5.80
WH	0.66-0.82	0.738	0.067	0.020	6.07
WP	0.83-1.05	0.944	0.099	0.030	7.03
WE	0.91-1.14	1.006	0.102	0.031	6.79
B. Setae on left elytron.					
Interval 3	5- 7	6.2			
Interval 5	5- 7	6.3			
Interval 7	3- 4	3.5			
Total	14-18	16.0	1.6	0.5	6.72
C. Proportions.					
WF/WH	0.66-0.72	0.688	0.023	0.007	2.27
LP/WP	0.95-1.01	0.982	0.033	0.010	2.22
DP/LP	0.80-0.86	0.824	0.023	0.007	1.86
LP/WE	0.88-0.96	0.918	0.036	0.011	2.61
Ta/Ti	0.64-0.75	0.708	0.052	0.015	4.86
PS/LP	0.63-0.76	0.701	0.050	0.015	4.75

2.48 mm) and male (LE, 2.41 mm) are from Long Beach, New York, the smallest female (LE, 1.66 mm) is from Columbus, Texas, and the smallest male (LE, 1.69 mm) is from Clark Co., Kansas. There is an apparent slight tendency for larger size toward the northeast than toward the southwest, but population samples generally are too small for worthwhile comparisons.

Etymology. - Latin, *ferrugineus* = rust colored, in reference to the body color; Latin, *sulcatus* = sulcate, in reference to the sulci on the frons and pronotum.

Distribution. - *S. ferrugineus* ranges at low elevations in sandy places from southern Ontario south to northern Florida and west to southeastern Arizona (Fig. 100). I examined 505 specimens from the following localities.

CANADA

No locality (1; UKSM). ONTARIO (1; CAS): Tilbury (1; KHSt); Toronto (5; CAS, CUNY, KSUM, MCZ).

UNITED STATES

No locality (3; ANSP, IRSB). ALABAMA: Washington Co., Leroy (2; CUNY). ARIZONA: Cochise Co., Douglas (1; UCB); Graham Co., Aravaipa (1; CAS); Pima Co., Robles Ranch (1; UCD). ARKANSAS: Carroll Co., Eureka Springs (1; UKSM); Hempstead Co., Hope (3; CUNY, USNM); Washington Co., Mount Sequoyah (1; INHS). COLORADO: Logan Co. (1; USNM). DELAWARE (1; MCZ). FLORIDA: Nassau Co., Fernandina Beach (2; USNM). GEORGIA (2; ANSP). ILLINOIS: Mason Co., Havana (1; USNM); Pike Co., Pittsfield (2; UCD). INDIANA (1; CNHM): Lake Co., Pine (6; CNHM, MGFT); Sterben Co., Fremont (1; CNMH); Tippecanoe Co. (1; UCD). IOWA: Johnson Co., Iowa City (4; USNM); Des Moines Co., Burlington (2; MCZ). KANSAS (14; CNHM, CUNY, KSUM, MCZ, USNM): Clark Co. (1; UKSM); Douglas Co. (1; UKSM), Lawrence (4;

INHS); Kiowa Co. (1; UKSM); Leavenworth Co. (3; USNM); Pottawatomie Co., Onaga (1; UASM); Reno Co. (8; CAS, MCZ, USNM), Medora (2; KSUM); Riley Co. (7; KSUM, USNM), Manhattan (1; KSUM); Sedgwick Co. (6; USNM), Mount Hope (9; CAS, USNM). KENTUCKY (1; AMNH). LOUISIANA: Winn Co., Winnfield (1; MCZ). MAINE: Oxford Co., Paris (1; MCZ). MARYLAND: Difficult (4; CUNY, MCZ); Calvert Co., Chesapeake Beach (19; USNM), Kenwood Beach (14; DRWh, JNeg, UCD, USNM); Montgomery Co., Plummers Island (2; USNM). MASSACHUSETTS: Essex Co., Ipswich (4; MCZ); Hampden Co., Chicopee (3; MCZ), Springfield (1; MCZ); Middlesex Co., Tewksbury (1; MCZ), Tyngsboro (13; MCZ). MICHIGAN: Huron Co. (1; MSUL); Monroe Co., Monroe (10; MCZ, MSUL, USNM). MINNESOTA: Houston Co., Mississippi Bluff (1; MSUL). MISSISSIPPI: George Co., Lucedale (2; CUNY). MISSOURI (1; ANSP). NEBRASKA: Cuming Co., West Point (2; USNM); Thomas Co., 2.5 mi. w. Halsey (1; CAS). NEW HAMPSHIRE: Grafton Co., Rumney (10; CNC, DRWh, MCZ). NEW JERSEY (2; ANSP, MCZ): Atlantic Co., Atlantic City (1; MCZ), Brigantine (3; CAS, RUNB); Burlington Co., Atsion (8; CAS); Camden Co., Cramer Hill (1; USNM), Westville (10; ANSP, MCZ, RUNB, USNM); Cape May Co., Anglesea (18; ANSP, LACM, MCZ, RUNB), Five Mile Beach (4; USNM), Ocean City (1; CAS); Gloucester Co., Woodbury (1; ANSP); Warren Co., Phillipsburg (1; CAS). NEW MEXICO: Curry Co., Clovis (2; UKL). NEW YORK (8; CAS, USNM): New York City and vicinity (13; AMNH, CAS, RUNB); Long Island (4; CAS, USNM); Brooklyn Co., Coney Island (7; CAS, MCZ); Nassau Co., Long Beach (17; AMNH, CAS, USNM); Queens Co., Rockaway Beach (10; CAS, CUNY, USNM); Suffolk Co., Plum Island (1; MCZ), Riverhead (2; CUNY), Sound Beach (1; AMNH); Tompkins Co., Groton (2; CAS). NORTH CAROLINA (1; MSUL). OHIO: Athens Co., Athens (2; UWLW), Hamilton Co., Cincinatti (1; MCZ). OKLAHOMA: Caddo Co., Hinton (6; MSUL); Love Co., Oswalt (2; MSUL); McCurtain

Co., Sherwood (1; MSUL); Woodward Co., Woodward (3; USNM). PENNSYLVANIA (1; USNM). SOUTH CAROLINA (2; CAS, MCZ): Charleston Co., Charleston (1; CAS), Folly Beach (1; USNM), Isle of Palms (5; ANSP, RUNB, USNM). TEXAS (65; AMNH, ANSP, CAS, CNHM, INHS, IRSB, KSUM, MCZ, MSUL, UKSM, USNM): Bexar Co., San Antonio (2; CAS); Blanco Co., Cypress Mills (6; CAS, USNM), Rome Mountain (16; CAS), Round Mountain (25; CAS, MCZ, RUNB); Brown Co., Brownwood (1; AMNH); Burnet Co. (2; USNM); Comal Co. (1; CAS); Colorado Co., Columbus (21; USNM); Harris Co., Hockley (2; AMNH, CAS); Lee Co. (2; MCZ), Fedor (6; CAS), Lexington (1; MCZ); Llano Co., Enchanted Rock (1; CNC); Travis Co., Austin (1; USNM); Wharton Co., Wharton (2; CUNY). VIRGINIA: Elizabeth City, Fort Monroe (1; USNM); Fairfax Co., Arlington (1; USNM); Nelson Co. (1; USNM); Princess Anne Co., Cape Henry (5; AMNH), Virginia Beach (2; USNM). WISCONSIN: Grant Co., Boscobel (1; FDAG).

Collecting notes. - *S. ferrugineus* differs from most other species of the subgenus *Schizogenius* in that individuals live in sand rather than in gravel bars. Specimens from Iowa City, Iowa, are labelled "Butler's Landing sand area." Specimens from Kenwood Beach, Maryland, were found "under wash-up." P. J. Darlington collected specimens "under log on beach" at Ipswich, Massachusetts, and others in "galleries in dry sand under logs, Baker River" at Rumney, New Hampshire. Additional specimens were collected in "drift" along the Merrimack River at Tyngsboro, Massachusetts.

Specimens of this species have been collected from 13 March at Charleston, South Carolina, to 16 October at Lawrence, Kansas. Many flew in to lights at various localities. I can add no additional observations, having collected no specimens of this species.

3.352 *Schizogenius auripennis* Bates

Schizogenius auripennis Bates 1881:38. *Type locality* Teleman, Guatemala; type in BMNH, specimen labelled "holotype" here designated as lectotype (!).

Schizogenius peninsularis Van Dyke 1949:50. *Type locality* 5 mi. s. Miraflores, Baja California; type in CAS, not studied. NEW SYNONYMY.

Diagnostic combination. - The shiny, unmicrosculptured abdomen separates specimens of *S. auripennis* from those of *S. ferrugineus*, the only other known member of the group. The apex of the male median lobe is strikingly different in form from that of any other species in the genus.

Description. - Body cylindrical. Color dark rufopiceous above and dark rufous below, elytral apices, legs, palpi, and antennae testaceous or rufotestaceous; dorsal surface with slight to strong aeneous luster.

Integument. Smooth, shiny. Fine microsculpture on paramedian frontal sulci, genae, mouthparts, pronotal base, front tibiae and anterior surfaces of front femora, middle legs except trochanters, hind tibiae and posterior surfaces of hind femora, elytral epipleura at extreme base, and at least small patch in coxal depression of sternum three; some specimens with microsculpture on sternum two, sides of sterna three and four, and margin of sternum seven.

Head. Fig. 88. As described for *S. ferrugineus* except: median field of clypeus narrower at base, between 1.0 and 1.5 apical width of median field of frons; second frontal carina broadened at base, fifth nearly obsolete; eye larger, globose; neck densely and coarsely punctate; and gena strongly rugose in front.

Pronotum. Fig. 88. Smaller, more transverse than in *S. ferrugineus*, paramedian sulci shorter and slightly hooked basally, anterior transverse impression finely punctate.

Legs. Paronychia more conspicuous, slightly shorter than tarsal claws.

Elytra. Five to eight setigerous punctures on interval three, five to seven on interval five, and four to seven on interval seven. Otherwise as in *S. ferrugineus*.

Abdomen. As in *S. ferrugineus*.

Male genitalia. Median lobe (Fig. 94) with form of apex diagnostic; endophallus, Fig. 99. Eleven specimens examined.

Measurements and proportions. See Table 6.

Variation. - Since *S. auripennis* has no known close relatives, and as available material was limited, I did not study geographic variation in detail. Specimens from the south tend to have more abdominal microsculpture, more elytral setae, more elongate paramedian pronotal sulci, and more cylindrical body form, but this variation seems gradual. The smallest specimens seen are males and females from Arizona and Baja California (LE, 2.07 mm) and the largest is a female from Tucson, Arizona (LE, 2.88 mm).

Etymology. - Of *auripennis*, Latin, *aurum* = gold plus *penna* = wing, in reference to elytral coloration of the slightly teneral type; of *peninsularis*, Latin, *peninsula* = peninsula, a reference to the type locality in peninsular Baja California.

Distribution. - The known distribution of this species (Fig. 101) extends from southern Arizona south to Costa Rica in Pacific drainage areas, from elevations near sea-level to as high as 4500' in Guatemala. I studied 118 specimens from the following localities.

Table 6. Descriptive statistics for *S. auripennis*, based on 20 males from Hermosillo, Sonora.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.46-4.23	3.824	0.329	0.098	5.73
LE	2.14-2.60	2.362	0.194	0.058	5.47
WH	0.73-0.88	0.789	0.071	0.021	5.98
WP	0.97-1.21	1.080	0.108	0.032	6.64
WE	1.10-1.34	1.201	0.105	0.031	5.85
B. Setae on left elytron.					
Interval 3	6 - 8	6.7			
Interval 5	5 - 7	6.3			
Interval 7	4 - 7	5.4			
Total	16- 22	18.4	1.6	0.7	8.64
C. Proportions.					
WF/WH	0.60-0.66	0.623	0.029	0.009	3.13
LP/WP	0.88-0.95	0.914	0.027	0.008	0.95
DP/LP	0.84-0.88	0.866	0.018	0.005	1.42
LP/WE	0.79-0.86	0.822	0.032	0.010	2.59
Ta/Ti	0.63-0.73	0.680	0.053	0.016	5.18
PS/LP	0.56-0.63	0.599	0.035	0.011	3.94

UNITED STATES

ARIZONA: Cochise Co., Douglas (1; CAS); Graham Co., Aravaipa (1; CAS); Maricopa Co., Phoenix (2; CUNY, DRWh), Wickenburg (5; MCZ, MSUL); Pima Co., Organ Pipe National Monument (1; LBSC), Quitobaquito (1; UATA), Tucson (3; AMNH, CAS, USNM); Santa Cruz Co., Nogales (2; CAS, UCD), Pena Blanca (4; UASM, UATA).

MEXICO

BAJA CALIFORNIA: 5 mi. s. Miraflores (17; CAS), 5 mi. w. San Bartolo (3; CAS), 6 mi. sw. Santiago (4; UATA), Triunfo (3; CAS). CHIAPAS: 20.9 mi. n. Arriaga (1; UASM), Puente Macuilapa (2; FDAG). JALISCO: Pitillal (1; UASM). NAYARIT: Jesus Maria (1; UCB), San Blas (1; CAS). PUEBLA: Tepexco (2; UASM). SINALOA: 19 mi. s. Culiacan (1; UCB), Real de Piaxtla (2; AMNH), 4 mi. s. Villa Union (1; UCB), 26 mi. ne. Villa Union (2; LBSC). SONORA: Alamos (5; CAS, LACM), 5 mi. w. Alamos (2; UATA), 10 mi. w. Alamos (4; AMNH), 7 mi. se. Alamos (4; UCB), Hermosillo (34; CAS), Minas Nuevas (1; AMNH), 10 mi. e. Navajoa (1; UATA).

GUATEMALA

ALTA VERAPAZ: Teleman (1; BMNH). EL QUICHE: Sacapulas (1; AMNH).

HONDURAS

CORTES: La Lima (1; INHS).

COSTA RICA

PUNTARENAS: Palmar Sur (1; UAFA). SAN JOSE: Barranca (1; JNeg), 3-7 mi. n. Puerto Viejo (1; UAFA).

Collecting notes. - Nearly all specimens were takan at lights, so little is known of the biology of *S. auripennis*. I collected one specimen from Arriaga along a small stream, but precise circumstances are unrecorded. Individuals of this species probably live in sand rather than gravel bars, as do those of *S. ferrugineus*; this supposition is supported by the cylindrical body form, which is not suited for life in gravel bars. If the normal habitat is sand, and particularly if it is dry sand, then the distribution of the species is likely to be unaffected by the location and substrate of drainage systems. Specimens have been collected throughout the year.

Taxonomic notes. - I have seen topoparatypes of both *S. auripennis* and *S. peninsularis*. These names are clearly synonyms. Southern specimens differ slightly as noted, but the male genitalia are constant throughout the known range. Exact relationships of this species with *S. ferrugineus* are unclear, but are quite apparently not close.

3.36 The *basalis* group

Diagnostic combination. - Specimens referred to this group have the following combination of characters: body convex; paramedian clypeal carinae not extended to median tooth; clypeal field triangular, at base more than 1.5 apical width of median frontal sulcus; clypeal suture sharply impressed; antennal articles five to ten short but filiform, distinctly longer than wide; submentum without accessory setae; pronotum without distinct paralateral carinae, with well developed paramedian sulci; front and middle tarsi quite narrow in both sexes; elytra with discal setae on intervals three, five, and seven, intervals not carinate; sternum seven with paramedian ambulatory setae in both sexes; paramedian carinae of sternum three not or slightly curved at apices;

and pygidium apex weakly to strongly crenulate in females.

Distribution. - Members of this group are known only from Brazil, Uraguay, and Argentina. I examined 18 specimens of the *basalis* group.

Taxonomic notes. - I assign to this group four species, two described here as new. I examined the type of *S. basalis* Putzeys, and saw some Brazilian specimens which agree well with the original description of *S. multipunctatus* Kult, but I doubt that any additional described species belong to this group. I have not provided full species descriptions, as none of the species are well represented in collections.

This group seems an important phylogenetic link, as it seems to share a common ancestry with the *ferrugineus* group (which has no clear derivatives), and probably also with all the remaining groups of *Schizogenius*.

3.361 *Schizogenius basalis* Putzeys

Schizogenius basalis Putzeys 1866:230. *Type locality* Santa Lucia River, 12 leagues north of Montevideo, Uruguay; holotype female in IRSB (!). Kult 1950:148.

Diagnostic combination. - The only specimen of this species seen by me differs from specimens of *S. multipunctatus* by its larger size (LE about 2.5 mm), less metallic coloration, and sparsely punctate occiput. It differs from specimens of *S. cearaensis* by its larger size, more numerous discal setae, and less metallic pronotal coloration, and from specimens of *S. negrei* by larger size, more numerous discal setae, and darker coloration.

Description. - With the characters of the *basalis* group. Body coloration faded from aging, but according to original description aeneopiceous, with elytral base fuscous; legs and antennae ferrugineous; palpi testaceous. Head and pronotum, Fig. 89; antennal article five about 1.3 times longer than wide; occiput sparsely punctate. Elytral striae distinctly punctate in basal half; left elytron with 16, 17, and 14 setae on intervals three, five, and seven, respectively. Male genitalia not known.

Measurements and proportions. TL, 4.01 mm; LE, 2.50 mm; WH, 0.79 mm; WP, 1.16 mm; WE, 1.33 mm; WF/WH, 0.67; LP/WP, 0.87; DP/LP, 0.86; LP/WE, 0.76; PS/LP, 0.61.

Etymology. - Latin, *basilaris* = at the base, in reference to the pale elytral base.

Distribution. - I examined only the type specimen from near Montevideo, Uruguay.

Taxonomic notes. - As the type specimen of *S. basalis* is faded, I can't judge what the color in life would be. Since Putzeys indicated that the elytra were pale at base only, I doubt that the forms named *S. basalis* and *S. cearaensis* are conspecific, but they may be geographic forms of a single species.

3.362 *Schizogenius cearaensis* new species

Type material. - Holotype male and allotype female labelled "Fortaleza Ceara, BRAZIL III -29/IV-2-63 F. G. Werner" (MCZ). Nine additional specimens with the same label data are paratypes (DRWh, IRSB, MCZ, UASM).

Diagnostic combination. - Within the *basalis* group, specimens of this species are distinguished by the combination of: occiput sparsely punctate; elytra uniformly pale; pronotum strongly metallic; and elytral disc with fewer than 40 setae.

Description. - With general characters of *basalis* group. As in *S. basalis* except as follows. Color ferrugineous; pronotum strongly aeneopiceous to metallic green; elytra, antennae, palpi, front tibiae and tarsi, and middle and hind legs testaceous. Head and pronotum, Fig. 90. Left elytron with 10 to 12 setae on interval three, 12 to 14 on interval five, and 9 to 13 on interval seven, total 33 to 38 in specimens examined. Male genitalia, Fig. 95; one specimen examined.

Measurements and proportions. Of holotype, the smallest specimen: TL, 3.07 mm; LE, 1.88 mm; WH, 0.65 mm; WP, 0.87 mm; WE, 1.07 mm; WF/WH, 0.65; LP/WP, 0.90; DP/LP, 0.88; LP/WE, 0.73; PS/LP, 0.54; Ta/Ti, 0.65. Of allotype, the largest specimen: TL, 3.37 mm; LE, 2.09 mm; WH, 0.67 mm; WP, 0.85 mm; WE, 1.12 mm; WF/WH, 0.67; LP/WP, 0.89; DP/LP, 0.88; LP/WE, 0.76; Ta/Ti, 0.73.

Etymology. - I name this species for its type locality, in the Brazilian state of Ceara.

Distribution. - *S. cearaensis* is known only from the type series from Fortaleza, Ceara, Brazil.

Taxonomic notes. - I distinguish *S. cearaensis* as a species distinct from the related *S. basalis* because all known specimens are smaller, have fewer elytral setae, and differ in coloration. It remains possible, however, that the two forms are merely geographic variants. More material of the group is required to study geographic variation, and to obtain more information about *S. basalis* including information about male genitalia.

3.363 *Schizogenius multipunctatus* Kult

Schizogenius multipunctatus Kult 1950:147. *Type locality* Corumba, Mato Grosso, Brazil; holotype and paratype in Kult collection, present location not known.

Diagnostic combination. - Within the *basalis* group, specimens with occiput densely punctate belong to this species. All known specimens of this species differ further from the type of *S. basalis* by smaller body size (LE under 2.3 mm), and from specimens of *S. cearaensis* and *S. negrei* by the dark elytra.

Description. - With characters of *basalis* group. Body bright aeneopiceous to metallic green, elytra unicolorous; legs and antennae ferrugineous; palpi testaceous. Head and pronotum, Fig. 91; antennal article five about 1.3 times longer than wide; occiput densely punctate. Elytral striae finely punctate in basal half; left elytron with about 14-18 setae on interval three, 15-17 on interval five, 11-13 on interval seven; total 41-46 in specimens examined. Male genitalia, Fig. 96; one specimen examined.

Measurements and proportions. Largest specimen, female: TL, 3.55 mm; LE, 2.24 mm; WH, 0.73 mm; WP, 0.98 mm; WE, 1.15 mm; WF/WH, 0.62; LP/WP, 0.87; DP/LP, 0.91; LP/WE, 0.74; Ta/Ti, 0.66; PS/LP, 0.59. Smallest specimen, male: TL, 3.17 mm; LE, 2.00 mm; WH, 0.66 mm; WP, 0.85 mm; WE, 1.02 mm; WF/WH, 0.60; LP/WP, 0.88; DP/LP, 0.92;

LP/WE, 0.74; Ta/Ti, 0.58; PS/LP, 0.57.

Etymology. - Latin, *multus* = much, plus *punctum* = small hole, in reference to the numerous discal setae on the elytra.

Distribution. - Specimens of this species have been collected in various localities in central Brazil. I studied three specimens from the following localities.

BRAZIL

GOIAS: Santa Isabel do Morro (1; DRWh). PIAUI: Terezina (2; MGFT).

Collecting notes. - As the above specimens were collected in January and June, adults of *S. multipunctatus* are probably active throughout the year.

Taxonomic notes. - Specimens here identified as *S. multipunctatus* differ strongly from specimens of *S. basalis* and *S. cearaensis* in coloration and in punctation of occiput, and doubtless are reproductively isolated from them. Although I did not see type material of *S. multipunctatus*, the specimens reported here fit the original description quite well and seem correctly assigned.

3.364 *Schizogenius negrei* new species

Type material. - Holotype male (MNHP) and allotype female (JNeg) labelled "Tucuman Concepcion 31-xii-46 Coll A. Golbach" ex collection J. Negre. One female specimen with the same label data is a paratype (DRWh).

Diagnostic combination. - Specimens of this species are distinguished from all others in the group by entirely ferrugineous body coloration.

Further, known females have the pygidium apex only indistinctly crenulate.

Description. - With the characters of the *basalis* group. As in *S. basalis* except as follows. Color ferrugineous, pronotum slightly aeneous; antennae, palpi, front tibiae and tarsi, and middle and hind legs testaceous. Head and pronotum, Fig. 92; antennal article five about 1.2 times longer than wide. Left elytron with 12-13 setae on interval three, 13-17 on interval five, and 10-13 on interval seven, total 35-41 in specimens examined. Male genitalia, Fig. 97; one specimen examined.

Measurements and proportions. Of holotype: TL, 3.38 mm; LE, 2.08 mm; WH, 0.71 mm; WP, 0.93 mm; WE, 1.07 mm; WF/WH, 0.66; LP/WP, 0.91; DP/LP, 0.88; LP/WE, 0.79; Ta/Ti, 0.73; PS/LP, 0.62. Of allotype: TL, 3.48 mm; LE, 2.15 mm; WH, 0.72 mm; WP, 0.99 mm; WE, 1.13 mm; WF/WH, 0.65; LP/WP, 0.89; DP/LP, 0.89; LP/WE, 0.78; Ta/Ti, 0.71; PS/LP, 0.63.

Etymology. - It is with pleasure that I name this species for my friend, J. Negre.

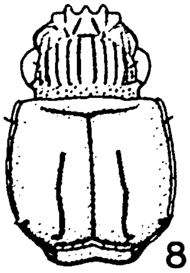
Distribution. - This species is known only from the type series of three specimens, collected at Concepcion, Tucuman, Argentina. It is the only member of the group known from Argentina.

Taxonomic notes. - *S. negrei* is well differentiated morphologically from other members of the *basalis* group, and is no doubt reproductively isolated from them.

3.37 The *elongatus* group

Diagnostic combination. - Specimens of this group have the following

Fig. 87-92. Head and pronotum, dorsal aspect. 87. *S. ferrugineus* Putzeys, Kenwood Beach, Maryland. 88. *S. auripennis* Bates, Arriaga, Chiapas. 89. *S. basalis* Putzeys, Rio Santa Lucia, Uruguay. 90. *S. cearaensis* new species, Fortaleza, Brazil. 91. *S. multipunctatus* Kult, Terezina, Brazil. 92. *S. negrei* new species, Concepcion, Argentina. Fig. 93-97. Male median lobe, lateral aspect. 93. *S. ferrugineus* Putzeys, Logan County, Colorado. 94. *S. auripennis* Bates, Miraflores, Baja California. 95. *S. cearaensis* new species, Fortaleza, Brazil. 96. *S. multipunctatus* Kult, Terezina, Brazil. 97. *S. negrei* new species, Concepcion, Argentina. Fig. 98-99. Male endophallus. 98. *S. ferrugineus* Putzeys, Kenwood Beach, Maryland. 99. *S. auripennis* Bates, Hermosillo, Sonora. Fig. 100-101. Known distributions. 100. *S. ferrugineus* Putzeys; hollow symbols represent state records only. 101. *S. auripennis* Bates.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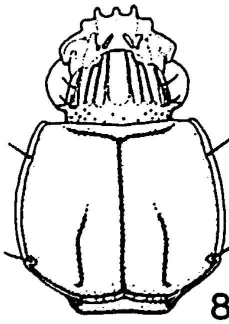
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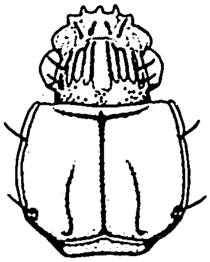
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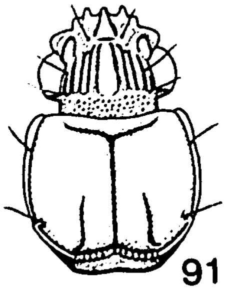
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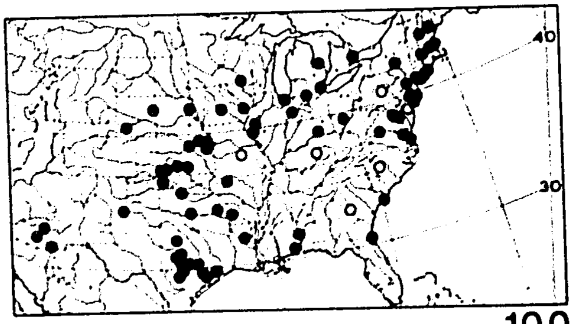

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combination of characters: body convex; paramedian clypeal carinae extended to median tooth or not; clypeal field triangular, at base more than 1.5 apical width of median frontal sulcus; clypeal suture sharply impressed; antennal articles five to ten moniliform, slightly longer than wide; submentum without accessory setae; pronotum with paramedian sulci distinct at base only, and with distinct paralateral carinae; front and middle tarsi slightly broadened in both sexes; elytra without discal setae, intervals not carinate; sternum seven with paramedian ambulatory setae in males, not in females; paramedian carinae of sternum three not or hardly curved at apices; and pygidium apex strongly crenulate in females.

Distribution. - Members of this group are known only from Argentina and Brazil. I studied 13 specimens of the *elongatus* group.

Taxonomic notes. - I assign here two described species, *S. costiceps* Steinheil and *S. elongatus* Kult, though I have seen type material of neither. Specimens from near the type locality of *S. elongatus* agree well with its original description. My association of a specimen from Argentina with the name *S. costiceps* is less definite, but I have no reason to doubt the association. As I have seen no type material of the group, I give no detailed redescriptions of the two described species here assigned to it.

3.371 *Schizogenius costiceps* Steinheil

Schizogenius costiceps Steinheil 1869:242. *Type locality* San Luis, Argentina; location of type unknown.

Diagnostic combination. - One specimen seen by me which may belong to this species differs from specimens of *S. elongatus* by its larger size (LE over 2.9 mm), brighter green color, more elongated paramedian pronotal sulci, and less distinctly punctate elytral striae.

Description. - With characters of *elongatus* group. Body piceous, strongly metallic green; legs and antennae ferrugineous; palpi testaceous. Head and pronotum, Fig. 102; clypeal carinae extended to median tooth, but weakly developed in apical third; antennal article five about 1.1 times longer than wide. Elytral striae indistinctly punctate. Male genitalia not known.

Measurements and proportions. TL, 4.69 mm; LE, 2.96 mm; WH, 0.91 mm; WP, 1.27 mm; WE, 1.50 mm; WF/WH, 0.62; LP/WP, 0.93; DP/LP, 0.91; LP/WE, 0.79; Ta/Ti, 0.66; PS/LP, 0.49.

Etymology. - Latin, *costa* = rib, plus *caput* = head, in reference to the frontal carinae.

Distribution. - Two specimens are known, both from central Argentina. The type is from San Luis, San Luis province. The specimen reported here is labelled "Rep. Arg. Pronunciamento Pro-Entre Rios XI-63." (JNeg).

Taxonomic notes. - The original description of *S. costiceps* is inadequate, as Steinheil thought that the eight long longitudinal carinae on the frons distinctive. But the Entre Rios specimen fits the description in other characteristics recorded, such as the size and bright green color, and is from a sufficiently close locality that it may well be conspecific. Steinheil's description indicates a more pale body color, but his specimen was probably teneral. Further evidence that the Entre Rios specimen is conspecific with or closely related to the type of

S. costiceps is in what Steinheil did not say: he particularly omitted any mention of discal setae on the elytra.

3.372 *Schizogenius elongatus* Kult

Schizogenius elongatus Kult 1950:146. *Type locality* Corumba, Mato Grosso, Brazil; type and paratype in Kult collection, present location not known.

Diagnostic combination. - Within the *elongatus* group, specimens of this species are distinguished by small body size (LE under 2.5 mm), narrow body, aeneopiceous coloration, nearly obsolete paramedian pronotal sulci, and finely but distinctly punctate elytral striae.

Description. - With characters of *elongatus* group. Body piceous, strongly aeneous; legs and antennae ferrugineous; palpi testaceous. Head and pronotum, Fig. 103; clypeal carinae broken in apical third; antennal article five about 1.1 times longer than wide. Elytral striae finely but distinctly punctate in basal half. Male genitalia, Fig. 108; 1 specimen examined.

Measurements and proportions. Largest specimen, male: TL, 3.88 mm; LE, 2.40 mm; WH, 0.79 mm; WP, 1.07 mm; WE, 1.20 mm; WF/WH, 0.59; LP/WP, 0.94; DP/LP, 0.86; LP/WE, 0.84; Ta/Ti, 0.61; PS/LP, 0.22. Smallest specimen, female: TL, 3.39 mm; LE, 2.13 mm; WH, 0.71 mm; WP, 0.94 mm; WE, 1.04 mm; WF/WH, 0.58; LP/WP, 0.91; DP/LP, 0.92; LP/WE, 0.83; Ta/Ti, 0.64; PS/LP, 0.26.

Etymology. - Latin, *elongatus* = prolonged, in reference to the elongate body form.

Distribution. - Specimens of *S. elongatus* have been collected in two states in central Brazil. I studied 12 specimens from the following localities.

BRAZIL

GOIAS: Santa Isabel do Morro (8; DRWh, MGFT, UASM). MATO GROSSO: Barra do Tapirape (1; MZSP), Caceres (2; MGFT), Jacare (1; MGFT).

Collecting notes. - Adults of this species have been collected in June, November, and December, and thus are probably active throughout the year.

Taxonomic notes. - Although I did not study type material of *S. elongatus*, the specimens here reported agree well with the original description and were collected near the type locality. Kult erred in suggesting a relationship with members of the *optimus* group, which lack a distinct clypeal suture and differ in numerous additional ways.

3.38 The *carinatus* group

Diagnostic combination. - Members of this group are readily recognized by the following combination of characters: antennal articles five to ten filiform; elytral intervals strongly carinate; and elytral disc without setae. Also: body convex; paramedian clypeal carinae extended to median tooth or not; clypeal field triangular, at base less than 1.5 apical width of median frontal sulcus; clypeal suture sharply impressed; median frontal sulcus strongly microsculptured, with median carina distinct; submentum without accessory setae; pronotum with paramedian sulci well developed and with distinct paralateral carinae; front and middle tarsi distinctly expanded, especially in males; sternum seven with paramedian ambulatory setae in males, not in females; paramedian carinae of sternum three not curved at apices; and pygidium apex crenulate in females.

Distribution. - Seven specimens of this group are known from Brazil.

Taxonomic notes. - I assign here two quite different species, *S. carinatus* Whitehead and a new species described below. The characteristics of members of this group are so distinctive that all described species not seen by me may safely be excluded from the group.

3.381 *Schizogenius carinatus* Whitehead

Schizogenius carinatus Whitehead 1966:2. *Type locality* Santa Isabel, Mato Grosso, Brazil; holotype male in CAS (!).

Diagnostic combination. - Within the *carinatus* group, specimens of this species are distinguished from the only known specimen of *S. costipennis* by the following: body color piceous; clypeal carinae clearly extended to median tooth; dorsum not extensively microsculptured; pronotum not rugose; and elytral intervals more distinctly carinate.

Description. - I have nothing to add to the original description (Whitehead, 1966), except pygidium apex crenulate in female.

Etymology. - Latin, *carina* = keel, in reference to the carinate elytra.

Distribution. - I studied six specimens of *S. carinatus* from the following localities in central Brazil.

BRAZIL

GOIAS: Santa Isabel do Morro (2; DRWh). MATO GROSSO: Jacare (3; MGFT), Santa Isabel (1; CAS).

Collecting notes. - Adults of this species probably are active throughout the year, as specimens have been collected in June, August, and November.

3.382 *Schizogenius costipennis* new species

Type material. - Holotype female labelled "S. Isabel do Morro Ilha do Bananal Bras. Goias VI.1961 leg. M. Alvarenga" (MGFT).

Diagnostic combination. - The only known specimen of this species differs from specimens of *S. carinatus*, the only other known member of the *carinatus* group, by the following: body color rufotestaceous; integument extensively microsculptured; pronotum strongly rugose; paramedian clypeal carinae interrupted before median tooth; and elytral intervals distinctly but weakly carinate.

Description. - Body broad, moderately convex. Color rufotestaceous, without metallic luster.

Integument. Entire body apparently microsculptured, but under surface not examined in detail; median frontal sulcus as well as paramedian sulci coarsely microsculptured. Pronotum strongly rugose.

Head. Fig. 104. Paramedian clypeal carinae straight, parallel, abbreviated at apices; median field triangular, no wider at base than apex of median field of frons. Clypeal suture sharply defined. Median frontal sulcus dividied by longitudinal carina. Eye uniformly faceted.

Neck rugose-punctate. Antennal articles four to ten elongate, filiform, article five about 1.8 times longer than wide.

Pronotum. Fig. 104. Sides bisetose, hind angles strongly reduced, entire surface rugose. Paramedian longitudinal sulci long, impunctate, sinuate, shallow toward apices, strongly hooked basally. Anterior transverse impression finely punctate. Paralateral longitudinal carinae strongly developed.

Legs. Front and middle tarsi strongly dilated; hind tarsi slender, short. Paronychia about half as long as tarsal claws. Front tibia narrowed evenly to base. Front femur strongly constricted near apex.

Elytra. Discal setae absent. Striae deep, sharply engraved, finely punctate in basal two-thirds. Interval one moderately convex; intervals two to seven strongly raised, finely carinate; interval eight sharply carinate at apex; apices of intervals three, five, and seven broadly joined. Humeral denticles moderately prominent.

Abdomen. Sternum three with paramedian carinae straight. Sternum seven without paramedian ambulatory setae. Pygidium with apical margin crenulate.

Male genitalia. Not known.

Measurements and proportions. Holotype: TL, 4.15 mm; LE, 2.68 mm; WH, 0.92 mm; WP, 1.21 mm; WE, 1.56 mm; WF/WH, 0.63; LP/WP, 0.76; DP/LP, 0.96; LP/WE, 0.59; PS/LP, 0.70.

Etymology. - Latin, *costa* = rib, plus *penna* = wing, in reference to the strongly sculptured elytra.

Distribution. - This species is known only from the holotype, from central Brazil.

Collecting notes. - The holotype was collected in June. Specimens of the following additional species were taken at the same time and place: *S. carinatus*, *S. elongatus*, *S. jacarensis*, and *S. multipunctatus*. I presume that adults of *S. costipennis* are active throughout the year, as adults of the other species probably are, and that they probably live in riparian gravel bars.

Taxonomic notes. - *S. costipennis* is peculiar in numerous ways, and perhaps is not closely related to *S. carinatus*. In addition to characteristics mentioned in the diagnostic combination, the form of the thorax is quite different, and the elytra are much more strongly ovate. However, I doubt that the peculiar combination of elytral intervals carinate, elytral disc without setae, and pronotum with strong paralateral carinae is the result of convergence. And the two species are sympatric, so at least there is no evidence that this combination of characteristics had independent origins in separate areas. If these two species indeed are related, then additional species of the group should exist and, if found, should verify the relationship.

3.39 The *strigicollis* group

Diagnostic combination. - Specimens of this group are distinguished from all others of the genus by numerous accessory setae on submentum. They have the following additional combination of characters: body convex; paramedian clypeal carinae extended to median tooth, moderately elevated basally; clypeal field triangular, at base less than 1.5 apical width of median frontal sulcus; clypeal suture sharply impressed; antennal articles five to ten filiform, distinctly longer than wide; pronotum with well developed paralateral carinae and paramedian sulci; front and middle tarsi moderately dilated in males and females; elytra with numerous discal setae on intervals three, five, and seven, intervals not carinate; sternum seven with paramedian ambulatory setae in males only; paramedian carinae of sternum three not curved at apices; and pygidium apex not crenulate in females.

Distribution. - This group is known only from three specimens from Colombia.

Taxonomic notes. - Lindroth (1961) designated *S. strigicollis* as the type species of the genus, as it was the first species of the genus listed by Putzeys (1846). This species is the only known member of the group.

3.391 *Schizogenius strigicollis* Putzeys

Schizogenius strigicollis Putzeys 1846:650. *Type locality* Colombia, here restricted to Aracataca, Magdalena; male specimen in IRSB (!) labelled lectotype here so designated. Putzeys 1863:24. Putzeys 1866:222. Bates 1881:38. Lindroth 1961:164.

Diagnostic combination. - *S. strigicollis* is the only known species of *Schizogenius* characterized by numerous accessory setae on submentum.

Description. - With characters of *strigicollis* group. Body convex, bright aeneopiceous, elytra margined in metallic green; legs, antennae, and mouthparts rufotestaceous. Head and pronotum, Fig. 105; antennal article five about 1.8 times longer than wide; pronotum distinctly rugose at sides and base. Elytral striae indistinctly punctate basally; left elytron with about 13-15 setae on interval three, 13 on interval five, 9-10 on interval seven; total 35-38 in specimens examined. Male median lobe, Fig. 109; one specimen examined.

Measurements and proportions. Largest specimen, a female: TL, 4.90 mm; LE, 3.12 mm; WH, 1.06 mm; WP, 1.35 mm; WE, 1.67 mm; WF/WH, 0.59; LP/WP, 0.84; DP/LP, 0.91; LP/WE, 0.68; Ta/Ti, 0.63; PS/LP, 0.53. Smallest specimen, a male: TL, 4.69 mm; LE, 2.88 mm; WH, 1.10 mm; WP, 1.35 mm; WE, 1.62 mm; WF/WH, 0.61; LP/WP, 0.86; DP/LP, 0.89; LP/WE, 0.72; Ta/Ti, 0.62; PS/LP, 0.59.

Etymology. - Latin, *strigosus* = strigose, plus *collum* = neck, in reference to the rugose pronotum.

Distribution. - I studied three specimens of this species, all from Colombia.

COLOMBIA

No locality (1; IRSB). MAGDALENA: Aractaca (2; MCZ).

Collecting notes. - Specimens from Aracataca were collected by P. J. Darlington in March and May.

Taxonomic notes. - Records of this species from Mexico (Putzeys, 1846; Bates, 1881) are no doubt erroneous.

3.40 The *arechavaletae* group

Diagnostic combination. - Specimens of this group differ from other members of the subgenus by having three or four setae on interval three of elytron, and two setae only on basal half of interval five. They have the following additional characters: body moderately convex; paramedian clypeal carinae abbreviated before median tooth; clypeal field triangular, at base more than 1.5 apical width of median frontal sulcus; clypeal suture sharply impressed; antennal articles five to ten filiform, distinctly longer than wide; pronotum without paralateral carinae, with short paramedian sulci; front and middle tarsi moderately dilated in both sexes; elytral intervals not carinate; sternum seven with paramedian ambulatory setae in males only; paramedian carinae of sternum three curved outward at apices; and pygidium apex crenulate in females.

Distribution. - Two species are known, one from Uruguay and the other from northeastern Brazil. I studied ten specimens of the *arechavaletae* group.

Taxonomic notes. - The two species included in this group are quite different in body form, but as they agree in all important ways except length of paronychia they probably are quite closely related.

3.401 *Schizogenius arechavaletae* Putzeys

Schizogenius arechavaletae Putzeys 1866:227. *Type locality* Santa Lucia River, north of Montevideo, Uruguay; male specimen in IRSB labelled lectotype (!), here so designated.

Schizogenius angusticollis Putzeys 1866:231. *Type locality* Santa Lucia River, north of Montevideo, Uruguay; holotype male in IRSB (!). NEW SYNONYMY.

Diagnostic combination. - Specimens of *S. arechavaletae* are distinguished from specimens of *S. reichardti*, the only other known member of the *arechavaletae* group, by longer paramedian pronotal sulci, more convex body form, and rounded humeral angles of elytra.

Description. - Body broad, convex. Color of type specimens faded; originally described by Putzeys as aeneocupreous, appendages fuscous.

Integument. Microsculpture generally as in *S. reichardti* except on abdomen: less developed on sternum two, in coxal depressions and on small paralateral patches on sternum three, otherwise largely unmicrosculptured.

Head. Fig. 106. Clypeal carinae tuberculate, in some specimens evidently but weakly extended to median tooth; median clypeal field triangular, broad, width at base about 1.5 apical width of median field of frons. Clypeal suture sharply engraved. Eye prominent, subglobose, uniformly faceted. Neck densely, coarsely punctate. Gena rugose in front. Antenna filiform, short, article five about 1.5 times wider than long.

Pronotum. Fig. 106. Sides bisetose, hind angles weakly developed, base and sides moderately rugose. Paramedian sulci short, impunctate, distinctly engraved apically, deep and broadly hooked basally. Anterior transverse impression distinctly punctate.

Legs. Front and middle tarsi distinctly dilated, particularly in males, in males with dense ventral pubescence; hind tarsus slender, short. Paronychia nearly as long as tarsal claws. Front tibia evenly narrowed to base where much narrower than at base of antennal cleaner. Front femur not strongly constricted near apex.

Elytra. Three or four setigerous punctures on interval three, two on basal half of interval five. Striae deep and sharply engraved, finely punctate in basal half. Intervals one to seven broad and convex, interval eight carinate at apex; intervals three and five broadly joined apically with interval seven. Humeral angles rounded.

Abdomen. Sternum three with paramedian carinae curved at apices. Sternum seven with paired paramedian ambulatory setae in males only. Pygidium with apical margin crenulate in females.

Male genitalia. Median lobe, Fig. 110, 111; three specimens studied.

Measurements and proportions. Largest specimen, a female: TL, 4.66 mm; LE, 2.95 mm; WH, 0.91 mm; WP, 1.34 mm; WE, 1.60 mm; WF/WH, 0.65; LP/WP, 0.82; DP/LP, 0.93; LP/WE, 0.69; Ta/Ti, 0.67; PS/LP, 0.58. Smallest specimen, a male: TL, 3.61 mm; LE, 2.27 mm; WH, 0.75 mm; WP, 0.99 mm; WE, 1.27 mm; WF/WH, 0.65; LP/WP, 0.86; DP/LP, 0.93; LP/WE, 0.67; Ta/Ti, 0.69; PS/LP, 0.59.

Etymology. - The name *arechavaletae* was given in honor of the collector, M. Arechavaleta. The name *angusticollis* is derived from Latin, *angustus* = narrow, plus *collum* = neck, in reference to the narrowly prominent pronotal front angles.

Distribution. - I studied seven specimens of this species from Uruguay, all from type series (IRSB) of *S. arechavaletae* and *S. augusticollis*.

Taxonomic notes. - If the holotype specimen of *S. angusticollis* is correctly labelled, it unquestionably is conspecific with specimens named *S. arechavaletae*, and was from the same series. According to original descriptions, however, there is some possibility of error; the description of *S. angusticollis* suggests an animal more like *S. reichardti* than *S. arechavaletae*. This question cannot be resolved until other specimens of the type series are found, and, for the present, I prefer to place the names *S. angusticollis* and *S. arechavaletae* in synonymy.

Paronychia apparently are primitively short in the subgenus *Schizogenius*, and secondarily elongate in *S. arechavaletae* and all following species groups. I suspect that the ancestor of the *arechavaletae* group had secondarily elongated paronychia, and that the shortened paronychia of *S. reichardti* represents a reversion to the ancestral condition.

3.402 *Schizogenius reichardti* new species

Type material. - Holotype female labelled "PARAIBA Corema - VI-1957 Exp. Dep. Zoologia" (MZSP). Two additional females with the same label data, from Brazil, are paratypes (MZSP, DRWh).

Diagnostic combination. - Specimens of this species are readily distinguished from others in the *arechavaletae* group by numerous characteristics, including prominent humeral angles of elytra.

Description. - Body broad, dorsum flattened. Color dark castaneous, elytra with slight aeneous luster; legs, antennae, and palpi ferrugineous.

Integument. Distinct microsculpture on paramedian frontal sulci, genae, mouthparts, base of pronotum, anterior surfaces of front legs, middle legs except trochanters, hind tibiae and posterior surfaces of hind femora, elytral epipleura on base and apical two-thirds, sternum two, and portions of sterna three to seven.

Head. Fig. 107. Clypeal carinae tuberculate, convergent, not or weakly extended to median tooth; median clypeal field triangular, broad, width at base about 1.5 apical width of median field of frons. Clypeal suture sharply engraved. Eye prominent, subglobose, uniformly faceted.

Neck densely, coarsely punctate. Gena rugose in front. Antenna filiform, short, article five about 1.3 to 1.4 times longer than wide.

Pronotum. Fig. 107. Sides bisetose, hind angles weakly developed, base and sides moderately rugose. Paramedian sulci short, impunctate, shallow and indistinctly engraved apically, deep and broadly hooked basally. Anterior transverse impression distinctly punctate.

Legs. Front and middle tarsi distinctly dilated, without dense ventral pubescence; hind tarsus slender, short. Paronychia distinct, about half length of tarsal claws. Front tibia evenly narrowed to base where much narrower than at base of antennal cleaner. Front femur not strongly constricted near apex.

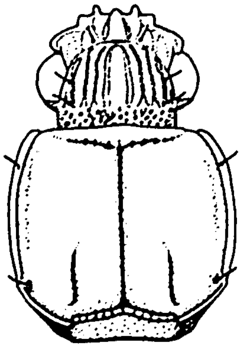
Elytra. Three or four setigerous punctures on interval three, two on basal half of interval five. Striae deep and sharply engraved, distinctly punctate in basal three-fourths. Intervals one to seven broad and moderately convex, interval eight carinate at apex; intervals three and five broadly joined apically with interval seven. Humeral angles prominent.

Abdomen. Sternum three with paramedian carinae curved at apices. Sternum seven without paramedian ambulatory setae in female. Pygidium with apical margin crenulate in female.

Male genitalia. Unknown.

Measurements and proportions. Largest specimen: TL, 4.99 mm; LE, 3.09 mm; WH, 1.15 mm; WP, 1.42 mm; WE, 1.65 mm; WF/WH, 0.65; LP/WP, 0.88; DP/LP, 0.90; LP/WE, 0.73; Ta/Ti, 0.73; PS/LP, 0.44. Smallest specimen: TL, 4.47 mm; LE, 2.75 mm; WH, 1.02 mm; WP, 1.28 mm; WE, 1.58 mm; WF/WH, 0.66; LP/WP, 0.86; DP/LP, 0.93; LP/WE, 0.70; Ta/Ti, 0.68; PS/LP, 0.49.

Fig. 102-107. Head and pronotum, dorsal aspect. 102. *S. costiceps* Steinheil, Entre Rios, Argentina. 103. *S. elongatus* Kult, Caceres, Brazil. 104. *S. costipennis* new species, Santa Isabel do Morro, Brazil. 105. *S. strigicollis* Putzeys, Aracataca, Colombia. 106. *S. arechavaletae* Putzeys, Rio Santa Lucia, Uruguay. 107. *S. reichardti* new species, Corema, Brazil.
Fig. 108-111. Male median lobe, lateral aspect. 108. *S. elongatus* Kult, Santa Isabel do Morro, Brazil. 109. *S. strigicollis* Putzeys, Aracataca, Colombia. 110, 111. *S. arechavaletae* Putzeys, Rio Santa Lucia, Uruguay.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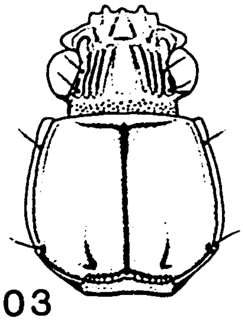
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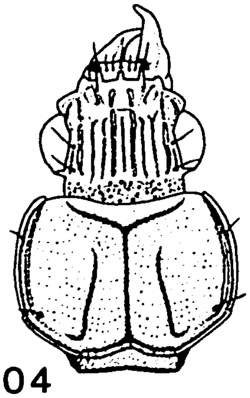
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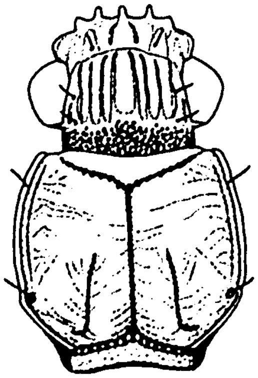
0.5 mm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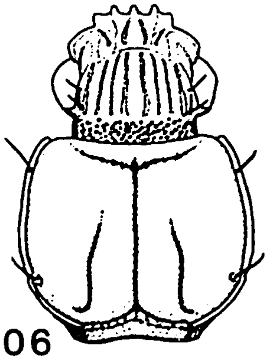
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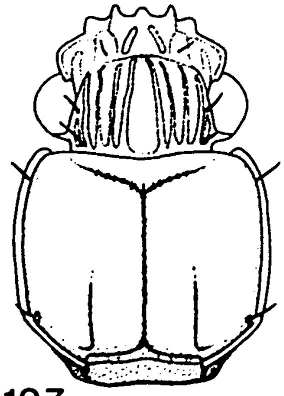
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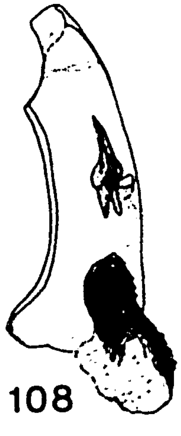
0.2 mm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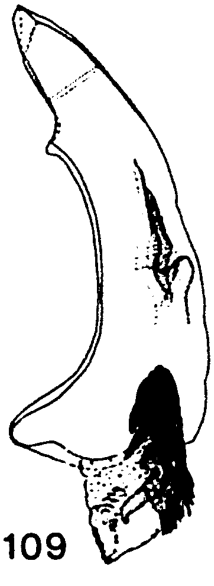
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111

Variation. - On one paratype basal halves of all femora are strongly rugose.

Etymology. - I take pleasure in naming these distinctive beetles for my friend, Hans Reichardt, who made specimens of them available for study.

Distribution. - Only the type specimens from northeastern Brazil are known.

3.41 The *ocellatus* group

Diagnostic combination. - Specimens of this group differ from all others of the genus by remarkably reduced, bubble-like eyes, and plurisetose antennal pedicels. They have the following additional combination of characters: body flattened; prothoracic pleura and abdominal sterna microsculptured; paramedian clypeal carinae extended to median tooth; clypeal field triangular, at base less than 1.5 apical width of median frontal sulcus; clypeal suture sharply impressed; inner paramedian frontal carinae not grossly thickened; median frontal sulcus not or weakly microsculptured, without median longitudinal carina; antennal articles five to ten filiform, elongate; submentum without accessory setae; pronotum with elongate paramedian sulci, without paralateral carinae; front and middle tarsi broadened in both sexes, particularly in males; elytra with discal setae on interval three only; hind wings brachypterous; sternum seven with paramedian ambulatory setae in males, not in females; paramedian carinae of sternum three strongly curved at apices; and pygidium apex crenulate in females.

Distribution. - Eight specimens of one species were collected in a cave in southern Brazil.

Taxonomic notes. - The plurisetose pedicel is reminiscent of antennae in *Halocoryza* species, but is clearly a secondary adaptation. Relationships are uncertain; castaneous color, ventral microsculpture, prominent hind angles, curved sternal carinae, reduced elytral setation, and other characteristics suggest relationship with members of the *darlingtoni* group. The reduced eyes are quite unlike any others seen by me in Carabidae, and lend the head a peculiar appearance.

3.411 *Schizogenius ocellatus* new species

Type material. - Holotype male and allotype female labelled "Grutas das Areias Sao Paulo Bresil 30.VII.68 P. Strinati" (MHNG). Six additional specimens with the same label data are paratypes (DRWh, MHNG, MZSP, UASM).

Diagnostic combination. - The peculiarly reduced eyes readily distinguish members of this species from all others of the genus so far known.

Description. - Body flattened, elytra ovate. Color castaneous, no aeneous luster, appendages paler.

Integument. Conspicuous microsculpture on paramedian frontal sulci, genae, mouthparts, prothoracic pleura, front tibiae and anterior surfaces of front femora, middle legs except trochanters, hind tibiae and posterior surfaces of hind femora, elytral epipleura, and most of abdomen except on midline of sternum seven.

Head. Fig. 112. Paramedian clypeal carinae straight, extended to median tooth; median field narrow, not or hardly wider at base than apex of median frontal sulcus. Clypeal suture sharply defined. Eye reduced, bubble-like, not apparently faceted. Neck coarsely punctate. Gena rugose-punctate. Antennal articles five to ten elongate, article five about 2.0 times longer than wide.

Pronotum. Fig. 112. Sides bisetose, hind angles prominent, base not rugose. Paramedian longitudinal sulci elongate, impunctate, deep throughout, slightly hooked basally. Anterior transverse impression punctate. Front angles sharply produced.

Legs. Front and middle tarsi slightly dilated and pubescent ventrally in females, strongly so in males; hind tarsus slender, short. Paronychia conspicuous, nearly as long as tarsal claws. Front tibia narrowed evenly to base. Front femur not strongly constricted near apex.

Elytra. Three or four setae on interval three, none on intervals five or seven. Striae deep and sharply engraved, distinctly punctate in basal two-thirds. Intervals one to seven broad and convex, interval eight carinate at apex; apices of intervals three, five, and seven broadly joined. Hind wings brachypterous.

Abdomen. Sternum three with paramedian carinae curved at apices. Sternum seven with paired ambulatory setae in males, not in females. Apex of pygidium entire in males, crenulate in females.

Male genitalia. Median lobe, Fig. 116; one specimen examined.

Measurements and proportions. Holotype: TL, 3.65 mm; LE, 2.10 mm; WH, 0.50 mm; WP, 1.07 mm; WE, 1.17 mm; WF/WH, 0.79; LP/WP, 0.98; DP/LP, 0.78; LP/WE, 0.90; Ta/Ti, 0.64; PS/LP, 0.67. Allotype: TL, 3.82, mm; LE, 2.24 mm; WH, 0.80 mm; WP, 1.08 mm; WE, 1.21 mm; WF/WH, 0.81; LP/WP, 1.00; DP/LP, 0.80; LP/WE, 0.89; Ta/Ti, 0.63; PS/LP, 0.67.

Etymology. - Latin, *ocellatus* = having little eyes, in reference to the ocellus-like eye.

Distribution. - Only the type series of eight specimens is known, from a cave in southeastern Brazil.

Taxonomic notes. - The only true troglobitic scaritines heretofore described are *Spelaeodytes mirabilis* Miller and *Italodytes stammeri* Müller from Europe and *Antroforceps bolivari* Barr from Mexico (see Barr, 1967). Specimens of *S. ocellatus* differ from all other known specimens of *Schizogenius* by brachyptery, plurisetose antennal pedicel, and greatly modified eye structure, and in these ways are reminiscent of *A. bolivari*. Specimens of other *Schizogenius* species have been taken in caves, and in particular specimens of *S. tibialis* from Indian Creek Cave in Texas have markedly reduced eyes. But though measures of relative eye size (WF/WH) for *S. ocellatus* and cavernicolous *S. tibialis* are similar, they are not comparable because of grossly different eye structures.

3.42 The *darlingtoni* group

Diagnostic combination. - Specimens of this group have the following combination of characters: body flattened; paramedian clypeal carinae extended to median tooth; clypeal field triangular, at base less than 1.5 apical width of median frontal sulcus; clypeal suture sharply impressed or not; inner paramedian frontal carinae grossly thickened; median frontal sulcus microsculptured, with or without median longitudinal carina; antennal articles five to ten filiform; submentum without accessory setae; pronotum with elongate paramedian sulci, without paralateral carinae; front and middle tarsi broadened in both sexes, particularly in males; elytra with discal setae on intervals three and five only; sternum seven with paramedian ambulatory setae in males only; paramedian carinae of sternum three strongly curved at apices; and pygidium apex crenulate in females or not.

Distribution. - *S. darlingtoni* Kult was described from Panama. I studied ten specimens of other species from Colombia, Venezuela, and Peru.

Taxonomic notes. - I studied type material of no members of this group, and am therefore unable to review them at this time. As here defined, the group contains specimens with enlarged inner paramedian frontal carinae, microsculptured frontal sulcus, normally developed eyes, and setae on elytral intervals three and five. The type specimens of *S. darlingtoni* Kult (1950:140), described from Volcan de Chiriqui, Panama (BMNH), have strong microsculpture on the apical two-thirds of the elytra. I judge from original descriptions that *S. interstriatus* Putzeys (1878: 54, from Medellin, Colombia) and *S. riparius* Putzeys (1878:54, from Ibague, Colombia) are members of this group. These descriptions are not adequate, and I do not know the present location of type specimens. However, as an aid to future students, I made tentative identifications of the following specimens.

Seven specimens from Rio Frio, Magdalena, Colombia (DRWh, MCZ) agree well with Putzeys' description of *S. interstriatus* in all characteristics reported. Additional characteristics are: paramedian pronotal sulci elongate (PS/LP, 0.76-0.81); front femur strongly angulate on midventral margin; elytral interval three with four setae, interval five with five or six setae; abdomen without extensive microsculpture; and female pygidium not crenulate at apex. No other known species in the genus have the angulate front femur characteristic of this species.

Three additional specimens are in general agreement with Putzeys' description of *S. riparius*, but may represent at least two different species, and as none are from Colombia perhaps none are conspecific with *S. riparius*. These specimens are from the following localities: Chanchamayo, Peru (MCZ); Cueva Alfredo Jahn Miranda, Venezuela (MNHG); and El Valle, Venezuela (CNHM). The Venezuelan specimens (LE, 2.53-2.66 mm) agree in the body size reported for *S. riparius*, but the Peruvian specimen is much larger (LE, 3.04 mm). Additional characteristics of these specimens are: paramedian pronotal sulci less elongate (PS/LP, 0.68-0.71); front femur not angulate midventrally; elytral interval three with five or six setae, interval five with six setae; abdomen extensively microsculptured; and female pygidium crenulate at apex.

3.43 The *capitalis* group

Diagnostic combination. - Specimens referred to this group have the following combination of characters: body flattened; paramedian clypeal carinae extended to median tooth; clypeal field triangular, at base less than 1.5 apical width of median frontal sulcus; clypeal suture sharply impressed; inner paramedian frontal carinae not grossly thickened; median frontal sulcus not microsculptured, without median longitudinal carina; antennal articles five to ten elongate, filiform; submentum without accessory setae; pronotum with elongate paramedian sulci, without paralateral carinae; front and middle tarsi broadened in both sexes, particularly in males; elytra with discal setae on intervals three and five only; sternum seven with paramedian ambulatory setae in males, not in females; paramedian carinae of sternum three strongly curved at apices; and pygidium apex not crenulate in either sex. Members of this group differ most notably from members of the related *lindrothi* group by less convex body and much more strongly filiform antennae.

Distribution. - I have seen 12 specimens of this group from the following countries in western South America: Argentina, Bolivia, Colombia, Ecuador, and Peru.

Taxonomic notes. - A female specimen in IRSB (!) is labelled as the type of *S. capitalis* Putzeys (1863:25, from Carracas, Venezuela), and is labelled "capitalis P." in Putzeys' script. However, the specimen is labelled "Medellin" (Colombia), and differs from the original description by having four setae each on intervals three and five rather than five setae each on intervals three, five, and seven. Despite these discrepancies, the specimen otherwise fits the description, and until shown otherwise I think it best to regard this specimen as holotype of *S. capitalis*.

I have not seen type material of *S. putzeysi* Kirsch (1873:129, from Peru), but this seems quite clearly from the original description to be a member of the *capitalis* group, and I suspect the type specimen is teneral. I have tentatively identified as *S. putzeysi* six specimens, all smaller (LE, 2.50-2.79 mm) than the specimen of *S. capitalis* (LE, 3.05 mm) reported above, and all with distinct microsculpture on the sides of the pronotum. These specimens are from the following localities.

BOLIVIA

BENI: Huachi (2; USNM).

ECUADOR

EL ORO: 9 mi. s. Santa Rosa (3; CAS).

PERU

HUANUCO: 24 mi. e. Yurac (1; CAS).

I labelled five additional specimens as an undescribed species near *S. putzeysi*. These are also smaller (LE, 2.54-2.84 mm) than the specimen of *S. capitalis*, but lack distinct microsculpture on the sides of the pronotum. These specimens are from the following localities.

ARGENTINA

TUCUMAN (1; MCZ): Tacanas (3; MGFT), Villa Monti (1; CAS).

As I have seen no definite type material of the *capitalis* group, and few specimens from a broad geographic area, I attempt no detailed revision. Specimens reported above may represent as few as one to as many as three species; tentative identifications are intended as an aid to future students, but the group requires additional study before definite identifications are possible.

3.44 The *lindrothi* group

Diagnostic combination. - This group includes those species with three to six evenly distributed setae in elytral intervals three and five, but none in interval seven; antennal articles five to ten submoniliform, not strongly elongated; median field of frons not microsculptured, not bounded by unusually thickened carinae; and pygidium not crenulate in either sex. Also: body nearly cylindrical; paramedian clypeal carinae extended to median tooth, not strongly raised in basal half; clypeal field not or hardly wider at base than apex of median frontal sulcus; clypeal suture sharply impressed; anterior tarsi of males broadened and with dense ventral pubescence; abdomen not extensively microsculptured; paramedian carinae of sternum three curved at apices; sternum seven with paramedian ambulatory setae normally in males only; and endophallus with short basal collar spines.

Distribution. - I have seen 38 specimens of this group, representing at least two species, from Florida, Guatemala, Costa Rica, Venezuela, and Brazil.

3.441 *Schizogenius lindrothi* new species

Type material. - Holotype male and allotype female labelled "FLORIDA. Bay Co. 7 mi. n. Southport 10 July 1967 D. R. Whitehead" (MCZ). An additional 18 specimens from various localities in Florida are paratypes (BMNH, CAS, CUNY, DRWh, IRSB, UASM, USNM).

Diagnostic combination. - Specimens of this species are the only known specimens of North and Middle American *Schizogenius* with three or four setae each on elytral intervals three and five but none or only one on interval seven.

Description. - Body nearly cylindrical, elytra convex. Color dark rufopiceous, without strong aeneous luster; legs ferrugineous; palpi and antennae testaceous.

Integument. Conspicuous microsculpture on paramedian frontal sulci, genae, mouthparts, pronotal base, front tibiae and anterior surfaces of front femora, middle legs except trochanters, hind tibiae and posterior surfaces of hind femora, elytral epipleura in apical two-thirds and at extreme base, part of sternum two, and coxal depressions of sternum three.

Head. Fig. 113. Paramedian clypeal carinae straight, evenly elevated, extended to median tooth; median field narrow, not or hardly wider at base than apex of median frontal sulcus. Clypeal suture sharply defined. Eye globose, finely and uniformly faceted. Neck densely punctate. Gena rugose in front, strongly punctate. Antennal articles five to ten slightly but distinctly elongate, submoniliform, article five 1.3 times as long as wide.

Pronotum. Fig. 113. Sides bisetose, hind angles not prominent, base not rugose. Paramedian longitudinal sulci moderately elongate, impunctate, nearly straight, deep throughout, slightly hooked basally. Anterior transverse impression finely punctate.

Legs. Front and middle tarsi slightly dilated and pubescent ventrally in male, less so in female; hind tarsus slender, rather short. Paronychia conspicuous, more than half length of tarsal claws. Front tibia narrowed evenly to base. Front femur not strongly constricted near apex.

Elytra. Three to four setae each on intervals three and five, none or rarely one on interval seven. Striae deep and sharply engraved, distinctly punctate in basal two-thirds. Intervals one to seven broad and convex, interval eight carinate at apex; apices of intervals three, five, and seven broadly joined.

Abdomen. Sternum three with paramedian carinae curved at apices. Sternum seven with ambulatory setae in males, normally not in females.

Apex of pygidium entire in both sexes.

Male genitalia. Median lobe, Fig. 117; endophallus, Fig. 120, with short basal collar spines; nine specimens examined.

Measurements and proportions. See Table 7. Of holotype: TL, 4.19 mm; LE, 2.52 mm; WH, 0.85 mm; WP, 1.15 mm; WE, 1.30 mm; WF/WH, 0.57; LP/WP, 0.95; DP/LP, 0.83; LP/WE, 0.84; Ta/Ti, 0.69; PS/LP, 0.76. Of allotype: TL, 4.15 mm; LE, 2.52 mm; WH, 0.68 mm; WP, 1.15 mm; WE, 1.32 mm; WF/WH, 0.59; LP/WP, 0.92; DP/LP, 0.85; LP/WE, 0.80; Ta/Ti, 0.62; PS/LP, 0.71.

Variation. - There is not enough material in collections for an analysis of geographic variation, but if *S. lindrothi* is restricted to Florida such variation is probably negligible. In addition to variation in the Florida specimens listed in Table 7, I noted one female from Southport with a single seta on interval seven of the left elytron, and one female from Enterprise with a pair of paramedian ambulatory setae on sternum seven.

I tentatively associate with this species single females from Guatemala and Costa Rica. The Guatemala specimen differs by having a broad (LP/WP, 0.88), deep (DP/LP, 0.89), and relatively smaller (LP/WE, 0.70) thorax, and by having more prominent pronotal hind angles and stronger humeral angles on the elytra. The Costa Rican specimen falls outside the observed range of variation in Florida specimens by having a smaller thorax (LP/WE, 0.71), sharper hind angles and prominent humeral denticles, legs darker with femora rufopiceous, and more elytral setae; four or five setae each on intervals three and five.

Etymology. - I take pleasure in naming this new species after C. H.

Table 7. Descriptive statistics for *S. lindrothi*, based on 9 males from northern and central Florida.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.76-4.32	4.006	0.275	0.122	4.58
LE	2.28-2.65	2.419	0.180	0.080	4.97
WH	0.78-0.90	0.840	0.053	0.024	4.20
WP	1.01-1.20	1.084	0.096	0.043	5.90
WE	1.18-1.38	1.258	0.095	0.042	5.01
B. Setae on left elytron.					
Interval 3	3 - 4	3.3			
Interval 5	3 - 4	3.3			
Interval 7	nil				
Total	6 - 8	6.7	1.3	0.6	1.30
C. Proportions.					
WF/WH	0.55-0.58	0.564	0.013	0.006	1.54
LP/WP	0.94-0.99	0.958	0.025	0.011	1.73
DP/LP	0.83-0.86	0.841	0.016	0.007	1.26
LP/WE	0.80-0.85	0.830	0.022	0.010	1.81
Ta/Ti	0.63-0.69	0.663	0.029	0.013	2.91
PS/LP	0.72-0.79	0.748	0.031	0.014	2.75

Lindroth, who first mentioned its existence in his 1961 review of the genus.

Distribution. - If all specimens listed here are conspecific, then the distribution of *S. lindrothi* is disjunct, in Florida and southern Middle America but not in Mexico (Fig. 121). Inclusion of the Middle American specimens is, however, tentative. I studied 31 specimens which I include under the name *S. lindrothi*, from the following localities.

UNITED STATES

FLORIDA (2; CAS, USNM): Bay Co., 7 mi. n. Southport (9; BMNH, DRWh, IRSB, MCZ, UASM); De Soto Co., Arcadia (1; CUNY); Hernando Co., Weeke Wachee Springs (2; CNC); Highlands Co., Lake Placid (1; CAS); Marion Co. (1; CAS); Orange Co., Winter Park (3; MCZ); Sumpter Co. (1; USNM); Volusia Co., Enterprise (1; MCZ, USNM).

GUATEMALA

ALTA VERAPAZ: Trece Aguas (1; USNM).

COSTA RICA

LIMON: Los Diamantes (1; FDAG).

Collecting notes. - I collected the Southport specimens in the sandy margins of a small, spring-fed pond, and most probably *S. lindrothi* is exclusively an inhabitant of sand. Specimens of this or related species are not likely to be found in Mexico or far west of Florida along the Gulf of Mexico, if, as I suspect, their distribution agrees with that of the so-called Carribean pines (Mirov, 1967). For the same reason, it would be no surprise to find specimens of the *lindrothi* group in the West Indies.

Taxonomic notes. - Specimens of this species differ sufficiently from those of *S. banningeri* in details of male genitalia that there is no reason to suspect them conspecific. Whether Middle American specimens are conspecific with *S. lindrothi*, or even with one another, is a question that cannot now be satisfactorily answered.

3.442 *Schizogenius banningeri* Kult

Schizogenius banningeri Kult 1950:148. *Type locality* Corumba, Mato Grosso, Brazil; type in Kult Collection, present location not known; type not seen.

Diagnostic combination. - I assign to this species all specimens of the *lindrothi* group seen from South America. They differ from specimens of *S. lindrothi* by details of male genitalia (median lobe, Fig. 118; one specimen examined), and form and sculpture of head and pronotum (Fig. 114). In particular, the median frontal sulcus is less sharply defined and is more strongly narrowed in front. As I have seen only seven specimens of the *lindrothi* group from South America, I am not certain they are all conspecific and I therefore do not give a detailed description here.

Variation. - I did not study these specimens closely for variation, but only the Mato Grosso specimen is as small as specimens reported by Kult.

Etymology. - Kult named this species in honor of M. Bänninger.

Distribution. - Just as limits of the species are unknown, so is the extent of its distribution. I studied the following seven specimens.

BRAZIL

MATO GROSSO: Cerceres (1; MGFT). PIAUI: Terezina (5; DRWh,MGFT).

VENEZUELA

CARACAS: Caracas (1; IRSB).

Collecting notes. - Specimens of this species were collected in January and December.

Taxonomic notes. - Though I have not seen type material, the specimen from Cerceres matches the original description and is from an appropriate locality. Whether or not the specimens from the other two localities are conspecific is not certain.

The Caracas specimen is labelled as the type of *S. sellatus* Putzeys (1866:228), from Caracas, Venezuela), but perhaps incorrectly. It does not have maculate elytra, though this may be the result of aging. More important, it does have a prominent median clypeal tooth, in contradiction to Putzeys' description. This is the specimen that Kult (1950) believed was the type of *S. sellatus*, and the one with which he compared his *S. banningeri*. The differences he noted in body size and convexity of elytral intervals are probably not important. If this Caracas specimen really is the type of *S. sellatus*, then the name *S. banningeri* may be a synonym. A re-examination of all material studied by Putzeys will be required to resolve this question. For now, I regard the Caracas specimen as one of *S. banningeri*, not as the type of *S. sellatus*.

3.45 The *quadripunctatus* group

Diagnostic combination. - Specimens of the only known species of this group have the following combination of characters: body moderately flattened; paramedian clypeal carinae extended to median tooth; antennal articles five to ten filiform; eyes normal; discal setae present on interval three only, intervals not carinate; and abdomen extensively microsculptured. Also: clypeal suture sharply impressed; clypeal field subtriangular, less than 1.5 apical width of median frontal sulcus; submentum without accessory setae; pronotum with distinct paramedian sulci, without paralateral carinae; front and middle tarsi broadened and with dense ventral pubescence, especially in males; sternum seven with paramedian ambulatory setae in males, not in females; paramedian carinae of sternum three curved at apices; pygidium not crenulate at apex in either sex; and endophallus with basal collar spines distinct.

Distribution. - One species of this group is known from southern Brazil and northern Argentina. I examined 200 specimens.

3.451 *Schizogenius quadripunctatus* Putzeys

Schizogenius quadripunctatus Putzeys 1866:225. *Type locality* Parana, Brazil; location of type male unknown. Whitehead 1966a:5.

Diagnostic combination. - Specimens of *S. quadripunctatus* are readily distinguished by large size, dark color, filiform antennae, microsculptured abdomen, and normally developed eyes.

Description. - Since *S. quadripunctatus* is the only known member of the *quadripunctatus* group, and since specimens may readily be identified from the original description, a detailed redescription is not required. Head and Pronotum, Fig. 115. Left elytron with four or five discal setae on interval three. Male genitalia, Fig. 119; three specimens examined.

Fig. 112-115. Head and pronotum, dorsal aspect. 112. *S. ocellatus* new species, Grutas das Areias, Brazil. 113. *S. lindrothi* new species, Southport, Florida. 114. *S. banningeri* Kult, Terezina, Brazil. 115. *S. quadripunctatus* Putzeys, Nova Teutonia, Brazil. Fig. 116-119. Male median lobe, lateral aspect. 116. *S. ocellatus* new species, Grutas das Areias, Brazil. 117. *S. lindrothi* new species, Southport, Florida. 118. *S. banningeri* Kult, Terezina, Brazil. 119. *S. quadripunctatus* Putzeys, Nova Teutonia, Brazil. Fig. 120. Male endophallus, *S. lindrothi* new species, Southport, Florida. Fig. 121. Known distribution of *S. lindrothi* new species.


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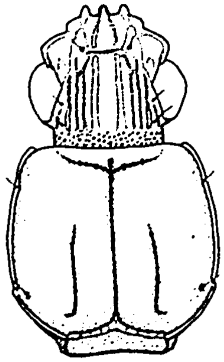
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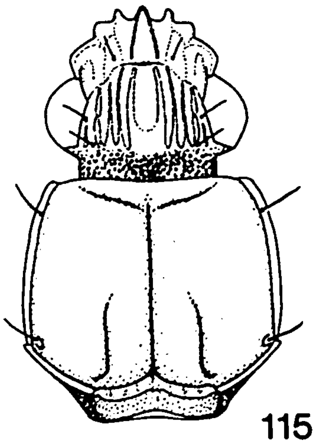
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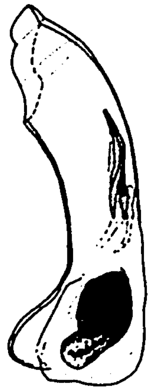
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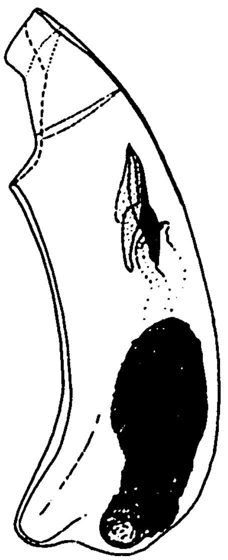
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Measurements and proportions. Largest specimen, female: TL, 6.20 mm; LE, 3.97 mm; WH, 1.20 mm; WP, 1.65 mm; WE, 2.06 mm; WF/WH, 0.59; LP/WP, 0.88; DP/LP, 0.87; LP/WE, 0.70; Ta/Ti, 0.69; PS/LP, 0.61. Smallest specimen, female: TL, 5.35 mm; LE, 3.37 mm; WH, 1.05 mm; WP, 1.39 mm; WE, 1.81 mm; WF/WH, 0.60; LP/WP, 0.91; DP/LP, 0.86; LP/WE, 0.70; Ta/Ti, 0.65; PS/LP, 0.59.

Etymology. - Latin, *quadri* = four, plus *punctum* = small hole, in reference to the normal number of setae on each elytron.

Distribution. - *S. quadripunctatus* is known from two localities in southern Brazil, including the type locality in Parana state, and from one locality in Argentina. I examined 199 specimens from Nova Teutonia, Santa Catarina, Brazil (DRWh, MCZ, MGFT), and one specimen from Pico, LaPampa, Argentina (MCZ).

Collecting notes. - Fritz Plaumann collected specimens of this species in January, February, March, April, August, September, and November, so adults probably are active throughout the year.

Taxonomic notes. - Although I saw no type material, specimens seen well match the original description of this distinctive species, and as the locality in Santa Catarina is near the type locality I have no doubt that I have associated the name correctly.

3.46 The *truquii* group

Diagnostic combination. - Members of this group are distinguished from all others in the genus by unusually elongated paramedian pronotal sulci, which extend nearly to the anterior transverse impression. They are further characterized by the following additional characters: body subcylindrical; paramedian clypeal carinae extended to median tooth, but more strongly raised in basal half; clypeal field triangular, its base over 1.5 apical width of median frontal sulcus; clypeal suture sharply impressed; antennal articles five to ten submoniliform, slightly elongate; anterior tarsi slender in both sexes; elytral disc with setae on intervals three, five, and seven; sternum seven with paramedian ambulatory setae in males only; paramedian carinae of sternum three usually curved at apices; pygidium not crenulate in either sex; and endophallus without enlarged spines.

Distribution. - The only known species in the group, *S. truquii* Putzeys, is probably restricted to the southern edge of the Trans-Volcanic Sierra of central Mexico, and northward along western slopes of the Sierra Madre Occidental to Sinaloa. I examined 42 specimens of the *truquii* group.

3.461 *Schizogenius truquii* Putzeys

Schizogenius truquii Putzeys 1866:224. *Type locality* Mexico, here restricted to Cuernavaca, Morelos; type in IRSB, female specimen labelled lectotype here so designated (!). Bates 1881:37.

Diagnostic combination. - *S. truquii* is the only species of the genus known to have paramedian pronotal sulci extended forward nearly to anterior transverse impression.

Description. - Body subcylindrical. Color dark rufopiceous, without metallic luster, appendages rufous.

Integument. Fine microsculpture on paramedian frontal sulci, genae, mouthparts, anterior surfaces of front tibiae and femora, middle legs except trochanters, hind tibiae and posterior surfaces of hind femora, and small patch near coxal depressions of sternum three.

Head. Fig. 122. Clypeal carinae extended to median tooth, more strongly raised in basal half; clypeal field triangular, narrow, wider at base than apex of median frontal sulcus. Clypeal suture sharply engraved. Frons with median field smooth, without median carina. Eye globose, finely and uniformly faceted. Neck sparsely, rather coarsely punctate. Gena rugose in front. Antennal articles five to ten distinctly elongate, submoniliform; article five 1.2-1.3 times as wide as long.

Pronotum. Fig. 122. Sides bisetose, hind angles prominent, base not rugose. Paramedian sulci elongated nearly to anterior transverse impression, impunctate, nearly straight, deep throughout, slightly hooked basally. Anterior transverse impression punctate. No evident paralateral carinae.

Legs. Front and middle tarsi slender, without dense ventral pubescence; hind tarsus slender, short. Paronychia conspicuous, nearly as long as tarsal claws. Front tibia evenly narrowed to base where much narrower than at base of antennal cleaner. Front femur not strongly constricted near apex.

Elytra. Six to eight setigerous punctures on interval three, five to eight on interval five, and three to five on interval seven. Striae deep and sharply engraved, distinctly punctate except at apex. Intervals one to eight broad, convex; interval eight carinate at apex; intervals three, five, and seven broadly joined at apices.

Abdomen. Sternum three with paramedian carinae usually suddenly curved outward at apices. Sternum seven with paramedian ambulatory setae in males only. Pygidium with apical margin entire in both sexes.

Male genitalia. Median lobe, Fig. 127; endophallus, Fig. 137, with poorly developed basal collar spines; five specimens examined.

Measurements and proportions. See Table 8.

Variation. - The smallest (LE, 2.15 mm) and largest (LE, 2.56 mm) specimens are females from La Garita, Jalisco. A female from Sinaloa has a flatter body (DP/LP, 0.77) and much smaller eyes (WF/WH, 0.67) than do other specimens.

Etymology. - *S. truquii* was named to honor E. Truqui, who collected the specimens which Putzeys first reported as this species.

Distribution. - Specimens of *S. truquii* have been found in central and western Mexico at moderate elevations, from about 1500' to 4000' (Fig. 145). I studied 42 specimens from the following localities.

MEXICO

JALISCO: San Diego Cocula (1; USNM), 0.4 mi. w. Cocula (2; DRWh), 8.5 mi. n. Juchitlan (2; MCZ), La Garita (32; BMNH, CAS, CNC, IRSB, UASM). MICHOACAN: 8.5 mi. n. Nueva Italia (1; USNM). MORELOS: Cuernavaca (2; BMNH). SINALOA: 21 mi. e. Villa Union (1; CNC).

Collecting notes. - At La Garita, the only locality at which a long series of this species was taken, I found no other species of *Schizogenius*. I noted nothing peculiar about the locality, and other carabid beetles taken there are found abundantly elsewhere along similar gravel streams. At other localities in Jalisco and Michoacan where I found specimens of *S. truquii*, the *Schizogenius* fauna included representatives of two or three additional species. Specimens from these states include nearly

Table 8. Descriptive statistics for *S. truquii*, based on 20 males from La Garita, Jalisco.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.67-4.06	3.854	0.188	0.056	3.26
LE	2.25-2.48	2.347	0.125	0.037	3.54
WH	0.75-0.85	0.805	0.039	0.012	3.26
WP	0.93-1.08	1.000	0.063	0.019	4.19
WE	1.15-1.27	1.204	0.060	0.018	3.40
B. Setae on left elytron.					
Interval 3	6 - 8	6.4			
Interval 5	5 - 8	6.6			
Interval 7	3 - 5	4.2			
Total	14 -20	17.3	2.0	0.6	7.74
C. Proportions.					
WF/WH	0.60-0.64	0.621	0.017	0.006	2.22
LP/WP	0.96-1.02	0.988	0.026	0.008	1.75
DP/LP	0.78-0.85	0.807	0.024	0.007	1.97
LP/WE	0.79-0.86	0.819	0.028	0.008	2.28
Ta/Ti	0.62-0.73	0.672	0.052	0.015	5.12
PS/LP	0.85-0.90	0.882	0.022	0.007	1.66

twice as many males as females, possibly because of the season; all were collected in January and March, and none of the collecting localities were revisited at a later season. The Sinaloa specimen was taken in July, at lights.

Taxonomic notes. - Putzeys (1866) described the body as strongly convex, and the elytron as having 12 setae each on intervals three, five, and seven. These observations are clearly erroneous. The lectotype specimen agrees with my description, and is undoubtedly one of the specimens studied by Putzeys; it has a printed label, "Truqui Mexique," as well as Putzeys' handwritten green determination label.

3.47 The *brevisetosus* group

Diagnostic combination. - Specimens of this group are distinguished by the following combination of characters: elytron with 35 or more short discal setae; abdomen without extensive microsculpture; body depressed; color castaneous; size large, LE over 2.70 mm in all specimens seen. Also: paramedian clypeal carinae extended to median tooth, more strongly raised in basal half; clypeal field triangular, its base under 1.5 apical width of median frontal sulcus; clypeal suture sharply impressed; antennal articles five to ten filiform; front and middle tarsi broadened and with dense ventral pubescence, especially in males; discal setae present on intervals three, five, and seven; sternum seven with paramedian ambulatory setae in males, not in females; paramedian carinae curved at apices; pygidium not crenulate in either sex; and endophallus with basal collar spines distinct.

Distribution. - *S. brevisetosus* is known from Coahuila, New Mexico, and Texas. The group is probably most closely allied to the *pluripunctatus* group, but differs in various ways, notably by short elytral setae. The two groups are allopatric but proximate in geographic distribution. I examined 42 specimens of the *brevisetosus* group.

3.471 *Schizogenius brevisetosus* new species

Type material. - Holotype male and allotype female labelled "Sanderson, TEX. April 27, 1959 Becker & Howden" (CNC). An additional 32 specimens collected at various times and places in Texas are paratypes (CAS, CNC, CUNY, DRWh, LACM, MCZ, UASM, USNM).

Diagnostic combination. - Specimens of this distinctive species are readily distinguished from all others in the genus by the combination of large size, pale coloration, deplanate body, numerous short discal setae on the elytra, and lack of extensive microsculpture on the abdomen.

Description. - Body deplanate. Color dark castaneous, without definite aeneous luster, appendages paler.

Integument. Conspicuous microsculpture on paramedian sulci of frons, genae, mouthparts, front tibiae and anterior surfaces of front femora, middle legs except trochanters, hind tibiae and posterior surfaces of hind femora, elytral epipleura in apical two-thirds and at extreme base, and coxal depressions of sternum three.

Head. Fig. 123. Labrum weakly biemarginate. Paramedian carinae of clypeus straight, extended to median tooth, strongly raised in basal half; median field triangular, narrow, slightly wider at base than apex of median frontal sulcus. Clypeal suture sharply defined. Eye globose, finely and uniformly faceted. Neck densely, coarsely punctate. Gena coarsely punctate, rugose in front. Antennal articles four to ten elongate, filiform; article five 1.7 times as long as wide.

Pronotum. Fig. 123. Sides bisetose, hind angles sharp and prominent, base not rugose. Paramedian sulci elongate, impunctate, nearly straight, deep throughout, slightly hooked basally. Anterior transverse impression finely punctate.

Legs. Front and middle tarsi slightly but distinctly dilated and pubescent ventrally; hind tarsus slender, quite short. Paronychia conspicuous, more than half length of tarsal claws. Front tibia narrowed evenly to base. Front femur not strongly constricted near apex.

Elytra. Left elytron with about 13-20 setae on interval three, 12-18 on interval five, and 10-14 on interval seven. Striae deep, sharply engraved, finely but distinctly punctate nearly to apex. Intervals one to seven broad and flat, interval eight carinate at apex; apices of intervals three, five, and seven broadly joined. Humeral denticles sharp and prominent.

Abdomen. Sternum three with paramedian carinae curved outward at apices. Sternum seven with paramedian ambulatory setae in male only. Pygidium with apical margin entire in both sexes.

Male genitalia. Median lobe, Fig. 128; endophallus (Fig. 138) with well developed basal collar spines. Three specimens examined.

Measurements and proportions. See Table 9. Of holotype: TL, 4.87 mm; LE, 3.05 mm; WH, 0.95 mm; WP, 1.26 mm; WE, 1.62 mm; WF/WH, 0.64; LP/WP, 0.95; DP/LP, 0.79; LP/WE, 0.74; Ta/Ti, 0.59; PS/LP, 0.72. Of

Table 9. Descriptive statistics for *S. brevisetosus*, based on 16 males from Texas.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	4.40-4.97	4.699	0.187	0.062	2.65
LE	2.79-3.12	2.949	0.118	0.039	2.66
WH	0.82-0.97	0.913	0.051	0.017	3.75
WP	1.11-1.32	1.220	0.064	0.021	3.48
WE	1.46-1.63	1.549	0.068	0.023	2.92
B. Setae on left elytron.					
Interval 3	13-20	15.6			
Interval 5	12-18	14.9			
Interval 7	10-14	11.9			
Total	35-50	42.4	5.3	1.8	8.35
C. Proportions.					
WF/WH	0.63-0.67	0.650	0.017	0.006	1.77
LP/WP	0.90-0.95	0.929	0.022	0.007	1.54
DP/LP	0.76-0.80	0.791	0.017	0.006	1.42
LP/WE	0.69-0.76	0.729	0.028	0.009	2.52
Ta/Ti	0.57-0.61	0.591	0.021	0.007	2.38
PS/LP	0.67-0.74	0.694	0.029	0.010	2.83

allotype: TL, 4.63 mm; LE, 2.98 mm; WH, 0.85 mm; WP, 1.17 mm; WE, 1.17 mm; WF/WH, 0.66; LP/WP, 0.92; DP/LP, 0.79; LP/WE, 0.72; Ta/Ti, 0.62; PS/LP, 0.68.

Variation. - Available material is too limited to permit any statement about geographic variation in this species. Males average about 0.2 mm smaller than females. The largest (LE, 3.33 mm) and smallest (LE, 2.83 mm) females are from Hope, New Mexico, and Limpia Canyon, Texas, respectively; the largest (LE, 3.05 mm) and smallest (LE, 2.74 mm) males are both from Sanderson, Texas.

Etymology. - Latin, *brevis* = short, plus *setosus* = bristly, in reference to the short discal elytral setae.

Distribution. - Specimens of *S. brevisetosus* have been collected from eastern New Mexico, east to central Texas, and south to Coahuila, from the Colorado River in the north to the Rio Grande drainage system in the south (Fig. 146). I examined 42 specimens from the following localities.

UNITED STATES

NEW MEXICO: Eddy Co., Hope (2; UKSM). TEXAS (1; USNM): Blanco Co., Cypress Mills (1; USNM); Brewster Co. (1; MCZ), Alpine (3; CUNY, MCZ); Jeff Davis Co., Davis Mountains (3; CAS), Limpia Canyon (6; DRWh, UASM), Barrel Springs Creek (1; DRWh), Fort Davis (4; CNC); Kerr Co., Kerrville (4; CNC); Terrell Co., Lozier Canyon (3; MCZ), Sanderson (6; CNC); Uvalde Co., Garner State Park (2; LACM).

MEXICO

COAHUILA: La Gloria, s. of Monclova (3; AMNH).

Collecting notes. - Specimens of this species have been collected from April to August, frequently at light, apparently not always near streams (e.g., Lozier Canyon and La Gloria). I collected two specimens in typical gravel streams near Fort Davis, Texas, along with specimens of *S. scopaeus*.

3.48 The *pluripunctatus* group

Diagnostic combination. - The most obvious diagnostic feature of members of this North and Middle American group is unusual length of discal setae on elytron; these setae generally are about 1.2 times as long as the maximum width of interval two, or longer. Specimens of some South American species also have long setae; from these, members of the *pluripunctatus* group are distinguished by the following additional characters in combination: setae present on intervals three, five, and seven of elytra; pronotum without marginal carinae; mentum without accessory setae; and pygidium of female not crenulate. Most included forms are densely setose, with more than ten setae on elytral interval three. Additional characters of members of the group are: form cylindrical to subcylindrical; paramedian clypeal carinae extended to median tooth, sometimes strongly raised in basal half; clypeal field triangular, its base under 1.5 apical width of median frontal sulcus; clypeal suture sharply impressed; antennal articles five to ten filiform; anterior and middle tarsi slightly to strongly broadened, especially in males; sternum seven with paramedian ambulatory setae in males, sometimes in females; paramedian carinae of sternum three curved at apices; abdomen without extensive microsculpture; endophallus with distinct basal collar spines. The group contains the only known species in the genus with more than two pairs of lateral setae on the pronotum.

Distribution. - This group includes several similar, allopatric forms, in two geographic subgroups. One subgroup ranges from northern California south to southern Baja California. The second subgroup ranges from southern Arizona and New Mexico, south to Guatemala, and north in the east to Nuevo Leon and Tamaulipas. I examined 575 specimens of the *pluripunctatus* group.

Taxonomic notes. - The two geographic subgroups could be termed "superspecies," and I relied in part on statistical analyses to sort out taxonomic relationships within them. The Californian subgroup, with two allopatric forms here treated as subspecies, is distinguished by more flattened body form and short deflexed apex of male median lobe. The second subgroup, with four allopatric forms here recognized as species, is distinguished by more cylindrical body form and relatively longer deflexed apex of male median lobe.

3.481 *Schizogenius seticollis* Fall

Diagnostic combination. - Specimens of this species, one of two species in the genus characterized by accessory marginal setae on the pronotum, differ from those of *S. plurisetosus* by form of male median lobe. *S. plurisetosus* is intermediate between the two subspecies of *S. seticollis* in numbers of elytral setae, but has fewer pronotal setae and normally only one seta in recessed pits at pronotal hind angles rather than two or three. The form of the median lobe, with deflexed apical portion proportionately short, is diagnostic of specimens of *S. seticollis* within the *pluripunctatus* group.

3.4811 *Schizogenius seticollis seticollis* new combination

Schizogenius seticollis Fall 1901:209. *Type locality* Pomona, California; type in MCZ; specimen labelled MCZ type 23859 here designated lectotype (!). Lindroth 1961:165.

Diagnostic combination. - Specimens of this subspecies are distinguished by fewer than 60 setae per elytron, and most specimens have fewer marginal pronotal setae.

Description. - Body subcylindrical. Color piceous; mandibles, mentum, front coxae, trochanters, tibiae, femoral apices, and in some specimens margin and apex of elytron rufopiceous; antennae, at least at base, rufous; and labial palpi, maxillae, and tarsi testaceous; no pronounced metallic or aeneous luster.

Integument. Fine but conspicuous microsculpture on mouthparts, genae, front legs except posterior surfaces of femora and trochanters, middle legs except anterior surfaces of trochanters, hind tibiae and posterior surfaces of hind femora, extreme bases of epipleura, and small areas in coxal depressions of sternum three. Microsculpture irregular and indistinct in paramedian frontal sulci.

Head. Fig. 124. Clypeal carinae straight, extended to median tooth, strongly elevated in basal half; median field triangular, narrow, no wider at base than apex of median frontal sulcus. Clypeal suture sharply defined. Eye prominent, globose, finely and uniformly faceted. Neck densely, coarsely punctate. Gena coarsely punctate, rugose in front. Antennal articles four to ten elongate, filiform, article five about 1.6 times as long as wide.

Pronotum. Fig. 124. Sides plurisetose, generally with seven to 11 setae on each side, two or three setae in pits recessed from hind angles; hind angles obsolete; base not rugose. Paramedian sulci rather short, impunctate, nearly straight, deep throughout, slightly hooked basally. Anterior transverse impression finely punctate.

Legs. Front and middle tarsi dilated and pubescent ventrally in both sexes, slightly more so in males; hind tarsus slender, rather short. Paronychia conspicuous, more than half length of tarsal claws. Front tibia narrowed evenly to base. Front femur not strongly constricted near apex.

Elytra. Discal setae about 1.2 times as long as maximum width of interval two. Among 20 specimens examined, 10-17 setae on interval three, 12-19 on interval five, and 11-23 on interval seven; most setae adjacent to corresponding inner striae, but up to 25% irregular, slightly biseriate. Striae deep and sharply engraved, finely to indistinctly punctate in basal half or two-thirds. Intervals one to seven broad and slightly convex, interval eight carinate at apex; apices of intervals three, five, and seven broadly joined. Humeral denticles small, sharp.

Abdomen. Sternum three with paramedian carinae straight or curved outward at apices. Sternum seven with paramedian ambulatory setae in male only. Pygidium with apical margin entire in both sexes.

Male genitalia. Median lobe (Fig. 129) elongate, narrow; apex deflected at weak angle, relatively short; endophallus with well developed basal collar spines (Fig. 139); four specimens examined.

Measurements and proportions. See Table 10.

Variation. - I found little noteworthy variation in this subspecies. In five selected samples (samples one to five), I found little significant clinal variation in size (Fig. 148, Table 11); slightly increased numbers of discal elytral setae to the south (Fig. 149, Table 12); slightly increased eye size to the south (Fig. 150, Table 13); and slightly narrowed pronotum to the south (Fig. 151, Table 14).

Etymology. - Latin, *seta* = bristle, plus *collis* = hill, in reference to the marginal setae of the pronotum.

Distribution. - Specimens of *S. seticollis seticollis* have been collected in central and western California, from Shasta County in the north to San Diego County in the south (Fig. 147). I examined 227 specimens from the following localities.

UNITED STATES

CALIFORNIA (9; ANSP, CAS, USNM): Colorado Desert (1; MCZ); Alameda Co., Berkeley (1; CUNY), 17.5 mi. s. Livermore (1; CAS); Calaveras Co., Mokelumne Hill (9; CAS); Colusa Co., Cooks Springs (1; CAS); El Dorado Co., Latrobe (2; CAS); Fresno Co., Camp Greeley (5; CAS, CNC, KSUM), Le Ferre Creek (2; CAS), Trimmer (1; CAS), 3.5 mi. e. Trimmer (8; DRWh, TLEr, UASM), 11.6 mi. s. Tollhouse (3; TLEr); Glenn Co., Elk Creek (1; CAS); Humboldt Co., Garberville (1; CAS); Kings Co., Stratford (1; CAS); Lake Co. (2; CAS), Kelsey Creek (2; CAS), Middle Creek (2; CAS); Los Angeles Co. (6; CAS, USNM), Azuza (1; CAS), 4 1/2 mi. ne. Claremont (1; INHS), La Canada (1; CAS), Los Angeles (1; INHS), Palmdale (1; CAS), Pasadena (5;

Table 10. Descriptive statistics for *S. seticollis seticollis*, based on 11 males from Los Angeles County, California.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.73-4.68	4.381	0.404	0.162	6.14
LE	2.29-2.86	2.686	0.238	0.096	5.91
WH	0.78-0.95	0.896	0.080	0.032	5.97
WP	1.00-1.26	1.187	0.111	0.045	6.23
WE	1.22-1.57	1.451	0.136	0.055	6.24
B. Setae on left elytron.					
Interval 3	12-17	13.8			
Interval 5	13-19	16.2			
Interval 7	12-23	17.3			
Total	40-58	47.3	8.6	3.5	12.11
C. Proportions.					
WF/WH	0.60-0.65	0.625	0.020	0.008	2.18
LP/WP	0.87-0.94	0.919	0.029	0.012	2.09
DP/LP	0.81-0.87	0.838	0.025	0.010	1.98
LP/WE	0.72-0.78	0.752	0.029	0.012	2.58
Ta/Ti	0.61-0.74	0.659	0.059	0.024	5.96
PS/LP	0.62-0.68	0.643	0.029	0.012	3.04

CAS), Pomona (3; MCZ, RUNB), Pomona Mountains (5; CUNY, MCZ), San Gabriel Mountains (2; TCBa), Saugus (1; CAS); Jujunga (4; MCZ); Mendocino Co. (5; JNeg), Dry Creek (13; CAS); Monterrey Co., Arroyo Seco Camp (1; TLEr), Bradley (2; MCZ, UCB); Napa Co. (1; CNHM), Monticello (1; UCD), Pope Creek (2; CAS), Rutherford (3; TLEr), Santa Helena (2; MCZ, CAS); Riverside Co., Riverside (3; CAS, USNM), San Jacinto Mountains (1; CAS); San Benito Co., Pinnacles National Monument (1; CAS), San Benito River (2; CAS); San Bernadino Co., 0.9 mi. ne. Cedar Springs (1; LBSC), Lytle Creek (4; MCZ), San Bernadino (1; CAS), San Bernadino Mountains (3; MGFT); San Diego Co., San Diego (5; MCZ, CAS), Warners (3; USKM); San Joaquin Co., Manteca (4; CAS); San Luis Obispo Co., Paso Robles (3; CAS, UKSM), Santa Margarita (4; CAS); San Mateo Co., Foster (1; CAS); Santa Barbara Co. (1; CAS), Santa Inez Mountains (3; CAS); Santa Clara Co., Gilroy Hot Springs (10; DJLa, TLEr), Mount Hamilton (5; CAS, TLEr); Santa Cruz Co. (1; CNHM); Shasta Co., Redding (15; CAS), 10 mi. ne. Redding (1; DHKa); Sonoma Co. (1; AMNH), Duncan Mills (2; CAS), Healdsburg (3; CAS), 2. mi. e. Healdsburg (1; CAS), Russian River (8; CAS, MCZ), Santa Rosa (2; MCZ), 2.5 mi. w. Skaggs Springs (8; CAS), Sobre Vista (2; CAS), Sylvania (3; CAS, MCZ); Stanislaus Co., 22 mi. w. Patterson (4; CAS); Tehama Co. (2; CAS); Tulare Co., Kaweah (1; CAS), Ventura Co., 9 mi. sw. Stauffer (1; UCB); Yolo Co., Davis (2; UCD), Rumsey (1; UCD).

Collecting notes. - Specimens have been collected from March through October, most of them along gravel streams. Some were taken at lights, indirect evidence that adults can fly. I have not collected specimens of this subspecies.

Taxonomic notes. - See discussion for *S. seticollis vandykei*.

Table 11. Variation in body size (LE, in mm) in selected samples of the *seticollis* subgroup; see Fig. 148.

Sample	N	Males	Range	Mean	1.5SD	2SE	CV(%)
S. s. seticollis.							
1	16	8	2.72-3.19	2.935	0.204	0.068	4.64
2	16	8	2.65-3.26	2.942	0.272	0.091	6.17
3	10	5	2.63-3.35	3.095	0.315	0.133	6.79
4	18	9	2.50-3.18	2.827	0.314	0.099	7.41
5	22	11	2.29-2.96	2.747	0.231	0.066	5.61
S. s. vandykei.							
6	10	5	2.54-3.34	2.886	0.406	0.171	9.39

Table 12. Variation in numbers of discal setae on left elytron in selected samples of the *seticollis* subgroup; see Fig. 149.

Sample	N	Males	Range	Mean	1.5SD	2SE	CV(%)
S. s. seticollis.							
1	16	8	35-49	39.9	5.4	1.8	9.05
2	16	8	33-46	37.4	5.9	2.0	10.47
3	10	5	42-51	46.3	4.8	2.0	6.98
4	18	9	33-53	41.2	7.7	2.4	12.39
5	22	11	40-53	46.7	7.6	2.2	10.91
S. s. vandykei.							
6	10	5	71-104	85.3	16.4	6.9	12.85

Table 13. Variation in eye size (WF/WH) in selected samples of the *seticollis* subgroup; see Fig. 150.

Sample	N	Males	Range	Mean	1.5SD	2SE	CV(%)
S. s. seticollis.							
1	16	8	0.62-0.66	0.631	0.017	0.006	1.81
2	16	8	0.62-0.66	0.639	0.018	0.006	1.88
3	10	5	0.62-0.65	0.633	0.017	0.007	1.83
4	18	9	0.59-0.65	0.629	0.023	0.007	2.41
5	22	11	0.60-0.65	0.626	0.018	0.005	1.89
S. s. vandykei.							
6	10	5	0.61-0.66	0.640	0.022	0.009	2.33

Table 14. Variation in pronotal form (LP/WP) in selected samples of the *seticollis* subgroup; see Fig. 151.

Sample	N	Males	Range	Mean	1.5SD	2SE	CV(%)
S. s. seticollis.							
1	16	8	0.88-0.94	0.914	0.028	0.009	2.07
2	16	8	0.90-0.95	0.918	0.023	0.008	1.66
3	10	5	0.89-0.95	0.917	0.029	0.012	2.12
4	18	9	0.88-0.96	0.924	0.030	0.009	2.17
5	22	11	0.87-0.94	0.920	0.026	0.007	1.91
S. s. vandykei.							
6	10	5	0.89-0.98	0.938	0.039	0.016	2.74

3.4812 *Schizogenius seticollis vandykei* new subspecies

Type material. - Holotype male and allotype female labelled "MEX. B.Cal. 3 mi.NW of Miraflores 19-I-1959" and "Canon San Bernadino. Boca de la Sierra" and "H. B. Leech Collector" (CAS). Nine additional specimens from various localities in southern Baja California are paratypes (CAS, DRWh, UASM).

Diagnostic combination. - All known specimens of this subspecies have more than 60 discal setae per elytron, and thus differ from specimens of *S. seticollis seticollis*.

Description. - As in *S. s. seticollis* except as follows. Base of frons (Fig. 125) more strongly calloused. Pronotum with 10-14 setae on each side. Elytron with 18-36 setae on interval three, 27-35 on interval five, and 22-37 on interval seven; arrangement of setae on intervals three, five, and seven strongly biseriate; discal setae about 1.5 times as long as the maximum width of interval two. Male genitalia, (Fig. 130) not distinctive, two specimens examined.

Measurements and proportions. See Table 15. Of holotype: TL, 4.63 mm; LE, 2.83 mm; WH, 0.92 mm; WP, 1.18 mm; WE, 1.48 mm; WF/WH, 0.61; LP/WP, 0.98; DP/LP, 0.82; LP/WE, 0.78; Ta/Ti, 0.66; PS/LP, 0.65. Of allotype: TL, 4.81 mm; LE, 2.96 mm; WH, 0.95 mm; WP, 1.28 mm; WE, 1.57 mm; WF/WH, 0.65; LP/WP, 0.93; DP/LP, 0.82; LP/WE, 0.76; Ta/Ti, 0.65; PS/LP, 0.65.

Variation. - See Tables 11-14.

Etymology. - I dedicate this subspecies to E. C. Van Dyke, who provided much of our knowledge about the Coleoptera of the southwestern

Table 15. Descriptive statistics for *S. seticollis vandykei*, based on 6 males and 5 females from southern Baja California.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	4.14-5.40	4.625	0.666	0.268	9.60
LE	2.54-3.34	2.856	0.414	0.166	9.67
WH	0.83-1.05	0.915	0.117	0.047	8.52
WP	1.06-1.38	1.199	0.179	0.072	9.97
WE	1.34-1.78	1.505	0.208	0.083	9.20
B. Setae on left elytron.					
Interval 3	18-36	24.0			
Interval 5	27-35	30.4			
Interval 7	22-37	30.0			
Total	71-104	84.4	16.3	6.5	12.86
C. Proportions.					
WF/WH	0.61-0.66	0.639	0.022	0.009	2.25
LP/WP	0.89-0.98	0.940	0.038	0.015	2.69
DP/LP	0.82-0.90	0.845	0.041	0.017	3.27
LP/WE	0.70-0.79	0.747	0.040	0.016	3.59
Ta/Ti	0.61-0.69	0.659	0.035	0.014	3.49
PS/LP	0.61-0.67	0.637	0.028	0.011	2.90

United States.

Distribution. - Specimens of this subspecies are known only from a few localities in southern Baja California (Fig. 147). I studied 11 specimens from the following localities.

MEXICO

BAJA CALIFORNIA: Arroyo Saltito near Las Cruces (5; CAS, DRWh, UASM), 20 mi. n. Comondu (1; CAS), Hamilton Ranch (1; CAS), 3 mi. nw. Miraflores (2; CAS).

Collecting notes. - Adults of *S. seticollis vandykei* are probably active throughout the year, as I have records for January, July, and August. I know nothing about their habits, but suspect they may be found along intermittent streams. Aside from *S. auripennis, S. falli*, and *S. pygmaeus*, the subspecies is the only member of the genus known from Baja California.

Taxonomic notes. - I recognize *S. seticollis vandykei* as a distinct subspecies because it clearly is closely related to *S. seticollis seticollis*, there is no evidence of reproductive isolation between them, and all known specimens of each subspecies are distinguished by numbers of discal elytral setae. I suspect that the ranges of the two subspecies are disjunct in central and northern Baja California, or at least they are joined only by steeply stepped character clines.

As shown in Tables 11-14 and Fig. 148-151, sample six, *S. seticollis vandykei* does not differ significantly in body size from samples one to five, *S. seticollis seticollis*; it is more different from southern than northern samples of *S. s. seticollis* in eye size, but not significantly different from any of them; and the pronotum is narrower than in any of the *S. s. seticollis* but not statistically significantly different from the southernmost samples. In the number of discal elytral setae, however, despite a slightly greater similarity of *S. s. vandykei* to southern rather than northern samples of *S. s. seticollis*, the differences are large, indeed are taxonomically significant at 1.5 standard deviations from means. Numbers of discal elytral setae are, in general, directly correlated with body size. From Tables 11 and 12, ratios formed of the mean values for number of setae to elytral length are, for samples one to six, respectively: 13.6, 12.7, 15.0, 14.6, 17.0, and 29.6 setae per mm. A definite increase from north to south is evident from samples one to five, but a large hiatus still exists between samples five and six. I conclude from these observations that reproductive isolation between the two subspecies is indeterminate, but that they are at least isolated geographically. Collections from central and northern Baja California are needed to better define geographic and reproductive relationships.

3.482 *Schizogenius plurisetosus* new species

Type material. - Holotype male and allotype female labelled "MEX. Tamaulipas Rio Purificacion nr. El Barretal Rte.85 800' X. 19. 65" and George E. Ball D. R. Whitehead collectors" (MCZ). An additional 15 specimens from various localities in Nuevo Leon and Tamaulipas are paratypes (BMNH, CAS, CNC, DRWh, IRSB, UASM, USNM).

Diagnostic combination. - Specimens of this species are readily distinguished from specimens of *S. seticollis* by having fewer accessory marginal pronotal setae, and only one seta in pits near hind angles.

Also: apical portion of male median lobe proportionately longer and more sharply deflexed; front and middle tarsi less expanded; and range, in northeastern Mexico, sharply disjunct.

Description. - As in *S. seticollis seticollis*, except as follows. Legs paler, femora uniformly rufopiceous. Form and sculpture of head and pronotum, Fig. 126; genae less coarsely sculptured; pronotum with five to seven setae on each side, usually with only one in a pit recessed from the hind angle; basal impression distinctly punctate; anterior transverse impression nearly impunctate. Elytron with 18-24 setae on interval three, 17-30 on interval five, and 17-22 on interval seven; setae moderately biseriate; discal setae about 1.5 times as long as the maximum width of interval two; striae indistinctly punctate. Front and middle tarsi much narrower. Male genitalia with apex of median lobe (Fig. 131) sharply deflexed, proportionately long; endophallus, Fig. 140; four specimens examined.

Measurements and proportions. See Table 16. Of holotype: TL, 3.98 mm; LE, 2.43 mm; WH, 0.80 mm; WP, 1.06 mm; WE, 1.24 mm; WF/WH, 0.61; LP/WP, 0.93; DP/LP, 0.81; LP/WE, 0.80; Ta/Ti, 0.60; PS/LP, 0.63. Of allotype: TL, 4.25 mm; LE, 2.65 mm; WH, 0.83 mm; WP, 1.11 mm; WE, 1.35 mm; WF/WH, 0.62; LP/WP, 0.92; DP/LP, 0.83; LP/WE, 0.76; Ta/Ti, 0.66; PS/LP, 0.66.

Variation. - See Table 16. Two specimens have two setae in a recessed pit on one side of the pronotum; all others have only one seta per pit.

Etymology. - Latin, *pluralis* = more than one, plus *setosus* = bristly, in reference to the large numbers of setae which characterize members of

Table 16. Descriptive statistics for *S. plurisetosus*, based on 7 males from Nuevo Leon and Tamaulipas.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.78-4.69	4.134	-	-	-
LE	2.33-2.92	2.546	-	-	-
WH	0.76-0.91	0.824	-	-	-
WP	0.98-1.25	1.086	-	-	-
WE	1.18-1.48	1.293	-	-	-
B. Setae on left elytron.					
Interval 3	18-24	21.0			
Interval 5	17-30	21.7			
Interval 7	17-23	20.7			
Total	52-74	63.4			
C. Proportions.					
WF/WH	0.60-0.64	0.613	-	-	-
LP/WP	0.92-0.95	0.936	-	-	-
DP/LP	0.80-0.82	0.810	-	-	-
LP/WE	0.77-0.80	0.784	-	-	-
Ta/Ti	0.59-0.69	0.633	-	-	-
PS/LP	0.63-0.70	0.661	-	-	-

this species.

Distribution. - Specimens of this species have been collected only in Nuevo Leon and Tamaulipas, from the Rio Salinas, a tributary of the Rio Grande, south to the Rio Corona, a tributary of the Rio Soto la Marina (Fig. 147). The species is not known to range into the United States, but may do so. I studied 17 specimens, all collected by G. E. Ball or me during 1964 to 1966, from the following localities.

MEXICO

NUEVO LEON: Cienega de Flores (5; UASM), Linares (2; DRWh). TAMAULIPAS: El Barretal (6; CAS, CNC, MCZ), 15.2 mi. n. Ciudad Victoria (1; BMNH), 21.3 mi. n. Ciudad Victoria (3; IRSB, USNM).

Collecting notes. - Specimens of *S. plurisetosus* were collected in riparian gravel bars, in July, September, and October, at elevations ranging from 500 to 1200'. I noted nothing remarkable about habits, but at all stations there were fewer specimens of this species than of others in the genus.

Taxonomic notes. - Despite accessory pronotal setae, this species is not closely related to *S. seticollis*, as judged from form of male genitalia. It is most closely related to the geographically proximate *S. multisetosus*, with similar male genitalia. Even so, the form of the apex is slightly but apparently constantly more broadly rounded. This detail, together with the apparently constant accessory pronotal setae, indicates that *S. plurisetosus* and *S. multisetosus* are reproductively isolated. Statistical comparisons between them confirm this distinction. Thus, as shown in Tables 18-23 and Fig. 152-157,samples one to four, there is no important difference in body size, eye size, or relative pronotal size, but numbers of discal elytral setae are much greater in sample one, *S. plurisetosus* than in any sample (see Fig. 153) of *S. multisetosus*. Also, the northernmost sample of *S. multisetosus* differs by having statistically significantly broader pronota and statistically significantly longer paramedian pronotal sulci.

3.483 *Schizogenius multisetosus* Bates

Schizogenius multisetosus Bates 1891:233. *Type locality* Huitzo, Oaxaca; type in BMNH, male specimen labelled holotype here designated lectotype (!).

Diagnostic combination. - The combination of two pairs of marginal setae on the pronotum, sharply deflexed apical portion of the median lobe, and lack of paramedian ambulatory setae in females, distinguishes this species from other members of the *pluripunctatus* group. Also, numbers of setae on the elytral disc, in specimens examined, range from 37 to 56.

Description. - As in *S. seticollis seticollis* except: legs paler, femora uniformly rufous to rufopiceous, tibiae paler; abdomen often paler toward apex. Form and sculpture of head and pronotum as in *S. plurisetosus*, Fig. 126, except sides of pronotum bisetose and basal transverse impression less distinctly punctate. In specimens studied, elytron with 12-18 setae on interval three, 12-21 or interval five, and 12-20 on interval seven; setae mostly adjacent to corresponding inner striae, not markedly biseriate. Male genitalia with median lobe (Fig. 132-134) with apical portion sharply deflexed, proportionately long; endophallus, Fig. 141-142; 24 specimens examined.

Measurements and proportions. See Table 17.

Variation. - Samples of sufficient size for statistical analysis were available from only three localities. Data on variation in six characteristics in these samples, numbered two to four as in Fig. 152-157, are given in Tables 19-23. All three samples differ significantly from one another in body size (Fig. 152, Table 18). Other statistically significant differences are: sample two, shorter paramedian pronotal sulci (Fig. 157, Table 23); sample three, proportionately smaller thorax (Fig. 156, Table 22); and sample four, broader pronotum (Fig. 155, Table 21). These samples therefore represent populations which are equally well isolated from one another geographically, so no analysis of clinal relationships is feasible. The median lobe, especially at base, varies in form; most specimens from the Rio Moctezuma at 300' have a reduced basal lobe, and those from the Rio Balsas usually have a less sharply angulate apical deflection. A male from Hidalgo, collected at 5300' in the Rio Moctezuma drainage system, is in most ways similar to the Rio Balsas specimens but has the large thorax characteristic of Tamazunchale specimens; it may represent a truly intermediate population.

Etymology. - Latin, *multus* = most, plus *setosus* = setose, in reference to the numerous discal setae of the elytra.

Distribution. - Specimens of *S. multisetosus* have been collected at altitudes ranging from near sea level in the north to at least 5300'. They are from four river systems in central Mexico (Fig. 147): the Rios Moctezuma and Papaloapan on the Atlantic slopes, and the Rios Balsas and Atoyac on the Pacific. I studied 73 specimens from the following localities.

Table 17. Descriptive statistics for *S. multisetosus*, based on 14 males from 72.5 miles south of Valle Nacional, Oaxaca.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.84-4.44	4.093	0.315	0.112	5.13
LE	2.34-2.78	2.546	0.201	0.072	5.27
WH	0.75-0.90	0.816	0.068	0.024	5.51
WP	0.95-1.15	1.049	0.096	0.034	6.07
WE	1.20-1.45	1.304	0.112	0.040	5.72
B. Setae on left elytron.					
Interval 3	12-17	14.5			
Interval 5	15-20	17.1			
Interval 7	12-18	15.9			
Total	40-54	47.5	5.9	2.1	8.27
C. Proportions.					
WF/WH	0.60-0.64	0.621	0.020	0.007	2.14
LP/WP	0.93-0.97	0.944	0.020	0.007	1.42
DP/LP	0.81-0.87	0.841	0.027	0.010	2.15
LP/WE	0.74-0.78	0.761	0.024	0.009	2.12
Ta/Ti	0.62-0.68	0.649	0.026	0.009	2.67
PS/LP	0.62-0.69	0.654	0.030	0.011	3.09

Table 18. Variation in body size (LE, in mm) in selected samples of the *pluripunctatus* subgroup; see Fig. 152.

Sample	N	Males	Range	Mean	1.5SD	2SE	CV(%)
S. plurisetosus.							
1	14	7	2.33-2.93	2.625	0.320	0.114	8.14
S. multisetosus.							
2	14	7	2.50-3.10	2.734	0.251	0.089	6.12
3	22	11	2.33-2.90	2.575	0.227	0.064	5.87
4	20	10	2.07-2.60	2.342	0.232	0.069	6.62
S. pluripunctatus.							
5	18	9	2.05-2.70	2.402	0.251	0.079	6.95
6	10	5	2.15-2.65	2.382	0.228	0.096	6.39
7	18	9	2.09-2.68	2.407	0.218	0.069	6.04
8	8	5	1.98-2.75	2.372	-	-	-
9	10	5	2.15-2.71	2.445	0.237	0.100	6.47
S. kulti.							
10	10	5	2.00-2.55	2.278	0.263	0.111	7.70
11	20	10	1.96-2.65	2.234	0.237	0.071	7.07
12	22	11	1.75-2.25	2.050	0.205	0.058	6.65
13	12	6	2.07-2.44	2.283	0.183	0.070	5.34
14	10	8	2.16-2.60	2.299	-	-	-

Table 19. Variation in numbers of discal setae on left elytron in selected samples of the *pluripunctatus* subgroup; see Fig. 153.

Sample	N	Males	Range	Mean	1.5SD	2SE	CV(%)
S. plurisetosus.							
1	14	7	52-74	64.4	7.4	2.6	7.62
S. multisetosus.							
2	14	7	42-56	48.8	6.0	2.1	8.16
3	22	11	42-55	47.4	5.6	1.6	7.91
4	20	10	37-54	47.0	7.9	2.4	11.28
S. pluripunctatus.							
5	18	9	39-56	47.2	7.4	2.3	10.50
6	10	5	41-57	47.1	8.1	3.4	11.40
7	18	9	39-55	45.3	7.1	2.2	10.51
8	8	5	35-55	43.0	-	-	-
9	10	5	45-61	52.3	8.0	3.4	10.20
S. kulti.							
10	10	5	28-41	34.6	6.0	2.6	11.66
11	20	10	18-28	22.6	3.6	1.1	10.55
12	22	11	19-26	21.8	3.8	1.1	11.72
13	12	6	21-27	22.9	3.0	1.1	8.62
14	10	8	23-31	26.3	-	-	-

Table 20. Variation in eye size (WF/WH) in selected samples of the *pluripunctatus* subgroup; see Fig. 154.

Sample	N	Males	Range	Mean	1.5SD	2SE	CV(%)
S. plurisetosus.							
1	14	7	0.60-0.66	0.622	0.025	0.009	2.68
S. multisetosus.							
2	14	7	0.59-0.65	0.620	0.027	0.010	2.89
3	22	11	0.60-0.66	0.625	0.021	0.006	2.25
4	20	10	0.60-0.64	0.620	0.015	0.004	1.61
S. pluripunctatus.							
5	18	9	0.61-0.66	0.631	0.020	0.006	2.14
6	10	5	0.59-0.66	0.627	0.030	0.013	3.19
7	18	9	0.61-0.66	0.633	0.022	0.007	2.27
8	8	5	0.61-0.67	0.642	-	-	-
9	10	5	0.60-0.63	0.614	0.013	0.005	1.37
S. kulti.							
10	10	5	0.59-0.63	0.606	0.019	0.008	2.08
11	20	10	0.58-0.63	0.604	0.020	0.006	2.24
12	22	11	0.60-0.65	0.617	0.020	0.006	2.20
13	12	6	0.58-0.61	0.595	0.014	0.005	1.52
14	10	8	0.58-0.63	0.605	-	-	-

Table 21. Variation in pronotal form (LP/WP) in selected samples of the *pluripunctatus* subgroup; see Fig. 155.

Sample	N	Males	Range	Mean	1.5SD	2SE	CV(%)
S. plurisetosus.							
1	14	7	0.90-0.95	0.932	0.019	0.007	1.34
S. multisetosus.							
2	14	7	0.93-1.00	0.959	0.032	0.012	2.25
2	22	11	0.93-0.98	0.950	0.021	0.006	1.51
4	20	10	0.92-0.95	0.936	0.013	0.004	0.93
S. pluripunctatus.							
5	18	9	0.88-0.93	0.907	0.017	0.005	1.25
6	10	5	0.91-0.94	0.919	0.016	0.007	1.19
7	18	9	0.87-0.93	0.910	0.022	0.007	1.64
8	8	5	0.90-0.93	0.915	-	-	-
9	10	5	0.90-0.96	0.931	0.027	0.011	1.92
S. kulti.							
10	10	5	0.90-0.93	0.916	0.018	0.007	1.28
11	20	10	0.89-0.95	0.925	0.024	0.007	1.76
12	22	11	0.90-0.97	0.932	0.025	0.007	1.80
13	12	6	0.90-0.95	0.925	0.021	0.008	1.49
14	10	8	0.88-0.94	0.913	-	-	-

Table 22. Variation in pronotal length relative to elytral width (LP/WE) in selected samples of the *pluripunctatus* subgroup; see Fig. 156.

Sample	N	Males	Range	Mean	1.5SD	2SE	CV(%)
S. plurisetosus.							
1	14	7	0.74-0.80	0.775	0.027	0.010	2.30
S. multisetosus.							
2	14	7	0.73-0.82	0.789	0.050	0.018	4.19
3	22	11	0.73-0.78	0.752	0.027	0.008	2.42
4	20	10	0.74-0.80	0.776	0.022	0.007	1.88
S. pluripunctatus.							
5	18	9	0.75-0.83	0.790	0.028	0.009	2.34
6	10	5	0.74-0.81	0.781	0.039	0.016	3.33
7	18	9	0.71-0.80	0.764	0.034	0.011	2.95
8	8	5	0.76-0.81	0.785	-	-	-
9	10	5	0.74-0.79	0.779	0.036	0.015	3.11
S. kulti.							
10	10	5	0.74-0.81	0.784	0.035	0.015	3.01
11	20	10	0.75-0.83	0.784	0.034	0.010	2.87
12	22	11	0.75-0.84	0.780	0.035	0.010	3.00
13	12	6	0.77-0.81	0.792	0.021	0.008	1.79
14	10	8	0.75-0.82	0.786	-	-	-

Table 23. Variation in length of paramedian pronotal sulcus relative to pronotal length (PS/LP) in selected samples of the *pluripunctatus* subgroup; see Fig. 157.

Sample	N	Males	Range	Mean	1.5SD	2SE	CV(%)
S. plurisetosus.							
1	14	7	0.63-0.70	0.664	0.026	0.009	2.61
S. multisetosus.							
2	14	7	0.58-0.65	0.629	0.028	0.010	3.02
3	22	11	0.62-0.69	0.658	0.025	0.007	2.51
4	20	10	0.63-0.70	0.656	0.032	0.009	3.21
S. pluripunctatus.							
5	18	9	0.61-0.68	0.647	0.030	0.009	3.09
6	10	5	0.63-0.73	0.663	0.042	0.018	4.27
7	18	9	0.63-0.71	0.653	0.030	0.010	3.09
8	8	5	0.63-0.68	0.660	-	-	-
9	10	5	0.63-0.70	0.673	0.032	0.013	3.14
S. kulti.							
10	10	5	0.59-0.68	0.656	0.039	0.017	4.01
11	20	10	0.61-0.68	0.646	0.029	0.009	3.02
12	22	11	0.59-0.66	0.628	0.028	0.008	2.93
13	12	6	0.63-0.70	0.658	0.034	0.013	3.42
14	10	8	0.58-0.66	0.628	-	-	-

MEXICO

GUERRERO: 5 mi. s. Iguala (1; CAS). HIDALGO: Rio Tula near Tasquillo 5300' (1; UASM). MORELOS: Tetecala 2800' (6; CNC, MCZ, UASM), Yautepec (1; BMNH). OAXACA: Huitzo (2; BMNH), 72.5 mi. s. Valle Nacional 4100' (25; UASM). PUEBLA: Tehuitzingo 3700' (1; MGFT), Tepexco (22; UASM). SAN LUIS POTOSI: Tamazunchale 300' (14; CAS, DRWh, IRSB, UASM, USNM).

Collecting notes. - Specimens of *S. multisetosus* were collected during June, August, September, and October. Some, including the entire Tepexco series, were collected at black lights, doubtless by flight. Others were hand collected in riparian gravel bars, the normal habitat for most species in the subgenus, but on the average in slightly drier places. Some inhabited streams, at least in Puebla, are dry during winter.

Taxonomic notes. - *S. multisetosus*, so far as known, is allopatric with respect to all other members of the group. It does share at least one drainage system, the Rio Papaloapan, with *S. kulti*, and may be sympatric with it. Lack of known sympatry and close similarity of members of the *pluripunctatus* subgroup provide no direct evidence of reproductive isolation between them, but statistical data provide indirect evidence that reproductive isolation exists. Selected samples of *S. plurisetosus, S. multisetosus, S. pluripunctatus*, and *S. kulti* are compared for six different characteristics in Tables 18-23 and Fig. 152-157. Satisfactory comparisons of *S. multisetosus* with the other species are made difficult by lack of good information on clinal variation. Still, certain facts support the notion that *S. multisetosus* is reproductively isolated from the other three forms.

S. plurisetosus is known from rivers just north of the Moctezuma drainage basin, and a direct comparison between those specimens (sample one) and those of *S. multisetosus* from Tamazunchale (sample two) is therefore relevant. The apex of the median lobe of the male genitalia is more broadly rounded; accessory pronotal setae are present in all specimens; and the number of discal elytral setae (Fig. 153, Table 19) is much greater. Additional, statistically significant, differences are in the form of the pronotum (Fig. 155, Table 21) and in the length of the paramedian pronotal sulci (Fig. 156, Table 23). In these two features, the *S. plurisetosus* sample is similar to one or both of the two southern *S. multisetosus* samples (samples three and four); the Tamazunchale sample may thus be considered divergent, indicating a lack of gene flow between it and *S. plurisetosus*. Differences in these five characteristics, and the geographic proximity of the two samples, indicate reproductive isolation of *S. multisetosus* from *S. plurisetosus*.

Known geographic ranges of *S. pluripunctatus* (samples five to nine) and *S. multisetosus* are so widely separated that statistical differences are equivocal. However, constant differences in form of male genitalia, constant presence of paramedian ambulatory setae on sternum seven in females of *S. pluripunctatus*, and apparent geographic isolation are sufficient reasons to recognize *S. pluripunctatus* and *S. multisetosus* as separate species.

S. kulti (samples 10 to 14), particularly in the south, is characterized by fewer elytral setae and smaller body size than is *S. multisetosus*. Sample 13 of *S. kulti*, Valle Nacional and sample three of *S. multisetosus*, 72.5 mi. s. Valle Nacional, are from the same river system. Statistically significant differences in eye size, pronotal form, and relative size of thorax represent divergences in these features, so there is little doubt that the two samples represent reproductively isolated taxa. Similar, though less conclusive, comparisons between other population samples of the two forms give similar results, even though northern samples of *S. kulti* (samples 10 and 14) are characterized by large body size and increased numbers of elytral setae. These facts, together with constant differences in form of male median lobe, strongly support the conclusion that *S. kulti* is reproductively isclated from *S. multisetosus*.

3.484 *Schizogenius pluripunctatus* LeConte

Schizogenius pluripunctatus LeConte 1852:197. *Type locality* Colorado River, California; type in MCZ, specimen labelled MCZ 5484 here designated lectotype (!). LeConte 1857:82. Putzeys 1863:24. Putzeys 1866:225. LeConte 1879:34. Lindroth 1961:165.

Schizogenius simplex LeConte 1852:197. *Type locality* Colorado River, California; type in MCZ, specimen labelled MCZ 5485 here designated lectotype (!). LeConte 1857:83, established synonymy.

Diagnostic combination. - Within the *pluripunctatus* group, specimens of this species are distinguished by the following combination of characters: pronotum without accessory marginal setae; females as well as males each with paramedian ambulatory setae on sternum seven; apex of median lobe deflected at a weak angle; and elytron with 35 or more discal setae.

Description. - As in *S. seticollis seticollis*, except: legs paler, femora uniformly rufous, tibiae paler; abdomen often paler toward apex.

Form and sculpture of head and pronotum as in *S. plurisetosus* (Fig. 126), except sides of pronotum bisetose and basal transverse impression less distinctly punctate. In specimens studied, elytron with 12-18 setae on interval three, 12-23 on interval five, and 11-19 on interval seven; setae mostly adjacent to corresponding inner striae, not markedly biseriate; total number of setae per elytron 35-61; striae usually indistinctly punctate. Females and males each with a pair of ambulatory setae on sternum seven. Male genitalia: median lobe (Fig. 135) with apical portion proportionately long, deflected at weak angle; endophallus, Fig. 143; 23 specimens examined.

Measurements and proportions. See Table 24.

Variation. - Data on variation in six characteristics among five samples (samples five to nine) are given in Tables 18-23 and Fig. 152-157. Three samples from Arizona and New Mexico (samples five to seven) are quite uniform, and are intermediate in most ways to the two Mexican samples. I therefore suspect that sample nine from Sinaloa and Nayarit is geographically isolated from sample eight from Durango, and that these two samples represent populations near the ends of a partial circle of races. This is a reasonable hypothesis, since these areas are well separated by high ranges of the Sierra Madre Occidental, but should be tested through additional collections.

One female specimen from Prescott, Arizona, has only one left paramedian ambulatory seta on sternum seven. I otherwise found this character to be constant, and presume that it remains stable southward where the range of *S. pluripunctatus* approaches that of *S. kulti*.

Etymology. - Latin, *plurimus* = most, plus *punctum* = small holes, in

Table 24. Descriptive statistics for *S. pluripunctatus*, based on nine males from 18.6 miles southeast of Tonala, Chiapas.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.38-4.26	3.819	0.418	0.186	7.29
LE	2.05-2.60	2.334	0.260	0.116	7.43
WH	0.71-0.89	0.800	0.090	0.040	7.52
WP	0.93-1.19	1.063	0.127	0.057	7.98
WE	1.06-1.33	1.206	0.147	0.065	8.13
B. Setae on left elytron.					
Interval 3	13-17	14.2			
Interval 5	12-20	16.1			
Interval 7	13-19	14.8			
Total	39-56	45.1	5.5	2.4	8.10
C. Proportions.					
WF/WH	0.61-0.65	0.630	0.021	0.009	2.24
LP/WP	0.88-0.91	0.903	0.015	0.007	1.11
DP/LP	0.81-0.85	0.830	0.018	0.008	1.47
LP/WE	0.77-0.83	0.797	0.026	0.012	2.17
Ta/Ti	0.62-0.72	0.664	0.054	0.024	5.38
PS/LP	0.62-0.68	0.650	0.031	0.014	3.17

reference to the numerous discal setae on the elytron.

Distribution. - Specimens of *S. pluripunctatus* have been collected in the Gila and Colorado River drainages in Arizona and New Mexico, south to the Rio Acaponeta drainage basin in northern Nayarit, and in the interior Rio Nazas drainage in Durango (Fig. 147). One specimen labelled "N. Y." (UKSM) is no doubt erroneous. I studied 125 additional specimens from the following localities.

UNITED STATES

ARIZONA (14; AMNH, CAS, UASM, USNM): Cochise Co., Cochise Co., Cochise Stronghold (1; UATA), Fairbanks (1; CAS); Coconino Co., Bill Williams Fork (9; KSUM, MCZ, UKSM); Gila Co., Carrizo Creek (12; UASM), Globe (1; CAS), Roosevelt Lake (1; AMNH), Salt River Canyon (3; ANSP, MCZ, UASM), Verde River (1; MCZ); Graham Co., Aravaipa (11; BMNH, CAS, CNC, DRWh, IRSB), San Carlos Reservoir (1; MCZ); Maricopa Co., Phoenix (2; LACM); Pima Co., Madera Canyon (1; UASM), Tucson (5; AMNH, CAS, JNeg, UATA); Santa Cruz Co., Nogales (3; CNHM, UASM), 5 mi. n. Nogales (1; MCZ), Patagonia (8; AMNH, CAS, UATA), 2 mi. sw. Patagonia (5; UATA), Pena Blanca (1; UASM); Yavapai Co., Bumble Bee (2; CAS), Haslampa District (2; CAS), Prescott (2; UASM). NEW MEXICO: Catron Co., Glenwood (1; UASM); Grant Co., Cliff (8; UASM), 26 mi. n. Silver City (9; TLEr), 36.4 mi. ne. Silver City (1; MGFT).

MEXICO

DURANGO: 12.2 mi. s. El Banco (8; UASM). NAYARIT: Acaponeta (1; UASM), 2.4 mi. s. Acaponeta (6; UASM), 8 mi. nw. Acaponeta (1; CAS). SINALOA: 26 mi. ne. Villa Union (3; LBSC).

Collecting notes. - Specimens of *S. pluripunctatus* have been collected from March to September in the United States, and in January, July, and September in Mexico. Many specimens were taken at lights, to which they no doubt flew. I have collected specimens in gravel bars along streams, usually further from water than specimens of most other species.

Taxonomic notes. - The type of *S. simplex*, taken at the same time and place as that of *S. pluripunctatus*, is a small specimen of the same species and was so recognized subsequent to its description. Though the name has line priority, it was treated as a junior synonym of *S. pluripunctatus* by LeConte (1857) and by all subsequent authors, and the latter is thus established as the proper name.

Though known distributions are allopatric, specimens of *S. pluripunctatus* and *S. kulti* have been taken within 75 miles of each other, and the two river systems involved, Acaponeta and Grande de Santiago, approach each other even more closely in places. A scarcity of material from this area precludes a definite statement about reproductive relationships, but all available evidence points toward reproductive isolation. In specimens seen, all females of *S. pluripunctatus* have paramedian ambulatory setae on sternum seven, and males have the apical portion of the median lobe deflected at a slight but evident angle.

Statistical evidence of distinctness of *S. pluripunctatus* and *S. kulti* is given in Tables 18-23 and Fig. 152-157. Northern specimens of *S. kulti* (sample ten) approach *S. pluripunctatus* in body size and in numbers of elytral setae, but the Nayarit sample of the latter (sample nine) is divergent in these ways. Northern specimens of *S. kulti* approach specimens of *S. pluripunctatus* from Nayarit, but diverge from those from Durango (sample eight), in eye size. And, they diverge from Nayarit

S. pluripunctatus in pronotal form. It is unlikely that there is any actual or potential gene flow between northern *S. kulti* and either southern form of *S. pluripunctatus*, and I therefore treat these taxa as distinct species.

3.485 *Schizogenius kulti* new species

Type material. - Holotype male and allotype female labelled "MEXICO. Chiapas. 18.6 mi. se. Tonala. Rte. 200 100' III.2.1966" and "George E. Ball D. R. Whitehad collectors" (MCZ). Thirty additional specimens from various localities in Chiapas are paratypes (CNC, DRWh, UASM, USNM).

Diagnostic combination. - The following characters combine to distinguish specimens of this species from all others in the *pluripunctatus* group: median lobe arcuate, apical deflection not angulate; females without paramedian ambulatory setae; and pronotum without accessory marginal setae. Most specimens have fewer than 30 setae on the disc of each elytron, a feature unique within the group, but some specimens from northern parts of the range cannot be so distinguished.

Description. - As in *S. seticollis seticollis* except: color paler, testaceous to rufopiceous; front femora, coxae, and trochanters ferrugineous; maxillae, labial palpi, antennae, front tarsi and tibiae, middle and hind legs except coxae, and apical margins of elytra and abdomen rufotestaceous; no metallic luster. Form and sculpture of head and pronotum as in *S. plurisetosus* (Fig. 126), except sides of pronotum bisetose and basal and anterior transverse impressions nearly impunctate. Elytral intervals three, five, and seven in specimens examined with 6-14, 6-14, and 4-14 setae, respectively; striae nearly impunctate. Male genitalia: median lobe, Fig. 136, nearly or quite arcuate, apical portion proportionately long and deflexed at a slight angle or not angulate; endophallus, Fig. 144; 11 specimens examined.

Measurements and proportions. See Table 25. Of holotype: TL, 3.43 mm; LE, 2.09 mm; WH, 0.71 mm; WP, 0.92 mm; WE, 1.04 mm; WF/WH, 0.63; LP/WP, 0.93; DP/LP, 0.83; LP/WE, 0.83; Ta/Ti, 0.65; PS/LP, 0.61. Of allotype: TL, 3.45 mm; LE, 2.10 mm; WH, 0.72 mm; WP, 0.92 mm; WE, 1.08 mm; WF/WH, 0.60; LP/WP, 0.95; DP/LP, 0.83; LP/WE, 0.82; Ta/Ti, 0.65; PS/LP, 0.59.

Variation. - Data on variation in six characteristics are given in Tables 18-23, for samples numbered 10 to 14 as in Fig. 152-157. Toward the north in both Atlantic and Pacific drainage basins, body size, pronotal width, and numbers of elytral setae increase, eye size decreases, and except for the Veracruz sample paramedian pronotal sulci lengthen. Northern populations are geographically isolated from one another, so that their similarities may be interpreted either as convergences or as relict characteristics. I suspect the latter is more likely, since related species are larger and more setose. I found no specimens with accessory pronotal setae, and no females with paramedian ambulatory setae on sternum seven. The form of the median lobe is constantly arcuate, the apical portion not or hardly deflected at an angle.

Etymology. - The name *S. kulti* is dedicated to the Czechoslovakian entomologist, K. Kult, whose numerous papers on the Scaritini contributed much to our knowledge of the group. A specimen from Rio Maria Linda, Guatemala, was treated by Bates (1881) as *S. tristriatus*, but was sub-

Table 25. Descriptive statistics for *S. kulti*, based on 14 males from 18.6 miles southeast of Tonala, Chiapas.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	2.85-3.53	3.280	0.349	0.140	7.09
LE	1.75-2.14	1.987	0.205	0.082	6.87
WH	0.62-0.75	0.696	0.066	0.027	6.34
WP	0.76-0.96	0.884	0.097	0.039	7.31
WE	0.92-1.09	1.016	0.090	0.036	5.93
B. Setae on left elytron.					
Interval 3	6- 9	7.5			
Interval 5	7-10	8.0			
Interval 7	5- 7	5.9			
Total	19-25	21.5	3.9	1.6	11.99
C. Proportions.					
WF/WH	0.60-0.65	0.620	0.024	0.010	2.60
LP/WP	0.90-0.97	0.935	0.029	0.012	2.04
DP/LP	0.81-0.85	0.832	0.018	0.007	1.41
LP/WE	0.75-0.84	0.807	0.040	0.016	3.32
Ta/Ti	0.60-0.71	0.668	0.051	0.020	5.04
PS/LP	0.61-0.65	0.629	0.020	0.008	2.07

sequently labelled as a paratype of "*S. brittoni*" Kult, a pin label name never published.

Distribution. - Specimens of *S. kulti* have been collected at altitudes ranging from near sea level to 4100', from the Rio Grande de Santiago system in Nayarit and Zacatecas and the Rio Atoyac system in Veracruz, south to Guatemala (Fig. 147). I studied 122 specimens of this species from the following localities.

MEXICO

CHIAPAS: 3.2 mi. n. Arriaga (1; USNM), 12.2 mi. ne. Chiapa de Corzo (4; DRWh, UASM), Pijijiapan (4; CNC), Tonala (1; USNM), 18.6 mi. se. Tonala (23; MCZ, UASM). GUERRERO: 41.4 mi. n. Acapulco (3; UASM), Coyuca (2; UASM). JALISCO: 0.4 mi. w. Cocula (1; UASM), Talpa de Allende (1; UASM). NAYARIT: Jesus Maria (2; UCB), 14 mi. e. San Blas (1; UASM). OAXACA: 17.7 mi. w. El Camaron (10; MGFT, UASM), 29.4 mi. e. El Coyul (33; UASM), 11.1 mi. n. Matias Romero (1; CAS), Valle Nacional (14; UASM), Zanatepec (3; IRSB). TABASCO: Teapa (3; BMNH). VERACRUZ: Cordoba (1; CAS), Fortin de las Flores (9; DRWh, FDAG), Catemaco (1; JNeg). ZACATECAS: 0.9 mi. n. Jalpa (1; UASM).

GUATEMALA

ESCUINTLA: Rio Maria Linda (1; BMNH). IZABAL: Los Amates (1; MCZ).

Collecting notes. - Adults of *S. kulti* are active throughout the year in gravel bars along streams. I noted no special habits, and found them together with specimens of one or more other *Schizogenius* species. Specimens from Fortin de las Flores, Veracruz, were taken at black lights, and no doubt flew there. None of the Fortin specimens were collected by hand, although suitable habitats are in the vicinity and

Fig. 122-123. Head and pronotum, dorsal aspect. 122. *S. truquii* Putzeys, Cocula, Jalisco. 123. *S. brevisetosus* new species, Barrel Springs Creek, Texas. Fig. 124. Habitus, dorsal aspect, *S. seticollis seticollis* Fall, Mokelumne Hill, California. Fig. 125-126. Head and pronotum, dorsal aspect. 125. *S. seticollis vandykei* new subspecies, Arroyo Saltito, Baja California. 126. *S. plurisetosus* new species, Linares, Nuevo Leon. Fig. 127-136. Male median lobe, lateral aspect. 127. *S. truquii* Putzeys, Cocula, Jalisco. 128. *S. brevisetosus* new species, Sanderson, Texas. 129. *S. seticollis seticollis* Fall, Dry Creek, California. 130. *S. seticollis vandykei* new subspecies, Arroyo Saltito, Baja California. 131. *S. plurisetosus* new species, Cienega de Flores, Nuevo Leon. 132. *S. multisetosus* Bates, Tepexco, Puebla. 133. Same, 72.5 mi. s. Valle Nacional, Oaxaca. 134. Same, Tamazunchale, San Luis Potosi. 135. *S. pluripunctatus* LeConte, Patagonia, Arizona. 136. *S. kulti* new species, Valle Nacional, Oaxaca.

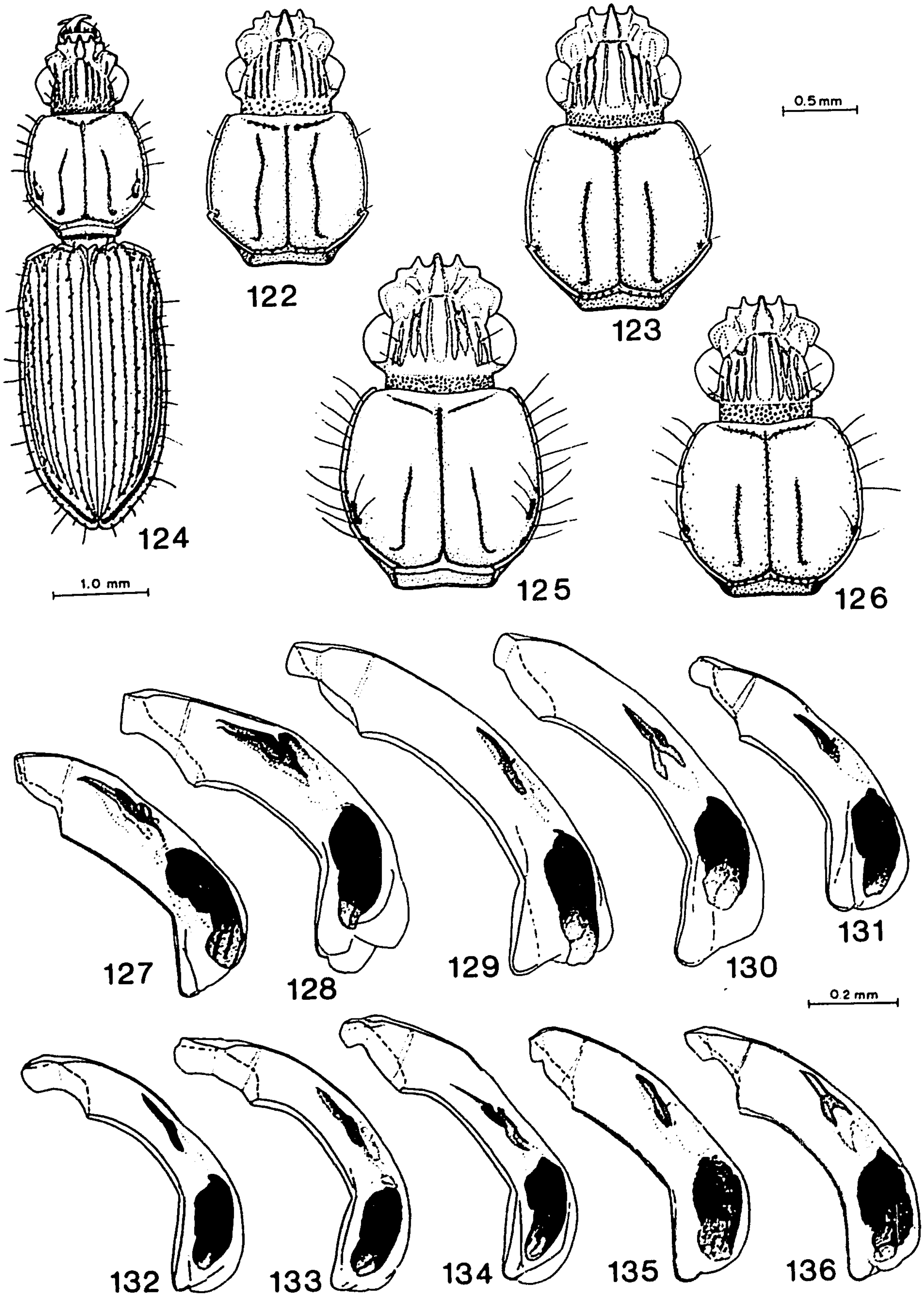
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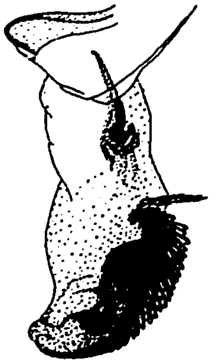
Fig. 137-144. Male endophallus. 137. *S. truquii* Putzeys, La Garita, Jalisco. 138. *S. brevisetosus* new species, Lozier Canyon, Texas. 139. *S. seticollis seticollis* Fall, Trimmer, California. 140. *S. plurisetosus* new species, El Barretal, Tamaulipas. 141. *S. multisetosus* Bates, 72.5 mi. s. Valle Nacional, Oaxaca. 142. Same, Tepexco, Puebla. 143. *S. pluripunctatus* LeConte, Acaponeta, Nayarit. 144. *S. kulti* new species, 41.4 mi. n. Acapulco, Guerrero. Fig. 145-147. Known distributions. 145. *S. truquii* Putzeys. 146. *S. brevisetosus* new species. 147. *S. seticollis seticollis* Fall, half-filled circles; *S. seticollis vandykei* new subspecies, filled circles; *S. pluripunctatus* LeConte, filled triangles; *S. kulti* new species, half-filled triangles; *S. multisetosus* Bates, half-filled squares; *S. plurisetosus* new species, filled squares. Fig. 148. Geographic variation in *S. seticollis seticollis* Fall, circles, and *S. seticollis vandykei* new subspecies, square; means of body size, Table 11.



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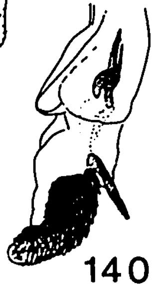

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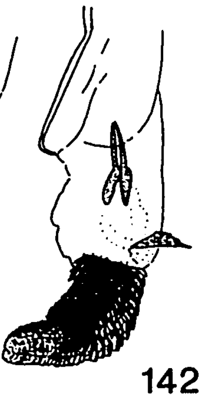

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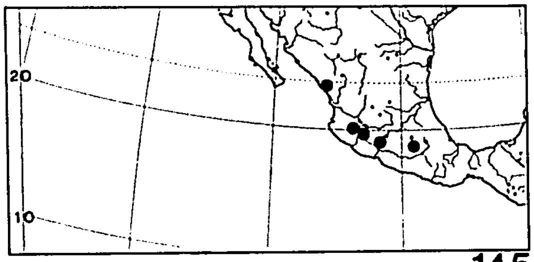

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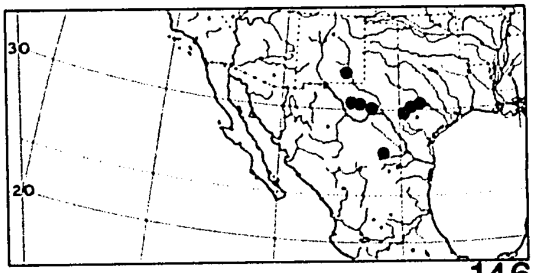

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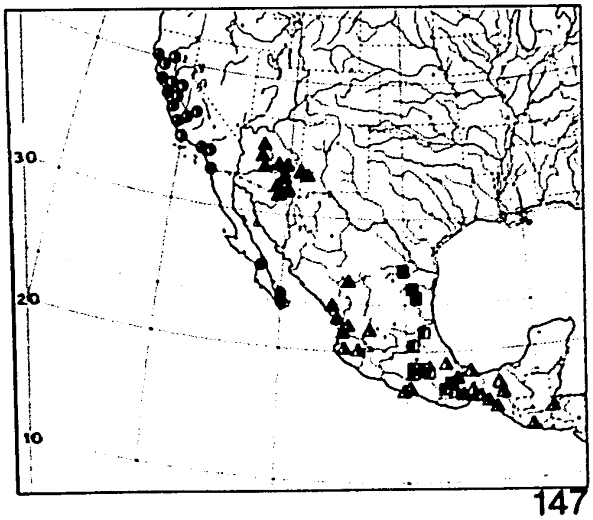

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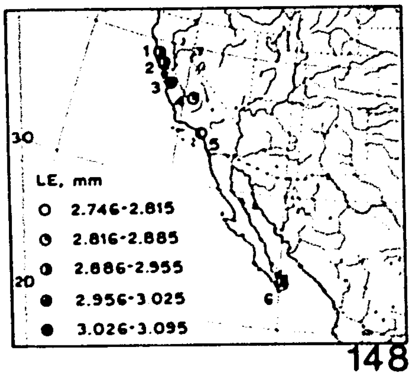

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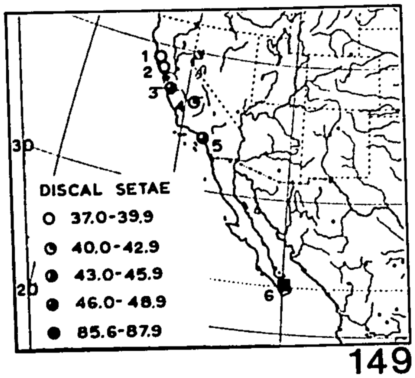
Fig. 149-151. Geographic variation in *S. seticollis seticollis* Fall, circles, and *S. seticollis vandykei* new subspecies, square. 149. Means of numbers of discal setae on left elytron, Table 12. 150. Means of relative eye size, Table 13. 151. Means of pronotal form, Table 14. Fig. 152-157. Geographic variation in *S. plurisetosus* new species, hexagon; *S. multisetosus* Bates, diamonds; *S. pluripunctatus* LeConte, circles; and *S. kulti* new species, squares. 152. Means of body size, Table 18. 153. Means of numbers of discal setae on left elytron, Table 19. 154. Means of relative eye size, Table 20. 155. Means of pronotal form, Table 21. 156. Means of relative pronotal size, Table 22. 157. Means of relative length of paramedian pronotal sulci, Table 23. Accompanying legends are for all included taxa.



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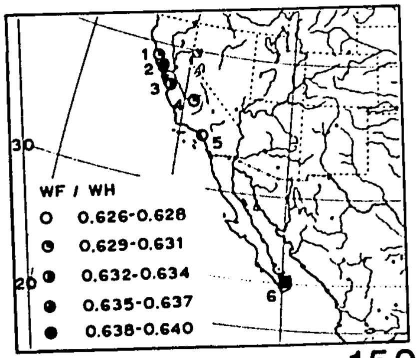

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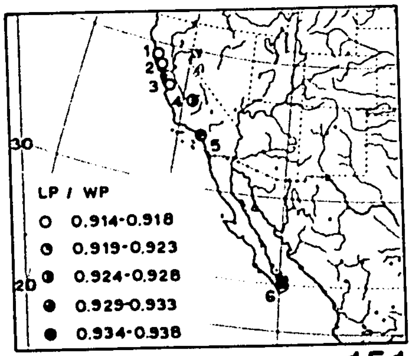

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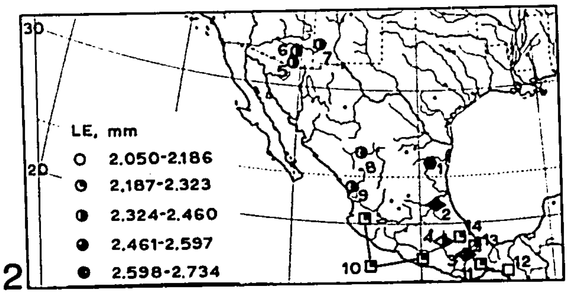

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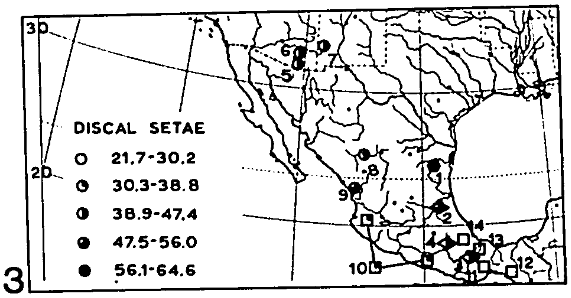

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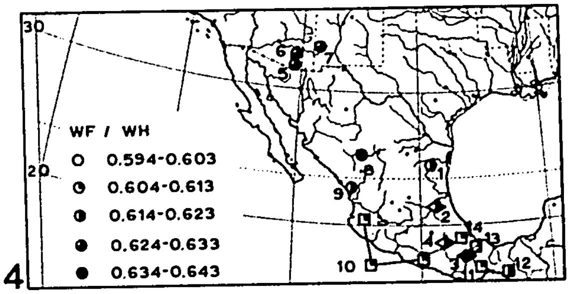

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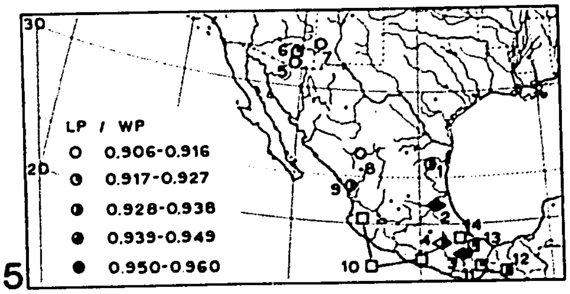

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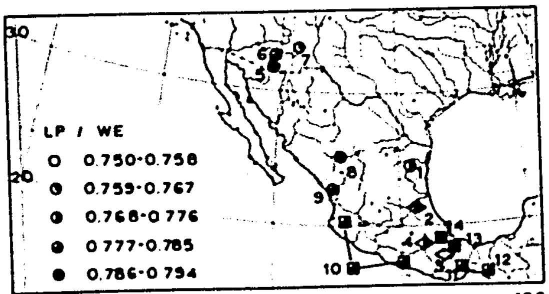

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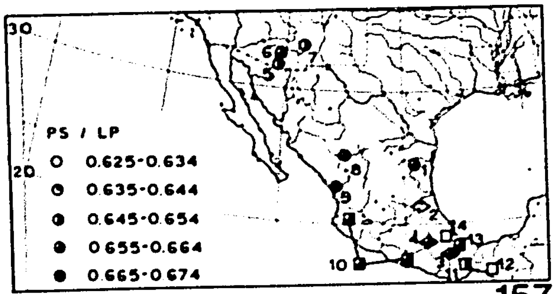


157

1000 mi

numerous specimens of *S. tristriatus* were collected there.

Taxonomic notes. - *S. kulti* is a variable species, and when more material is studied the more northern forms may be distinguished as subspecies. However, I do not suspect any reproductive isolation, and am convinced that all specimens referred to this taxon are conspecific.

My reasons for considering *S. kulti* as a species distinct from the related *S. multisetosus* and *S. pluripunctatus* are given in my discussions of those species.

3.49 The *sallei* group

Diagnostic combination. - Members of this monotypic group are distinguished by the following combination of characters: body strongly flattened; paramedian clypeal carinae extended to median tooth; clypeal field narrow, no wider at base than apex of median frontal sulcus; submentum without accessory setae; pronotum without paralateral carinae; discal setae present on intervals three, five, and seven, total normally less than 30, average length less than 1.0 times maximum width of interval two; abdomen microsculptured along midline, and with microsculpture in small lateral patches near coxal depressions of sternum three; endophallus with basal collar spines distinct. Also: clypeal suture sharply impressed; antennal articles five to ten filiform, elongate; front and middle tarsi broadened and with dense ventral pubescence, especially in males; sternum seven with paramedian ambulatory setae in males, not in females; paramedian carinae of sternum three curved outward at apices;

pygidium crenulate at apex in females; color rufocastaneous; and pronotal hind angles sharply developed.

S. sallei is the only *Schizogenius* species characterized by having strong microsculpture along the midline but not the margins of the abdomen.

Distribution. - *S. sallei* is known from the Great Plains region of North America, from Kansas south to the Rio Grande. I examined 372 specimens of the *sallei* group.

3.491 *Schizogenius sallei* Putzeys

Schizogenius sallei Putzeys 1866:228. *Type locality* Texas; type male in IRSB, specimen labelled lectotype by me so designated (!). LeConte 1879:34. Lindroth 1961:166.

Diagnostic combination. - Abdomen microsculptured along midline, otherwise mostly unmicrosculptured.

Description. - Body flattened. Color castaneous, unmetallic, legs and palpi paler.

Integument. Conspicuous microsculpture on paramedian frontal sulci, mouthparts, genae, front legs except posterior surfaces of femora and trochanters, middle legs except anterior surfaces of trochanters, hind tibiae and posterior surfaces of hind femora, elytral epipleura at base and on apical two-thirds, sternum three in coxal depressions and small paralateral patches, and middle of abdomen on sterna three to five or six.

Head. Fig. 158. Paramedian clypeal carinae straight, moderately elevated in basal half, extended to median tooth; median field triangular, narrow, no wider at base than apex of median frontal sulcus. Clypeal suture sharply defined. Eye prominent, finely and uniformly faceted. Neck densely punctate. Gena coarsely punctate, rugose in front. Antennal articles four to ten elongate, article five about 1.7-1.8 times longer than wide.

Pronotum. Fig. 158. Sides bisetose; base not rugose; hind angles prominent. Paramedian longitudinal sulci moderately long, nearly straight, strongly hooked basally. Anterior transverse impression strongly punctate.

Legs. Front and middle tarsi moderately dilated and pubescent ventrally, less so in females; hind tarsus slender, short. Paronychia nearly as long as tarsal claws. Front tibia narrowed evenly to base. Front femur not strongly constricted near apex.

Elytra. Left elytron with about 7-9 setae on interval three, 6-8 on interval five, 3-5 on interval seven; total 17-23 in specimens examined. Striae deep and sharply engraved, finely punctate in basal two-thirds. Intervals one to seven broad and flat, interval eight carinate at apex; intervals three, five, and seven broadly joined at apices. Humeral denticles prominent.

Abdomen. Sternum three with paramedian carinae curved outward at apices. Sternum seven with paramedian ambulatory setae in males only. Pygidium with apical margin crenulate in females, entire in males.

Male genitalia. Median lobe, Fig. 169; endophallus, Fig. 178; 8 specimens examined.

Measurements and proportions. See Table 26.

Variation. - See Table 26. I found no significant geographic variation in relative eye size, pronotal form, body size, or in numbers of

Table 26. Descriptive statistics for *S. pallei*, based on 20 males from 23 miles southwest of Brackettville, Texas.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	4.04-4.50	4.278	0.189	0.056	2.95
LE	2.51-2.80	2.660	0.126	0.038	3.16
WH	0.82-0.91	0.866	0.036	0.011	2.79
WP	1.05-1.14	1.096	0.041	0.012	2.52
WE	1.29-1.44	1.372	0.060	0.018	2.90
B. Setae on left elytron.					
Interval 3	7- 9	7.8			
Interval 5	6- 8	7.4			
Interval 7	3- 5	4.0			
Total	17-21	19.2	1.9	0.6	6.62
C. Proportions.					
WF/WH	0.59-0.64	0.610	0.022	0.007	2.40
LP/WP	0.91-0.96	0.935	0.023	0.007	1.61
DP/LP	0.78-0.84	0.804	0.025	0.007	2.03
LP/WE	0.71-0.77	0.743	0.027	0.008	2.43
Ta/Ti	0.59-0.68	0.636	0.033	0.010	3.51
PS/LP	0.66-0.72	0.692	0.030	0.009	2.86

elytral setae.

Etymology. - This species was named after Auguste Salle, who made important early collections of Coleoptera in Mexico.

Distribution. - The known range of this species extends from Kansas south to the Rio Grande Valley in Texas (Fig. 185). This is a peculiar distribution, especially since there is no evidence of restricted gene flow either between the Rio Grande and Colorado River systems, or north and south of the Red River. I have two doubtful records of unspecified localities in Canada (UKSM) and Ohio (CAS); both require confirmation. I studied 372 additional specimens from the following localities.

UNITED STATES

No locality (7; ANSP, LACM). KANSAS: Butler Co., Leon (6; UKSM); Riley Co. (1; USNM). OKLAHOMA: Carter Co., 10.7 mi. s. Drake (2; TLEr); Murray Co., 10.3 mi. n. Drake (6; TLEr). TEXAS (54; AMNH, ANSP, CAS, CNHM, INHS, IRSB, MCZ, MSUL, RUNB, UKSM, USNM, ZMLS): Andrews Co., Fullerton (3; CAS, USNM); Bexar Co., San Antonio (1; MCZ); Blanco Co., Cypress Mills (3; USNM), Johnson City (8; UASM), Twin Sisters (7; UASM); Brown Co., Brownwood (1; AMNH); Comal Co., New Braunfels (1; USNM); Colorado Co., Columbus (1; MSUL); Cooke Co., 4 mi. sw. Era (3; BMNH); Dallas Co. (1; INHS), Dallas (7; INHS, MCZ, MSUL, RTBe); Erath Co., Morgan Mill (2; IRSB); Guadalupe Co., Seguin (3; UKSM); Kerr Co., Kerrville (7; CNC); Kinney Co., 23 mi. sw. Brackettville (107; AMNH, ANSP, CAS, CUNY, DJLa, FDAG, HGou, INHS, JHen, JNeg, MCZ, MGFT, MZSP, TCBa, UAFA, UASM, UATA, UCB, ZMLS); Lampasas Co., Adamsville (10; UASM); Maverick Co., 8 mi. n. Quemado (1; DHKa); McCulloch Co., 16 mi. s. Brady (3; CAS); McLennan Co., Waco (1; DHKa); Randall Co., Canyon (2; MSU); Real Co., Leakey (1; UASM), 2 mi.

s. Leakey (34; UASM); Taylor Co., 25 mi. sw. Abilene (14; CNHM); Terrell Co., Chandler Ranch (7; UASM); Travis Co., Austin (4; UASM, USNM); Uvalde Co., Garner State Park (15; UASM), Sabinal (2; USNM), 17 mi. nw. Uvalde (1; UASM); Val Verde Co., 26 mi. n. Comstock (7; DRWh), Devel's River (1; UATA), 9 mi. se. Del Rio (8; UASM), 13 mi. nw. Del Rio (24; UASM), 14 mi. se. Del Rio (6; UASM).

Collecting notes. - Specimens of this species have been collected from March to September, in riparian gravel bars and at lights. At least in southern Texas, I found them abundant. The lack of pronounced geographic variation implies that *S. sallei* is a particularly vagile species.

Taxonomic notes. - This species is not closely related to any other, and I found no problems in infraspecific variation.

3.50 The *tristriatus* group

Diagnostic combination. - Members of this group are distinguished by the following combination of characters: body flattened; paramedian clypeal carinae extended to median tooth; bases of paramedian frontal carinae not broadly fused; antennal articles five to ten filiform; discal setae present on intervals three, five, and seven; and abdomen extensively microsculptured. Also: clypeal suture sharply impressed; clypeal field triangular, less than 1.5 apical width of median frontal sulcus; front and middle tarsi broadened and with dense ventral pubescence, especially in males; sternum seven with paramedian ambulatory setae in males, not in females; paramedian carinae of sternum three curved at apices; pygidium crenulate at apex in most females and some males; and endophallus with basal collar spines distinct.

Distribution. - Members of this group range from southeastern Canada, through the eastern and central United States, south to southern Mexico. I studied 398 specimens of the *tristriatus* group.

3.501 *Schizogenius tristriatus* Putzeys

Schizogenius tristriatus Putzeys 1846:651. *Type locality* Mexico; location of type unknown, possibly Hope Museum, Oxford. Putzeys 1863:24. Putzeys 1866:227. Bates 1881:37. Kult 1950:140.

Diagnostic combination. - Specimens of this species are readily recognized by characteristics given in the key to North and Middle American species of the subgenus *Schizogenius*. *S. tristriatus* is the only Mexican member of the *tristriatus* group which does not have basally broadened front tibiae.

Description. - Body flattened. Rufopiceous; elytral apices, abdomen, and legs rufous; palpi testaceous; no metallic luster. Microsculpture as in *S. dilatus*. Otherwise as in *S. tibialis* except as follows. Form and sculpture of head and pronotum, Fig. 159; eyes prominent; antennal article five 1.6-1.7 times longer than wide. Front tibia (Fig. 164) strongly tapered, distal tooth not spatulate. Left elytron with 6-8 setae on interval three, 5-7 on interval five, and 2-4 on interval seven, total 14-18 in specimens studied. Male genitalia with median lobe, Fig. 170; endophallus, Fig. 179; 6 specimens examined.

Measurements and proportions. See Table 27.

Table 27. Descriptive statistics for *S. tristriatus*, based on 20 males from Fortin de las Flores, Veracruz, Mexico.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	4.16-4.84	4.574	0.258	0.077	3.76
LE	2.60-3.02	2.854	0.154	0.046	3.59
WH	0.84-1.00	0.928	0.058	0.018	4.20
WP	1.10-1.30	1.215	0.081	0.024	4.44
WE	1.43-1.62	1.531	0.079	0.024	3.43
B. Setae on left elytron.					
Interval 3	6- 8	6.7			
Interval 5	5- 7	6.0			
Interval 7	3- 4	3.2			
Total	14-18	16.0	1.8	0.5	7.31
C. Proportions.					
WF/WH	0.59-0.63	0.604	0.018	0.005	2.02
LP/WP	0.87-0.93	0.905	0.024	0.007	1.77
DP/LP	0.78-0.84	0.814	0.020	0.006	1.66
LP/WE	0.69-0.74	0.719	0.024	0.007	2.25
Ta/Ti	0.60-0.67	0.625	0.034	0.010	3.62
PS/LP	0.62-0.71	0.668	0.030	0.009	2.95

Variation. - Two specimens from San Luis Potosi and Queretaro are slightly paler in color, but may simply be teneral.

Etymology. - Latin, *tres* = three, plus *stria* = furrow, in reference to the median and paramedian pronotal sulci.

Distribution. - Specimens of this species have been collected in eastern Mexico from San Luis Potosi and Queretaro south to Veracruz, at elevations ranging from 2900 to 4100' (Fig. 186). I studied 78 specimens from the following localities.

MEXICO

No locality (4; IRSB, MCZ). QUERETARO: Escanelilla (1; UASM). SAN LUIS POTOSI: Xilitla (2; CNC). VERACRUZ: 3.2 mi. sw. Coscomatepec (22; BMNH, CAS, CNHM, DRWh, IRSB, MCZ, MGFT, UASM, USNM): Fortin de las Flores (49; FDAG, UASM).

Collecting notes. - Specimens of *S. tristriatus* have been collected nearly throughout the year, from March to November, either in gravel bars along streams or at lights. Where I have collected them in numbers, I did not find specimens of other species, though at Fortin de las Flores specimens of other species were collected at lights.

Taxonomic notes. - There are two specimens of *S. tristriatus* in the Putzeys collection in the Institut Royal des Sciences Naturelles de Belgique labelled as syntypes, but I think these probably are the specimens mentioned in a subsequent paper (Putzeys, 1863). However, they were identified by him, and do match the original description, notably in coloration, and no doubt are conspecific with the types. *S. longipennis* Putzeys was described as a variety of *S. tristriatus*, and was considered as such by Bates (1881), but as noted by Kult (1950), is not closely related.

3.502 *Schizogenius dilatus* new species

Type material. - Holotype male and allotype female labelled "MEX. Nuevo Leon Rio Sabinas Hidalgo, 4.8 mi. e. Sabinas Hidalgo 800' X.22-23. 65" and "George E. Ball D. R. Whitehead collectors" (MCZ). An additional 26 specimens from various localities in Nuevo Leon and Tamaulipas are paratypes (BMNH, CAS, CNC, DRWh, IRSB, UASM, USNM).

Diagnostic combination. - Specimens of this species are distinguished from others in the group by having the front tibia strongly broadened basally and the femur distinctly constricted near the apex, but no pronounced microsculpture on the prothoracic pleura.

Description. - Strong microsculpture on paramedian frontal sulci, mouthparts, genae, sides and base of pronotum, front legs, middle legs except anterior surfaces of trochanters, hind tibiae and posterior surfaces of hind femora, elytral epipleura, and entire abdomen. Otherwise as in *S. tibialis* except as follows. Eyes prominent; antennal article five about 1.6-1.7 times longer than wide. Front tibia (Fig. 165) slightly more tapered, distal tooth not spatulate. Left elytron with 8-11 setae on interval three, 7-10 on interval five, and 3-5 on interval seven, total 18-23 in specimens studied. Male genitalia with median lobe, Fig. 171; and endophallus, Fig. 180; 6 specimens examined.

Measurements and proportions. See Table 28. Of holotype: TL, 4.57 mm; LE, 2.81 mm; WH, 0.90 mm; WP, 1.18 mm; WE, 1.45 mm; WF/WH, 0.61; LP/WP, 0.97; DP/LP, 0.74; LP/WE, 0.79; Ta/Ti, 0.65; PS/LP, 0.74. Of allotype: TL, 5.05 mm; LE, 3.10 mm; WH, 0.98 mm; WP, 1.33 mm; WE, 1.60 mm; WF/WH, 0.63; LP/WP, 0.95; DP/LP, 0.74; LP/WE, 0.79;

Table 28. Descriptive statistics for *S. dilatus*, based on 12 males from Nuevo Leon and Tamaulipas, Mexico.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	4.41-5.08	4.727	0.316	0.122	4.46
LE	2.74-3.11	2.903	0.176	0.068	4.03
WH	0.84-1.00	0.928	0.073	0.028	5.22
WP	1.12-1.33	1.227	0.095	0.037	5.17
WE	1.38-1.62	1.499	0.110	0.042	4.89
B. Setae on left elytron.					
Interval 3	8- 9	8.7			
Interval 5	7- 9	7.5			
Interval 7	3- 5	4.1			
Total	18-22	20.3	1.8	0.7	6.00
C. Proportions.					
WF/WH	0.60-0.65	0.624	0.023	0.009	2.51
LP/WP	0.94-1.00	0.967	0.027	0.010	1.84
DP/LP	0.74-0.77	0.755	0.016	0.006	1.44
LP/WE	0.76-0.81	0.789	0.019	0.007	1.57
Ta/Ti	0.58-0.65	0.618	0.037	0.014	3.95
PS/LP	0.65-0.74	0.702	0.039	0.015	3.74

Ta/Ti, 0.65; PS/LP, 0.65.

Etymology. - Latin, *dilatus* = expanded, in reference to the form of the front tibia.

Distribution. - Specimens of this species have been collected only in a few localities in northeastern Mexico (Fig. 187). I studied 28 specimens from the following localities.

MEXICO

NUEVO LEON: Cienega de Flores (4; CAS, IRSB), Linares (1; DRWh), 14.8 mi. w. Linares (2; USNM), 5 mi. s. Monterrey (1; CNC), 4.8 mi. e. Sabinas Hidalgo (17; MCZ, UASM). TAMAULIPAS: El Barretal (1; BMNH), 21.3 mi. n. Ciudad Victoria (1; CNC), 39 mi. s. Ciudad Victoria (1; DRWh).

Collecting notes. - Specimens of *S. dilatus* have been collected from June to October, in riparian gravel bars. The specimens from 14.8 miles west of Linares were taken at black lights. The facts that one good series was taken along a stream, and that the eyes are not reduced, indicate epigean habits.

Taxonomic notes. - The only other species having broadened front tibiae, *S. tibialis*, is well separated morphologically, and is also sympatric at least in Nuevo Leon. *S. dilatus* is otherwise most similar to *S. tristriatus*, but is clearly distinct.

3.503 *Schizogenius tibialis* new species

Type material. - Holotype male and allotype female labelled "MEXICO S.L.P. Rte.85, 19.3 mi. n.w. Tamazunchale 500' XI.14&20.65" and "George E. Ball D. R. Whitehead collectors" (MCZ). Ten additional specimens from various localities in San Luis Potosi, Mexico, are paratypes (CAS, CNC, DRWh, IRSB, UASM, UKSM).

Diagnostic combination. - Specimens of this species differ from all others in the genus by the following combination of characteristics. prothoracic pleura strongly microsculptured; front tibia strongly broadened basally; and front femur strongly constricted near apex.

Description. - Body flattened. Color castaneous to rufopiceous, without metallic luster, legs and antennae ferrugineous, tarsi and palpi testaceous.

Integument. Strong microsculpture on paramedian frontal sulci, mouthparts, genae, sides and base of pronotum, prothoracic pleura, front legs, middle legs except anterior surfaces of trochanters, hind legs, elytral epipleura, and entire abdomen.

Head. Fig. 160, 161. Generally as in *S. amphibius*, except eyes prominent to strongly flattened, and antennal article five about 1.7-1.8 times longer than wide.

Pronotum. Form and sculpture, Fig. 160. Otherwise as in *S. amphibius* except anterior transverse impression strongly punctate.

Legs. Front and middle tarsi strongly dilated and pubescent ventrally in males, less so in females; hind tarsus slender. Paronychia conspicuous, nearly as long as tarsal claws. Front tibia (Fig. 166) parallel sided, not or hardly narrowed toward base; distal tooth (Fig. 167-168) varied in form. Front femur strongly constricted near apex.

Elytra. Left elytron with 8-11 setae on interval three, 7-10 on interval five, and 3-6 on interval seven. Striae deep, sharply engraved, strongly punctate in basal two-thirds. Otherwise as in *S. amphibius*.

Male genitalia. Median lobe, Fig. 172, 173; endophallus, Fig. 181; eight specimens examined.

Measurements and proportions. Of holotype: TL, 4.56 mm; LE, 2.77 mm; WH, 0.87 mm; WP, 1.17 mm; WE, 1.45 mm; WF/WH, 0.63; LP/WP, 1.00; DP/LP, 0.75; LP/WE, 0.81; Ta/Ti, 0.65; PS/LP, 0.65. Of allotype: TL, 4.87 mm; LE, 2.95 mm; WH, 0.92 mm; WP, 1.25 mm; WE, 1.54 mm; WF/WH, 0.66; LP/WP, 1.01; DP/LP, 0.74; LP/WE, 0.82; Ta/Ti, 0.61 PS/LP, 0.72.

Variation. - As *S. tibialis* is poorly represented in collections, a statistical analysis of geographic variation is not yet possible. I do not suspect important variation in body size, body form, or in numbers of elytral setae. The largest (LE, 3.12 mm) and smallest (LE, 2.70 mm) males are from Encarnacion de Diaz and Saltillo, respectively, and the largest (LE,3.06 mm) and smallest (LE, 2.73 mm) females are from Monterrey and the Rio Balsas, respectively.

Despite paucity of material, a geographic pattern is evident from unusually pronounced variation in two characteristics. The distal tooth of the front tibia is swollen or spatulate apically in specimens from San Luis Potosi, Veracruz, Oaxaca, and Chiapas (Fig. 167), less so in specimens from Jalisco, and hardly or not at all in specimens from Coahuila, Guerrero, Tamaulipas, and Texas (Fig. 168). Relative eye sizes (WF/WH) are summarized in Fig. 188; eyes are prominent in specimens from San Luis Potosi and Veracruz (Fig. 160), less so in specimens from Oaxaca, decrease in prominence northward, and are especially flattened in specimens from Indian Creek Cave in Texas (Fig. 161). Only forms with prominent eyes have been taken in series, in San Luis Potosi and Oaxaca, and even they were not found as abundantly as were specimens of other species. The distribution of *S. tibialis* is probably correlated with the distribution of limestone, and perhaps of limestone caves, as all samples were obtained in regions in or near limestone out-croppings.

Probably there are no important barriers to gene flow along the Atlantic slope from San Luis Potosi south to Oaxaca, then back north along the Pacific slope to the Trans-Volcanic Sierra and inland along its northern drainages. As there is more similarity between Jalisco and San Luis Potosi samples in form of distal tooth of front tibia than between the latter and the Guerrero specimen, there may be some gene flow there. And the eye size pattern suggests that there is no serious barrier to gene flow between Jalisco and Atlantic drainage systems in Coahuila, Tamaulipas, and Texas. The particularly small eye of Indian Creek Cave specimens suggests a steeply stepped cline; those specimens might be reproductively isolated, but the existence of a reasonable geographic cline argues otherwise. However, large-eyed populations from San Luis Potosi are structurally isolated from smaller-eyed forms from Texas and Tamaulipas, and may be reproductively isolated and even sympatric. Thus, samples of *S. tibialis* probably represent a circle of races, as shown in Fig. 188. This hypothesis requires further investigation. In particular, further collections should be made in Tamaulipas, in the Sierra de Guatemala and Sierra de Tamaulipas, to determine whether sympatry exists.

Etymology. - Latin, *tibialis* = of the tibia, a reference to the peculiar structure of the front tibia.

Distribution. - Specimens of this species have been collected from the Nueces River system in southern Texas, south to southeastern Oaxaca (Fig. 188) and northern Chiapas, in a pattern strongly suggesting a circle of races. I studied 35 specimens of this species from the following localities.

UNITED STATES

TEXAS: Uvalde Co., Indian Creek Cave (2; TCBa); Val Verde Co., 9 mi. se. Del Rio (1; USNM).

MEXICO

CHIAPAS: 31 mi. w. Lazaro Cardenas (1; CNC). COAHUILA: 14 mi. n. Saltillo (1; BMNH). GUERRERO: Rio Balsas (1; MCZ). JALISCO: 9.7 mi. e. Encarnacion de Diaz (3; UASM). NUEVO LEON: 5 mi. s. Monterrey (2; CNC). OAXACA: 11.1 mi. n. Matias Romero (1; UASM), Tapanatepec (9; UKSM). SAN LUIS POTOSI: El Salto de Agua (1; CNC), Huichihuayan (3; UKSM), 17 ni. n. Palitla (1; DRWh), Rio Verde (1; IRSB), 2 mi. e. Tamazunchale (1; UASM), 5 mi. n. Tamazunchale (1; CAS), 19.3 mi. nw. Tamazunchale (4; DRWh, MCZ, UASM). TAMAULIPAS: 73.1 mi. n. Manuel (1; UASM). VERACRUZ: 20 mi. nw. Huatusco (1; FDAG).

Collecting notes. - Specimens of this species have been collected nearly throughout the year. Some were taken at lights. Both specimens from Indian Creek Cave were taken in a deep cave, and at that locality the species may be troglobitic. Elsewhere I suspect individuals are found near the surface only incidentally, and live at a much wider range of depths in gravel bars than do most other species in the genus.

Taxonomic notes. - The only other species known to have broadened front tibiae, *S. dilatus*, is sympatric with *S. tibialis* at least in

Nuevo Leon, and lacks marked subepigean adaptations. Specimens of *S. tibialis* have more strongly constricted front femora, and coarser microsculpture on the prothoracic pleura.

Specimens from Indian Creek Cave may represent a truly troglobitic species, reproductively isolated from the more southern epigean or subepigean forms. Or, they may represent a distinctive subspecies, since they are visibly distinct in eye size, and geographically are from an adjacent drainage system. But I think the eye size character varies in a direct, though steeply stepped, cline, and I prefer to take no further taxonomic action on them at least until additional material is available for analysis.

3.504 *Schizogenius amphibius* Haldeman

Clivina amphibia Haldeman 1843:299. *Type locality* southeastern Pennsylvania; type in MCZ, specimen labelled "amphibius 2" here designated lectotype (!). LeConte 1848:215.

Schizogenius amphibius, LeConte 1857:83. Putzeys 1863:24. Putzeys 1866:224. LeConte 1879:34. Lindroth 1961:168.

Clivina frontalis LeConte 1848:215. *Type locality* Westchester County, New York; type male MCZ, specimen labelled MCZ 5482 here designated lectotype (!).

Schizogenius frontalis, LeConte 1857:83, suggested synonymy.

Diagnostic combination. - Specimens of this species are easily distinguished from all others in the group by small size and coarsely punctate prothoracic pleura.

Description. - Body flattened. Color testaceous, without metallic luster.

Integument. Coarse microsculpture in paramedian frontal sulci and on sides of abdomen. Fine but conspicuous microsculpture on mouthparts, genae, front legs except posterior surfaces of femora and trochanters, middle legs except anterior surfaces of trochanters, hind tibiae and posterior surfaces of hind femora, elytral epipleura, and middle of abdomen. Indistinct microsculpture sometimes on median portion of frons and on prothoracic pleura. Prothoracic pleura coarsely punctate.

Head. Fig. 162. Paramedian clypeal carinae straight, extended to median tooth, strongly elevated in basal half; median field triangular, no wider at base than apex of median field of frons. Clypeal suture sharply defined. Eye small, slightly flattened, finely and uniformly faceted. Neck densely and coarsely punctate. Gena coarsely punctate, rugose in front. Antennal articles four to ten elongate, filiform, article five about 1.4 times longer than wide.

Pronotum. Form and sculpture, Fig. 162. Sides bisetose, hind angles sharp and prominent, base not rugose. Paramedian longitudinal sulci long, impunctate, nearly straight, deep throughout, in most specimens sharply hooked basally. Anterior transverse impression finely punctate.

Legs. Front tarsus slightly dilated and pubescent ventrally in both sexes; middle and hind tarsi slender, short. Paronychia nearly as long as tarsal claws. Front tibia narrowed evenly to base. Front femur not strongly constricted near apex.

Elytra. Left elytron with 9-14 setae each on intervals three and five, and 5-10 on interval seven, adjacent to corresponding inner striae.

Striae deep, sharply engraved, finely punctate in basal two-thirds. Intervals one to seven broad and flat, interval eight carinate at apex; apices of intervals three, five, and seven broadly joined. Humeral denticles sharp and prominent.

Abdomen. Sternum three with paramedian carinae curved outward at apices. Sternum seven with paramedian ambulatory setae in males only. Pygidium with apical margin entire in both sexes, or finely crenulate in a few females.

Male genitalia. Median lobe, Fig. 174, apex not sharply deflexed; endophallus with elongate basal collar spines; 6 specimens examined.

Measurements and proportions. See Table 29.

Variation. - I noted no obvious important variation, and because the only good population samples are clustered in a small geographic area, I did not study variation in detail. The largest (LE, 2.80 mm) and smallest (LE, 1.80 mm) specimens are females from New York.

Etymology. - For *S. amphibius*, Greek, *amphibios* = amphibius, a reference to the habitat. For *S. frontalis*, Latin, *frons* = frons, a reference to the sculpture of the frons.

Distribution. - *S. amphibius* is known to range from Michigan and Quebec south to Tennessee and North Carolina (Fig. 190). An isolated form may exist in Texas, as I have seen four specimens from there but without definite locality data (ANSP, UKSM, USNM), but confirmation is needed; no other specimens are known from west of the Mississippi River. I studied 188 additional specimens from the following localities.

CANADA

QUEBEC: Montreal (1; USNM). See Lindroth (1961) for additional records.

Table 29. Descriptive statistics in *S. amphibius*, based on 10 males from Ithaca, New York.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.18-3.38	3.307	0.101	0.042	2.03
LE	1.95-2.10	2.045	0.078	0.033	2.53
WH	0.62-0.68	0.651	0.024	0.010	2.45
WP	0.81-0.88	0.840	0.039	0.016	3.07
WE	0.99-1.05	1.025	0.039	0.016	2.51
B. Setae on left elytron.					
Interval 3	11-14	12.5			
Interval 5	10-14	11.5			
Interval 7	6-10	7.7			
Total	29-36	31.7	4.0	1.7	8.42
C. Proportions.					
WF/WH	0.68-0.71	0.698	0.021	0.009	2.00
LP/WP	0.93-0.98	0.952	0.024	0.010	1.70
DP/LP	0.76-0.81	0.781	0.024	0.010	2.05
LP/WE	0.76-0.81	0.781	0.029	0.012	2.45
Ta/Ti	0.55-0.65	0.607	0.045	0.019	4.91
PS/LP	0.69-0.78	0.742	0.039	0.017	3.52

UNITED STATES

No locality (6; ANSP, IRSB, USNM). CONNECTICUT: Hartford Co., West Hartford (1; MCZ). DISTRICT OF COLUMBIA: Washington (10; AMNH, ANSP, MCZ, USNM). ILLINOIS: Pike Co., Pittsfield (1; UCD). INDIANA: Tippecanoe Co. (1; UCD). KENTUCKY: Ballard Co., Wickliffe (2; TCBa); Jackson Co., Sand Gap (1; TCBa); Metcalfe Co., Edmonton (2; DRWh); Powell Co., Slade (1; TCBa). MAINE (1; MCZ); Oxford Co., Paris (2; MCZ). MARYLAND (4; INHS, USNM): Frederick Co., Frederick (1; RTBe). MICHIGAN (2; CAS). NEW HAMPSHIRE: Grafton Co., Franconia (4; AMNH, MCZ). NEW JERSEY: Burlington Co., Riverside (1; MCZ), Camden Co., Camden (1; MCZ), Cramer Hill (1; USNM); Essex Co., Irvington (1; CAS). NEW YORK (13; CAS, CNHM, INHS, KSUM, USNM): New York City vicinity (5; AMNH, CAS, MCZ); Long Island (1; USNM); Albany Co., Altamont (1; CUNY); Dutchess Co., Hyde Park (4; CAS); Herkimer Co., Newport (1; MCZ); Orange Co., West Point (21; USNM); Tompkins Co., Groton (4; CAS), Ithaca (20; CAS, CUNY, USNM, VMKi), Varna (2; UASM); Ulster Co., Esopus (2; CUNY), Phoenicia (3; CAS, CNHM); Westchester Co., Peekskill (20; CAS, CUNY, MCZ, PSUU), Tarrytown (3; LACM); Wyoming Co., Pike (2; MCZ). NORTH CAROLINA: Buncombe Co., Black Mountains (7; AMNH, CAS, MCZ). OHIO: Mohican Point (1; UMCG); Ashtabula Co., Ashtabula (1; MSU), Jefferson (1; MSU). PENNSYLVANIA (1; ANSP): Allegheny Co. (1; MCZ); Bucks Co., Parkland (3; RUNB); Philadelphia Co., Frankford (2; USNM); Pike Co., Milford (1; USNM); Warren Co., Warren (3; CAS); Gray's Ferry (2; RUNB). RHODE ISLAND: Providence Co., Providence (1; USNM). TENNESSEE: Jackson Co., Blackman Fork (2; TCBa); Smith Co., Lancaster (1; TCBa), Monoville (1; TCBa). VERMONT: Franklin Co., East Georgia (1; RTBe); Rutland Co., Clarendon

(1; USNM); Windham Co., Brattleboro (2; RTBe). VIRGINIA: Alexandria Co. (5; USNM); Fairfax Co., Mount Vernon (1; USNM); Spotsylvania Co., Fredericksburg (1; USNM). WEST VIRGINIA: Greenbrier Co., White Sulphur Springs (3; CAS, MCZ).

Collecting notes. - Specimens of *S. amphibius* have been collected from April until September, generally in small numbers. I collected two specimens near Edmonton, Kentucky, together with specimens of *S. sulcifrons*, *S. lineolatus*, and *S. planulatus*. But a long series was taken at West Point, New York, so habitat requirements of *S. amphibius* must differ in some way from those of other, sympatric species. Its range is more completely restricted to limestone regions than those of either *S. sulcifrons* or *S. lineolatus*, and the reduced eyes suggest a more subterranean habitat.

Taxonomic notes. - All of Haldeman's types are supposed to be in the LeConte Collection, at the head of each relevant series. However, the only specimens eligible for recognition as type material of *S. amphibius* are specimens 2, 3, 4, and 5, each so labelled and from Pennsylvania. The first specimen in the series is the only specimen representing type material of *S. frontalis* LeConte, and is the lectotype. I selected specimen 2 as lectotype of *amphibius*.

S. amphibius has no known close relatives, nor did I find any interesting patterns of variation within the species. If, however, specimens labelled "Texas" really were found there, they may not be conspecific. I doubt that *S. amphibius* will be found in any area between Texas and the Mississippi River, so that Texan populations, if they exist, would be markedly disjunct.

3.505 *Schizogenius planulatus* LeConte

Schizogenius planulatus LeConte 1863:5. *Type area* New York; type in MCZ; female labelled MCZ 5481 here designated lectotype (!). Putzeys 1866:224. LeConte 1879:34. Lindroth 1961:166.

Diagnostic combination. - Body strongly flattened. Dark testaceous to castaneous, unmetallic.

Integument. Conspicuous microsculpture on paramedian frontal sulci, mouthparts, apex of gula, genae, front legs except posterior surfaces of femora and trochanters, middle legs except anterior surfaces of trochanters, hind tibiae and posterior surfaces of hind femora, extreme base and sides of pronotum, apical two-thirds of elytral epipleura, and entire abdomen. Fine microsculpture on basal third of elytral epipleura, and sometimes on prothoracic pleura and median frontal sulcus.

Head. Fig. 163. Paramedian clypeal carinae straight, moderately elevated in basal half, extended to median tooth; median field triangular, narrow, no wider at base than apex of median frontal sulcus. Clypeal suture sharply defined. Eye small, slightly flattened, finely and uniformly faceted. Neck densely and coarsely punctate. Gena coarsely punctate, rugose in front. Antennal articles four to ten elongate, article five about 2.2 times longer than wide.

Pronotum. Fig. 163. Sides bisetose; base not rugose; hind angles small. Paramedian longitudinal sulci long, nearly straight, deep, sharply hooked basally. Anterior transverse impression finely punctate.

Legs. Front and middle tarsi moderately dilated and pubescent ventrally, less so in females; hind tarsus slender, short. Paronychia nearly as long as tarsal claws. Front tibia narrowed evenly to base. Front femur not strongly constricted near apex.

Elytra. Left elytron with 10-14 setae on interval three, 9-12 on interval five, 6-9 on interval seven; total 27-34 in specimens examined. Striae deep and sharply engraved, finely punctate in basal three-fourths. Intervals one to seven broad and flat, interval eight carinate at apex; intervals three, five, and seven broadly joined at apices. Humeral denticles sharp but not prominent.

Abdomen. Sternum three with paramedian carinae curved outward at apices. Sternum seven with paired paramedian ambulatory setae in males only. Pygidium with apical margin strongly serrate in females, entire in males.

Male genitalia. Median lobe, Fig. 175, apex characteristic; endophallus, Fig. 182; 5 specimens examined.

Measurements and proportions. See Table 29.

Etymology. - Latin, *planus* = flat, in reference to the body form.

Distribution. - I have seen specimens of this species only from Kentucky, New York, and West Virginia (Fig. 189) but it has been reported from Georgia (Fattig, 1949) and probably ranges throughout the Appalachian region at least in limestone areas. I studied 20 specimens from the following localities.

UNITED STATES

KENTUCKY: Metcalfe Co., 9 mi. e. Edmonton (3; DRWh, IRSB). NEW YORK: Erie Co., North Evans (2; CAS, MCZ); Tompkins Co., Ithaca (13; CAS, CUNY, UASM), Groton (1; JNeg). WEST VIRGINIA: Greenbrier Co., White Sulphur Springs (1; MCZ).

Table 30. Descriptive statistics for *S. planulatus*, based on 11 females plus 4 males from New York.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	4.85-5.30	5.133	0.236	0.081	3.06
LE	3.00-3.28	3.190	0.128	0.044	2.67
WH	0.97-1.08	1.042	0.052	0.018	3.34
WP	1.28-1.42	1.357	0.067	0.023	3.30
WE	1.55-1.68	1.629	0.060	0.021	2.44
B. Setae on left elytron.					
Interval 3	10-14	11.6			
Interval 5	9-12	10.5			
Interval 7	6- 9	7.3			
Total	27-34	29.3	3.0	1.0	6.78
C. Proportions.					
WF/WH	0.66-0.71	0.687	0.023	0.008	2.25
LP/WP	0.88-0.94	0.909	0.026	0.009	1.88
DP/LP	0.74-0.81	0.777	0.028	0.009	2.37
LP/WE	0.71-0.78	0.755	0.026	0.009	2.29
Ta/Ti	0.53-0.65	0.605	0.049	0.017	5.42
PS/LP	0.69-0.74	0.708	0.020	0.007	1.92

Collecting notes. - Specimens of this species have been collected from May to September. I collected the Kentucky specimens in a gravel bar, along with specimens of *S. amphibius*, *S. lineolatus*, and *S. sulcifrons*. Specimens of this species probably tend to be subepigean, as so few have been collected.

Taxonomic notes. - Specimens of this species differ radically from the related *S. ozarkensis* and *S. planuloides* in form of male genitalia, but otherwise probably are indistinguishable. As I found no important geographic variation in the form of the male genitalia in any of these species, I conclude that the form of the genitalia is constant and that the three geographic segregates truly represent distinct species. See discussion for *S. planuloides*, section 3.507.

3.506 *Schizogenius ozarkensis* new species

Type material. - Holotype male and allotype female labelled "5 mi. n. Stringtown Atoka Co. OKLAHOMA 7.IX.1964 Awram-Whitehead" (MCZ). 24 additional specimens from various localities in Arkansas, Missouri, and Oklahoma are paratypes (BMNH, CAS, CNC, DRWh, INHS, IRSB, UASM, UKSM, USNM).

Diagnostic combination. - Males of this species differ strikingly from those of *S. planulatus* and *S. planuloides* in form of apex of median lobe. This species is the only member of the *tristriatus* group known from the Ozark region, north of the Red River and west of the Mississippi River.

Description. - Superficially as in *S. planulatus*, except frontal lobes prominent. Left elytron with 10-14 setae on interval three, 9-12 on interval five, and 6-9 on interval seven; total 25-32. Male genitalia with median lobe, Fig. 176, apex characteristic; endophallus, Fig. 183; 6 specimens examined.

Measurements and proportions. See Table 30. Of holotype: TL, 4.74 mm; LE, 2.92 mm; WE, 0.95 mm; WP, 1.24 mm; WE, 1.48 mm; WF/WH, 0.68; DP/LP, 0.74; LP/WP, 0.93; LP/WE, 0.78; PS/LP, 0.76; Ta/Ti, 0.61. Of allotype: TL, 4.68 mm; LE, 2.90 mm; WH, 0.94 mm; WP, 1.18 mm; WE, 1.45 mm; WF/WH, 0.68; DP/LP, 0.76; LP/WP, 0.96; LP/WE, 0.81; PS/LP, 0.69; Ta/Ti, 0.65.

Etymology. - I name this species after the Ozark Mountains, as this species is known only from in or near this area.

Distribution. - This species is known from only a small area in eastern Oklahoma, western Arkansas, and southern Missouri (Fig. 189). I studied 27 specimens from the following localities.

UNITED STATES

ARKANSAS: Carroll Co., 5 mi. w. Berryville (4; BMNH, CNC), Eureka Springs (2; UKSM); Van Buren Co., Formosa (2; IRSB); Washington Co. (1; INHS), 7 mi. s. Fayetteville (8; UASM). MISSOURI: Butler Co., 12 mi. se. Elsinore (4; CAS). OKLAHOMA: Atoka Co., 5 mi. n. Stringtown (5; DRWh, MCZ, USNM); Ottawa Co., Wyandotte (1; MCZ).

Collecting notes. - Adults of this species have been found from June to September, in riparian gravel bars.

Taxonomic notes. - Although adults of this species cannot be distinguished from those of *S. planulatus* and *S. planuloides* by external morphology, details of the male genitalia differ radically and show no

Table 31. Descriptive statistics for *S. ozarkensis*, based on 10 females and 7 males from northwestern Arkansas.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	4.50-5.16	4.848	0.249	0.081	3.43
LE	2.80-3.22	3.006	0.155	0.050	3.44
WH	0.90-1.04	0.978	0.059	0.019	4.03
WP	1.10-1.32	1.225	0.062	0.020	3.40
WE	1.38-1.58	1.502	0.076	0.025	3.37
B. Setae on left elytron.					
Interval 3	10-14	11.2			
Interval 5	9-12	10.4			
Interval 7	6- 9	7.2			
Total	26-32	28.8	3.5	1.1	8.01
C. Proportions.					
WF/WH	0.64-0.74	0.671	0.038	0.012	3.76
LP/WP	0.92-0.98	0.948	0.024	0.008	1.69
DP/LP	0.73-0.77	0.751	0.017	0.006	1.52
LP/WE	0.74-0.80	0.771	0.027	0.009	2.29
Ta/Ti	0.60-0.68	0.643	0.041	0.014	4.28
PS/LP	0.66-0.74	0.690	0.033	0.011	3.16

sign of intergradation. Hence, I think that *S. ozarkensis* is reproductively isolated from them. See discussion for *S. planuloides*, section 3.507.

3.507 *Schizogenius planuloides* new species

Type material. - Holotype male labelled "Cypress Mills 7/1/88 Texas" and "2048" (USNM). An additional 19 specimens from various localities in Texas are paratypes (ANSP, CAS, CNHM, DHKa, DRWh, MSUL, UASM, UKSM, USNM).

Diagnostic combination. - Specimens of this species are readily distinguished from those of the related *S. planulatus* and *S. ozarkensis* only by details of the male genitalia and by the allopatric geographic distribution.

Description. - Superficially as in *S. planulatus*, except eyes in most specimens more strongly flattened and frontal lobes more prominent. Left elytron with 9-13 setae on interval three, 9-12 on interval five, and 6-8 on interval seven; total 26-31. Male genitalia with median lobe, Fig. 177, apex characteristic; endophallus, Fig. 184; 3 specimens examined.

Measurements and proportions. See Table 31. Of holotype: TL, 5.20 mm; LE, 3.20 mm; WH, 1.06 mm; WP, 1.34 mm; WE, 1.69 mm; WF/WH, 0.71; DP/LP, 0.75; LP/WP, 0.95; LP/WE, 0.76; PS/LP, 0.69; Ta/Ti, 0.70.

The claw-bearing article of the left hind tarsus of the type is lacking.

Table 32. Descriptive statistics for *S. planuloides*, based on 6 females and 12 males from Texas.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	4.94-5.54	5.194	0.244	0.077	3.13
LE	3.05-3.45	3.204	0.160	0.050	3.33
WH	1.02-1.15	1.084	0.050	0.016	3.07
WP	1.22-1.40	1.322	0.076	0.024	3.82
WE	1.50-1.75	0.628	0.095	0.030	3.88
B. Setae on left elytron.					
Interval 3	9-13	11.0			
Interval 5	9-12	10.4			
Interval 7	6- 8	6.9			
Total	26-31	28.3	2.3	0.7	5.25
C. Proportions.					
WF/WH	0.68-0.73	0.703	0.022	0.007	2.13
LP/WP	0.93-0.98	0.956	0.021	0.007	1.49
DP/LP	0.72-0.78	0.752	0.024	0.008	2.16
LP/WE	0.75-0.79	0.776	0.019	0.006	1.67
Ta/Ti	0.63-0.68	0.645	0.021	0.007	2.19
PS/LP	0.64-0.73	0.675	0.033	0.011	3.30

Etymology. - Latin, *planulatus* + *oides* = like *planulatus*, in reference to the great external similarity of this species to *S. planulatus*.

Distribution. - This species is known from only six definite localities throughout much of Texas (Fig. 189). Specimens labelled simply "Texas" may well have been collected at the type locality, since that was a favority early collecting locality in Texas. I studied 22 specimens of this species from the following localities.

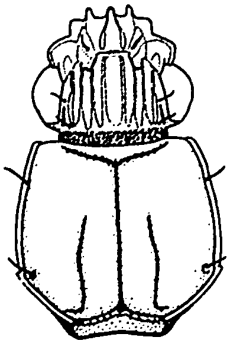
UNITED STATES

TEXAS (15; ANSP, CAS, MSUL, UKSM, USNM): Blanco Co., Cypress Mills (1; USNM); Coryell Co. (1; MCZ); Dallas Co., Dallas (1; MCZ); Kinney Co., 23 mi. sw. Brackettville (1; DRWh); McLennon Co., Waco (1; DHKa); Taylor Co., 25 mi. sw. Abilene (1; CNHM); Terrell Co., Independence Creek (1; UASM).

Collecting notes. - Specimens of this species have been collected from March through July, some at lights distant from water. I collected one specimen near Brackettville in a riparian gravel bar, along with several specimens of *S. scopaeus* and over 100 of *S. sallei*. Scarcity of specimens, and more strongly reduced eyes, suggest that this species is more strongly subepigean than either *S. planulatus* or *S. ozarkensis*. As in those species, I suspect that geographic distribution depends on surface and subsurface limestone.

Taxonomic notes. - The well differentiated male genitalia of this species indicates reproductive isolation from *S. planulatus* and *S. ozarkensis*. The geographically intermediate *S. ozarkensis* has less specialized male genitalia, but the genitalia of *S. planulatus* and *S. planuloides* are specialized in different ways. As shown in Tables

Fig. 158-163. Head and pronotum, dorsal aspect. 158. *S. sallei* Putzeys, Comstock, Texas. 159. *S. tristriatus* Putzeys, Coscomatepec, Veracruz. 160. *S. tibialis* new species, Tamazunchale, San Luis Potosi. 161. Same, Indian Creek Cave, Texas. 162. *S. amphibius* Haldeman, Edmonton, Kentucky. 163. *S. planulatus* LeConte, Edmonton, Kentucky. Fig. 164-166. Left front tibia, posterior aspect. 164. *S. tristriatus* Putzeys, Coscomatepec, Veracruz. 165. *S. dilatus* new species, Sabinas Hidalgo, Nuevo Leon. 166. *S. tibialis* new species, Tamazunchale, San Luis Potosi. Fig. 167-168. Distal portion of left front tibia, posterior aspect. 167. *S. tibialis* new species, Tamazunchale, San Luis Potosi. 168. Same, Indian Creek Cave, Texas. Fig. 169-173. Male median lobe, lateral aspect. 169. *S. sallei* Putzeys, Austin, Texas. 170. *S. tristriatus* Putzeys, Fortin de las Flores, Veracruz. 171. *S. dilatus* new species, Sabinas Hidalgo, Nuevo Leon. 172. *S. tibialis* new species, Encarnacion de Diaz, Jalisco. 173. Same, Indian Creek Cave, Texas.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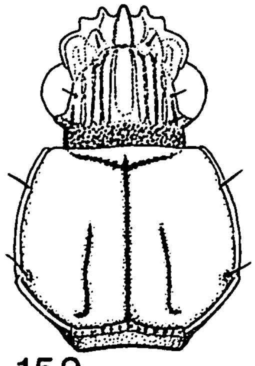
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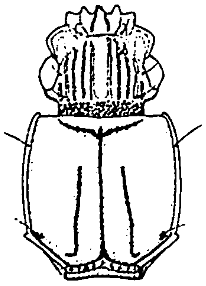
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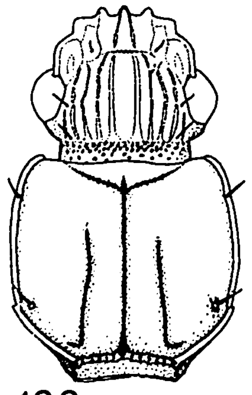
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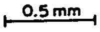

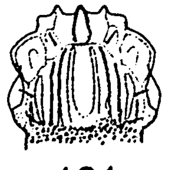
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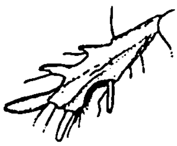
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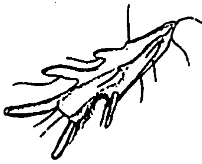
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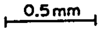

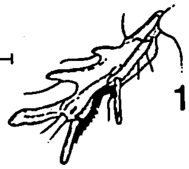
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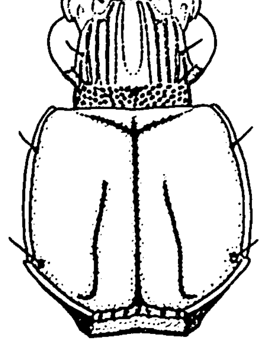
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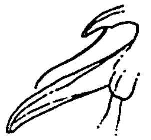
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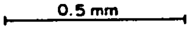

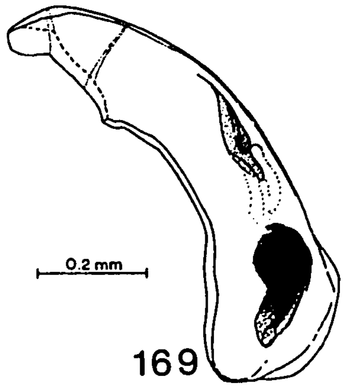

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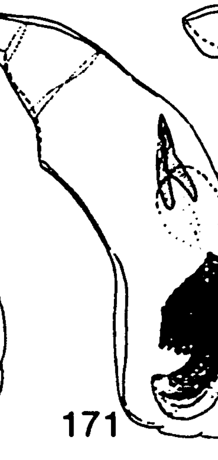
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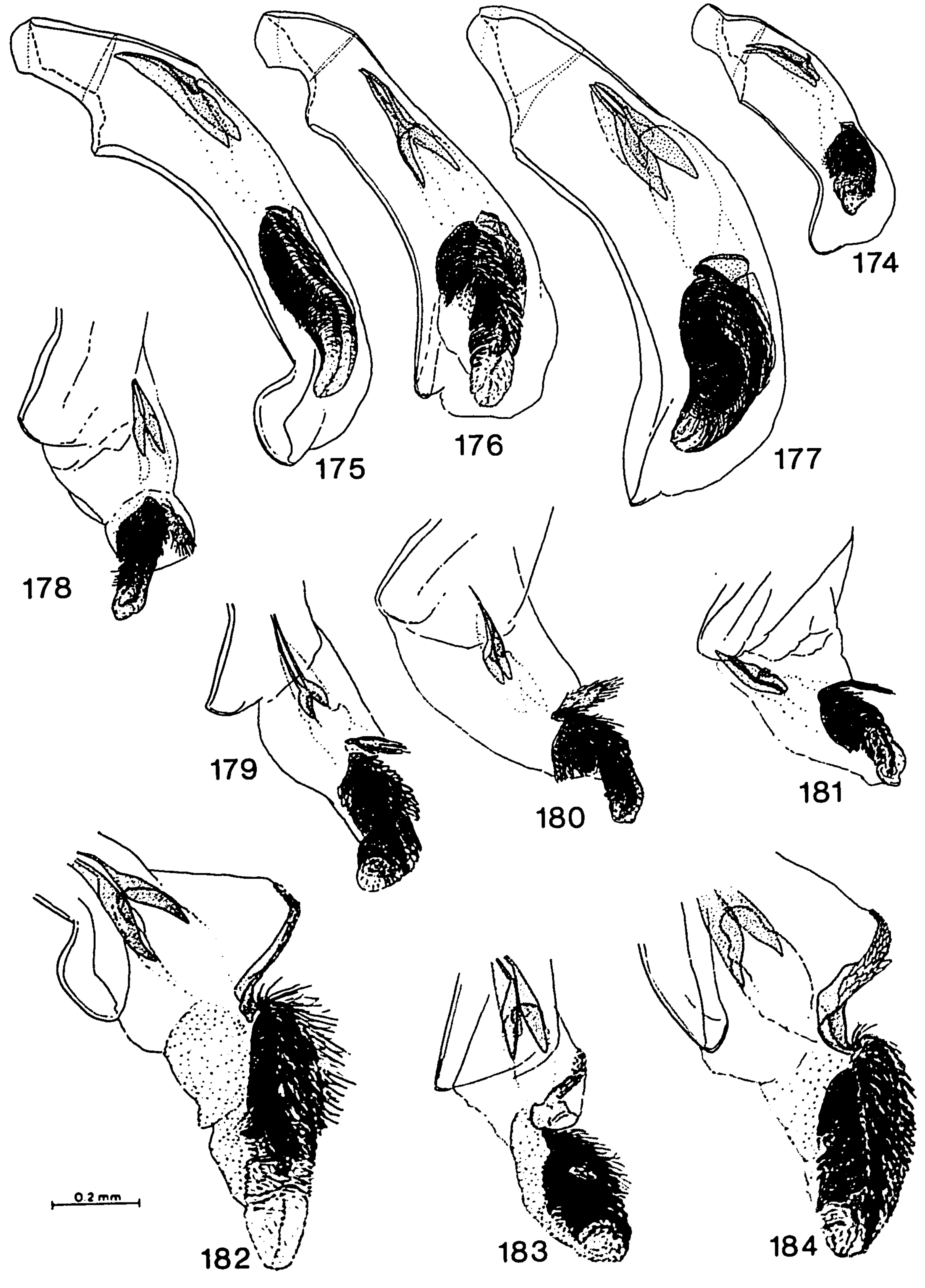
Fig. 174-177. Male median lobe, lateral aspect. 174. *S. amphibius* Haldeman, West Point, New York. 175. *S. planulatus* LeConte, North Evans, New York. 176. *S. ozarkensis* new species, Elsinore, Missouri. 177. *S. planuloides* new species, Texas. Fig. 178-184. Male endophallus. 178. *S. sallei* Putzeys, Sabinal, Texas. 179. *S. tristriatus* Putzeys, Fortin de las Flores, Veracruz. 180. *S. dilatus* new species, Sabinas Hidalgo, Nuevo Leon. 181. *S. tibialis* new species, Tapanatepec, Oaxaca. 182. *S. planulatus* LeConte, Ithaca, New York. 183. *S. ozarkensis* new species, Stringtown, Oklahoma. 184. *S. planuloides* new species, Cypress Mills, Texas.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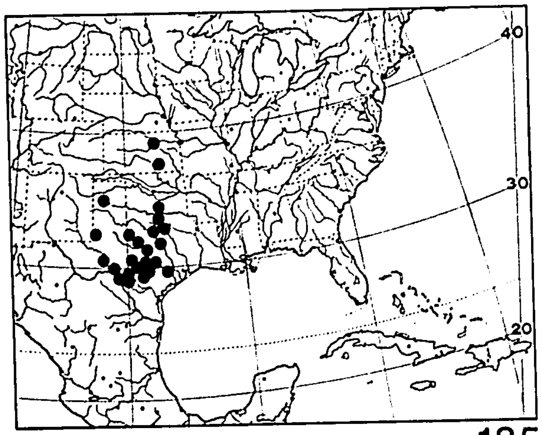
184
0.2 mm

Fig. 185-190. Known distributions. 185. *S. sallei* Putzeys. 186. *S. tristriatus* Putzeys. 187. *S. dilatus* new species. 188. *S. tibialis* new species (with clinal variation in relative eye size). 189. *S. planulatus* LeConte, circles; *S. ozarkensis* new species, triangles; *S. planuloides* new species, squares. 190. *S. amphibius* Haldeman; open symbol represents state record only.



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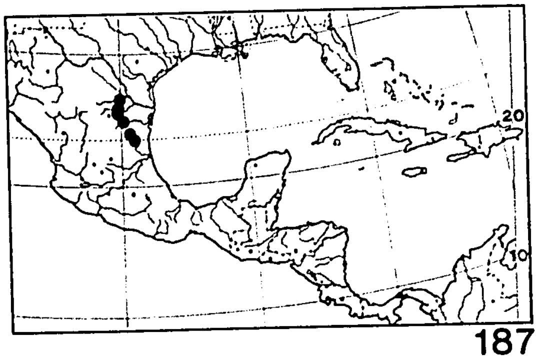
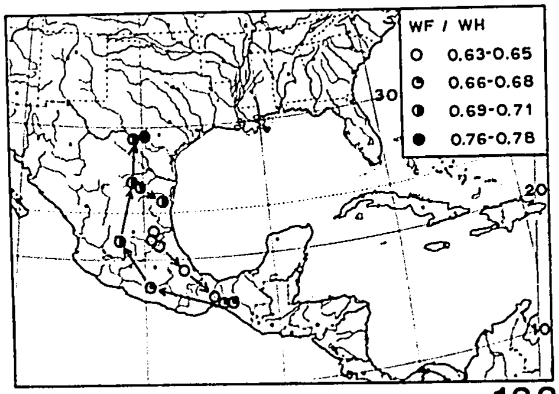
186

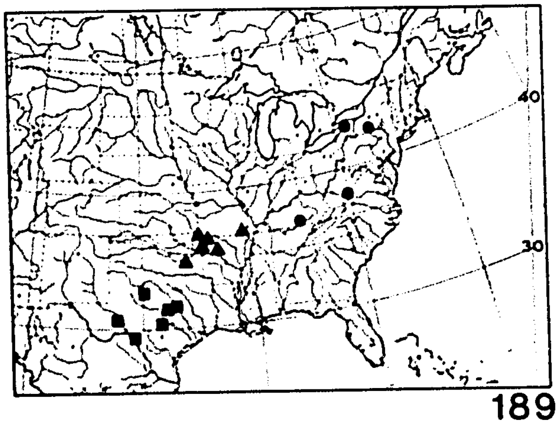


187

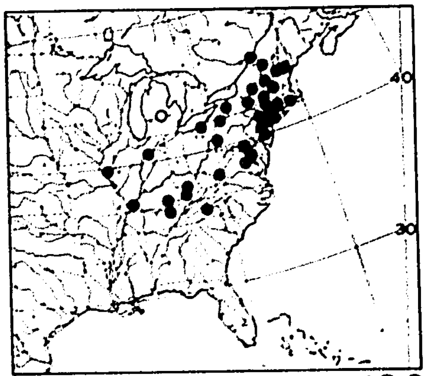


188

1000 mi



189



190

29-31, the sample of *S. planulatus* is characterized by statistically significantly broader pronota, the sample of *S. ozarkensis* by statistically significantly smaller body size, and the sample of *S. planuloides* by statistically significantly smaller eye size. As judged from comparisons with other members of the *tristriatus* group, the ancestor of the *planulatus* subgroup probably had larger eyes as in *S. planulatus* and *S. ozarkensis*, smaller size as in *S. ozarkensis*, and narrower pronota as in *S. ozarkensis* and *S. planuloides*. In all of these ways, *S. ozarkensis* is most like the probable ancestor of the subgroup. For reasons discussed in sections 4.14 and 4.3, I regard *S. ozarkensis* and *S. planulatus* as sister species.

Since I have no females from the type locality, I designate no allotype for *S. planuloides*.

3.51 The *lineolatus* group

Diagnostic combination. - From other members of the genus with antennae elongate, pronotal hind angles prominent, discal setae on intervals three, five, and seven, and paramedian sternal carinae curved at apices, members of this group are distinguished by the following combination of characters: body strongly flattened; elytra aeneopiceous, or rufocastaneous with pale apices; paramedian pronotal sulci not extended forward nearly to anterior transverse impression; elytron with total discal setae fewer than 30, their average length less than 1.0 times maximum width of interval two; and abdomen unmicrosculptured except in small patches near coxal depressions of sternum three. Also: paramedian clypeal carinae extended to median tooth; clypeal field narrow, no wider at base than apex of median frontal sulcus; clypeal suture sharply impressed; frontal carinae not confused at base; submentum without accessory setae; pronotum without paralateral carinae, without accessory marginal setae; front and middle tarsi broadened and with dense ventral pubescence, especially in males; sternum seven with paramedian ambulatory setae in males, not in females; pygidium crenulate at apex or not in females; and endophallus with basal collar spines distinct.

Distribution. - The range of the single included species, *S. lineolatus*, covers much of eastern North America south to the Rio Grande. I examined 876 specimens.

3.511 *Schizogenius lineolatus* Say

Clivina lineolata Say 1823:22. *Type locality* Allegheny, Pennsylvania (designated by Lindroth, 1961); neotype male designated by Lindroth and Freitag (1969). LeConte 1848:214.

Schizogenius lineolatus, LeConte 1857:82. Putzeys 1863:24. Putzeys 1866:228. LeConte 1879:34. Lindroth 1961:166.

Diagnostic combination. - Specimens of this species are best distinguished by characteristics given in the key. In eastern North America, the only other dark species of *Schizogenius* with setae on elytral interval seven is *S. sulcifrons*. Specimens of that species generally have less sharply developed pronotal hind angles, more elytral setae, and concolorous elytra and pronotum.

Description. - Body flattened. Color light to dark castaneous;

legs rufous; tarsi and palpi testaceous; elytra rufopiceous and in most specimens strongly aeneous, except in Rio Grande Valley where castaneous, paler toward apices, and weakly aeneous.

Integument. Conspicuous microsculpture on paramedian frontal sulci, mouthparts, genae, front legs except posterior surfaces of femora and trochanters, middle legs except anterior surfaces of trochanters, hind tibiae and posterior surfaces of hind femora, elytral epipleura on apical two-thirds and in most eastern specimens on shoulder and on basal third, and sternum three in coxal depressions and small paralateral patches.

Head. Fig. 191. Paramedian clypeal carinae straight, moderately elevated in basal half, extended to median tooth; median field triangular, narrow, no wider at base than apex of median frontal sulcus. Clypeal suture sharply defined. Eye prominent, finely and uniformly faceted. Neck densely punctate. Gena coarsely punctate, rugose in front. Antennal articles four to ten elongate, article five about 1.7-1.8 times longer than wide.

Pronotum. Fig. 191. Sides bisetose; base not rugose; hind angles prominent. Paramedian longitudinal sulci quite long, nearly straight, strongly hooked basally. Paralateral carinae absent. Anterior transverse impression strongly punctate in most specimens.

Legs. Front and middle tarsi moderately dilated and pubescent ventrally, less so in females; hind tarsus slender, short. Paronychia nearly as long as tarsal claws. Front tibia narrowed evenly to base. Front femur not strongly constricted near apex.

Elytra. Left elytron with about six to nine setae on interval three, five to eight on interval five, two to five on interval seven; total 13-20 in specimens examined. Striae deep and sharply engraved, finely punctate in basal two-thirds. Intervals one to seven broad and flat, interval eight carinate at apex; intervals three, five, and seven broadly joined at apices. Humeral denticles prominent.

Abdomen. Sternum three with paramedian carinae curved outward at apices. Sternum seven with paramedian ambulatory setae in males only. Pygidium with apical margin crenulate in some females, entire in males.

Male genitalia. Median lobe, Fig. 196; endophallus, Fig. 201; virga small; 20 specimens examined.

Measurements and proportions. See Table 33.

Variation. - Statistical data on variation in body size, numbers of elytral setae, relative eye size, and pronotal form are given in Tables 34-37 for 17 samples of *S. lineolatus* (Fig. 211-214). Body size (Table 34, Fig. 211) decreases quite regularly from northeast to southwest, with no geographically proximate samples statistically significantly distinct from one another. Numbers of elytral setae (Table 35, Fig. 212) tend to increase from northeast to southwest, and the Rio Grande sample (number 17) barely is statistically significantly distinct from the Guadalupe River sample (number 16). Eye size (Table 36, Fig. 213) increases generally southwest to the Guadalupe River (sample 16), with a statistically significant increase in the east between samples four and five, but is sharply reduced between samples 16 and 17. The pronotum (Table 37, Fig. 214) narrows from northeast to southwest, with statistically significant gaps between the Red River (sample 14), the Guadalupe River (sample 16), and the Rio Grande (sample 17).

Table 33. Descriptive statistics for *S. lineolatus*, based on 20 males from 5 miles north of Stringtown, Oklahoma.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.80-4.44	4.412	0.288	0.077	4.15
LE	2.35-2.74	2.558	0.153	0.046	4.00
WH	0.81-0.95	0.875	0.052	0.016	3.97
WP	1.00-1.20	1.092	0.083	0.025	5.08
WE	1.20-1.42	1.324	0.084	0.025	4.22
B. Setae on left elytron.					
Interval 3	6- 8	6.8			
Interval 5	5- 8	6.2			
Interval 7	2- 4	3.1			
Total	14-19	16.1	1.9	0.6	7.78
C. Proportions.					
WF/WH	0.55-0.59	0.567	0.017	0.005	1.99
LP/WP	0.87-0.94	0.910	0.021	0.006	1.55
DP/LP	0.80-0.86	0.830	0.024	0.007	1.93
LP/WE	0.73-0.77	0.749	0.019	0.006	1.73
Ta/Ti	0.60-0.69	0.643	0.037	0.011	3.85
PS/LP	0.76-0.82	0.786	0.025	0.007	2.08

Variation in extent of evident microsculpture on basal third of elytral epipleura and on shoulder follows a pattern of gradual reduction from east to west. Microsculpture on the basal third of the epipleura is present on most specimens from east of the Appalachians, absent from most specimens from west of the Mississippi River, and varied in specimens from intermediate areas. Microsculpture is evident on the shoulder of most specimens from all areas except in many from the most western localities such as in western Oklahoma and eastern Wyoming, but is most strongly developed in eastern specimens.

Specimens from the Rio Grande Valley (sample 17) differ from all others, except some teneral specimens, in elytral coloration: reddish rather than blackish, and paler toward apices. In this characteristic, these specimens do not intergrade with those from the nearest localities where *S. lineolatus* is known to exist, in the Guadalupe River system (sample 16) some 125-150 miles distant. These two samples also are statistically distinct in the number of elytral setae, relative eye size, and pronotal form, but are not distinct in epipleural microsculpture or in body size. Lack of differentiation in some characteristics, evidence of clinal continuity in others, and in particular the fine clinal sequence in variation in pronotal form shown by samples 14-16-17 strongly indicate that the Rio Grande population is not reproductively isolated. But the difference in coloration is constant, statistically significant differences exist for numbers of elytral setae, relative eye size, and pronotal form, and the direction of clinal variation is reversed in the relative eye size characteristic. I conclude from these facts that the Rio Grande form is geographically isolated from populations to the north, and predict

Table 34. Variation in body size (LE, in mm) in selected samples of *S. lineolatus*; see Fig. 211.

Sample	N	Males	Range	Mean	1.5SD	2SE	CV(%)
1	10	5	2.82-3.08	2.902	0.127	0.053	2.91
2	10	5	2.65-3.08	2.844	0.218	0.092	5.12
3	18	9	2.55-3.15	2.828	0.197	0.062	4.68
4	12	6	2.58-2.98	2.813	0.212	0.082	5.03
5	28	14	2.40-3.04	2.735	0.252	0.064	6.14
6	16	8	2.55-2.95	2.756	0.178	0.069	4.30
7	12	6	2.62-3.02	2.802	0.178	0.069	4.24
8	12	6	2.55-3.00	2.750	0.184	0.071	4.46
9	10	5	2.40-2.92	2.663	0.237	0.100	5.93
10	10	5	2.55-2.98	2.766	0.199	0.084	4.81
11	14	7	2.45-2.90	2.643	0.189	0.067	4.76
12	14	7	2.48-2.88	2.677	0.156	0.056	3.90
13	22	11	2.42-3.00	2.703	0.200	0.057	4.94
14	26	13	2.35-2.85	2.629	0.197	0.052	5.00
15	16	8	2.38-2.98	2.619	0.273	0.091	6.96
16	18	9	2.38-2.85	2.616	0.206	0.065	5.26
17	20	10	2.32-2.88	2.630	0.195	0.058	4.94

Table 35. Variation in numbers of discal setae on left elytron in selected samples of *S. lineolatus*; see Fig. 212.

Sample	N	Males	Range	Mean	1.5SD	2SE	CV(%)
1	10	5	13-17	15.3	1.7	0.7	7.58
2	10	5	16-19	16.6	1.6	0.7	6.48
3	18	9	15-19	15.9	1.6	0.5	6.62
4	12	6	15-17	16.2	1.3	0.5	5.16
5	28	14	14-17	15.6	1.2	0.3	5.04
6	16	8	15-17	15.6	1.2	0.4	5.23
7	12	6	15-18	15.9	1.5	0.7	6.26
8	12	6	13-17	15.5	1.9	0.7	8.02
9	10	5	14-17	15.6	1.3	0.5	5.41
10	10	5	15-18	16.0	1.6	0.7	6.58
11	14	7	15-20	17.1	1.5	0.9	9.60
12	14	7	14-17	16.1	1.1	0.4	4.77
13	22	11	14-19	16.3	1.7	0.5	7.17
14	26	13	14-18	16.2	1.5	0.4	6.30
15	16	8	15-19	16.5	1.5	0.5	6.26
16	18	9	14-18	16.0	1.8	0.6	7.43
17	20	10	16-19	17.2	1.4	0.4	5.28

Table 36. Variation in eye size (WF/WH) in selected samples of *S. lineolatus*; see Fig. 213.

Sample	N	Males	Range	Mean	1.5SD	2SE	CV(%)
1	10	5	0.59-0.63	0.614	0.023	0.010	2.57
2	10	5	0.60-0.62	0.612	0.012	0.005	1.29
3	18	9	0.58-0.63	0.607	0.021	0.006	2.26
4	12	6	0.58-0.62	0.601	0.016	0.006	1.80
5	28	14	0.56-0.61	0.590	0.016	0.004	1.87
6	16	8	0.58-0.61	0.592	0.017	0.006	1.87
7	12	6	0.57-0.60	0.582	0.015	0.006	1.77
8	12	6	0.56-0.60	0.579	0.020	0.008	2.26
9	10	5	0.56-0.60	0.579	0.022	0.009	2.50
10	10	5	0.56-0.59	0.577	0.014	0.006	1.64
11	14	7	0.54-0.59	0.579	0.023	0.008	2.70
12	14	7	0.55-0.59	0.574	0.018	0.006	2.12
13	22	11	0.56-0.59	0.576	0.015	0.004	1.75
14	26	13	0.55-0.59	0.569	0.017	0.004	1.95
15	16	8	0.55-0.58	0.565	0.015	0.005	1.83
16	18	9	0.54-0.60	0.564	0.020	0.006	2.37
17	20	10	0.57-0.60	0.579	0.015	0.004	1.67

Table 37. Variation in pronotal form (LP/WP) in selected samples of *S. lineolatus*; see Fig. 214.

Sample	N	Males	Range	Mean	1.5SD	2SE	CV(%)
1	10	5	0.86-0.90	0.880	0.022	0.009	1.69
2	10	5	0.84-0.91	0.880	0.030	0.012	2.14
3	18	9	0.85-0.91	0.882	0.025	0.008	1.92
4	12	6	0.84-0.94	0.883	0.041	0.016	3.07
5	28	14	0.85-0.93	0.888	0.015	0.006	1.87
6	16	8	0.86-0.93	0.886	0.023	0.008	1.74
7	12	6	0.86-0.94	0.898	0.033	0.013	2.46
8	12	6	0.84-0.92	0.882	0.037	0.014	2.82
9	10	5	0.87-0.94	0.899	0.035	0.015	2.59
10	10	5	0.87-0.91	0.885	0.019	0.008	1.43
11	14	7	0.88-0.93	0.901	0.023	0.008	1.73
12	14	7	0.88-0.94	0.909	0.026	0.009	1.90
13	22	11	0.86-0.93	0.903	0.030	0.008	2.19
14	26	13	0.87-0.93	0.902	0.025	0.007	1.85
15	16	8	0.89-0.95	0.912	0.022	0.007	1.63
16	18	9	0.88-0.94	0.922	0.023	0.007	1.64
17	20	10	0.90-0.98	0.940	0.031	0.009	2.18

that truly intermediate populations do not exist.

Etymology. - Latin, *lineola* = fine line, probably in reference to the presence of paramedian pronotal sulci.

Distribution. - Four specimens are labelled "Fla." I doubt that *S. lineolatus* really occurs in Florida, as I think there is no suitable habitat there. Otherwise, the known range of this species extends west from southern Canada and eastern United States to at least eastern Wyoming, and south to the Rio Grande Valley (Fig. 206). I studied 876 additional specimens from the following localities.

CANADA

No locality (5; ANSP, CNHM, MCZ, UKSM). ONTARIO: 16 mi. w. Bondhead (1; UASM), London (20; CNHM, UASM), Ottawa (1; TLEr), Port Credit (1; CUNY), Port Stanley (1; UASM), Saint Catherines (3; JNeg), Toronto (5; MCZ, UASM), Wheatley (1; KHSt). QUEBEC: Montreal (1; MCZ), Potton Springs (10; MCZ). For other Canadian records, see Lindroth (1961).

UNITED STATES

No locality (8; ANSP, CUNY, IRSB, USNM). ALABAMA: Tuscaloosa Co., 15 mi. n. Tuscaloosa (11; DJLa). ARKANSAS: Carroll Co., Berryville (1; MCZ), 4 mi. w. Berryville (27; UASM); Newton Co., Jasper (1; BMNH); Sevier Co., 6 mi. n. Lockesburg (1; MCZ); Van Buren Co., Formosa (2; IRSB); Washington Co. (2; INHS), 7 mi. s. Fayetteville (7; UASM). DISTRICT OF COLUMBIA: Washington (16; AMNH, CAS, MCZ, MSUL, USNM). ILLINOIS (8; INHS, MCZ, USNM): Cook Co., Palos Park (1; CNHM); La Salle Co., Ottawa (1; RTBe); McLean Co., Normal (1; INHS); Peoria Co., East Peoria (2; CNHM); Vermilion Co., Fairmount (1; RTBe). INDIANA (1; MSUL): Parke Co. (9; UCD), The Shades State Park (3; RTBe); Tippicanoe

Co. (2; MCZ); Wabash River (2; CAS). IOWA: Herrold (1; USNM); Boone Co., Boone (6; UASM); Cedar Co. (1; USNM); Johnson Co., Iowa City (1; USNM). KANSAS: Bourbon Co., Fort Scott (2; USNM); Douglas Co., Lawrence (1; DJLa); Pottawatomie Co., Onaga (1; USNM); Wilson Co., Benadict (2; CAS). KENTUCKY: Ballard Co., Wickliffe (9; TCBa); Cumberland Co., Marrowbone Creek (7; TCBa); Green Co., Greasy Creek (1; TCBa); Jackson Co., Sand Gap (2; TCBa); Jessamine Co., Indian Falls (2; TCBa); Metcalfe Co., 8 mi. e. Edmonton (20; UASM); Powell Co., Slade (2; TCBa); Hockcastle Co., Crooked Creek (1; TCBa). MARYLAND (3; CAS, MSUL, USNM): Difficult (1; MCZ); Baltimore Co., Baltimore (2; CAS); Frederick Co., Frederick (7; DRWh, RTBe); Harford Co., Edgewood (7; DRWh); Prince Georges Co., Bladensburg (1; CUNH). MISSOURI: Barry Co., Cassville (1; USNM); Boone Co., Columbia (3; USNM); Crawford Co., Meramec River (2; USNM); Laclede Co., Bennet Springs (7; USNM); McDonald Co., 3 mi. n. Noel (3; CAS); Ozark Co., Gainesville (18; UASM); Reynolds Co., Bunker (1; USNM); Ripley Co., Buffalo Creek (1; CAS), Doniphan (2; USNM); Saint Louis Co., Saint Louis (2; UMCG); Taney Co., 5 mi. e. Forsythe (2; MGFT); Wright Co., Mountain Grove (14; TCBa). MONTANA: Roosevelt Co., Wolf Point (1; CAS). NEW JERSEY (2; ANSP): Bergen Co., Westwood (1; CAS); Camden Co., Camden (9; CAS, LACM, RUNB), Cramer Hill (1; USNM); Essex Co., Irvington (2; AMNH); Gloucester Co., Westville (2; MCZ); Middlesex Co., Jamesburg (3; CUNY); Morris Co., Boonton (6; USNM); Somerset Co. (1; USNM); Warren Co., Phillipsburg (11; CAS, MSUL). NEW YORK (5; CAS, CNHM, INHS, USNM): New York City (2; CAS); West Hebron (3; CAS); Albany Co., Altamont (1; CUNY); Cattaraugus Co., Allegany State Park (1; USNM); Dutchess Co., Fishkill (6; CAS); Erie Co., Buffalo (2; CAS), North Evans (3; CAS); Greene Co., Ashland (4; CUNY, MCZ); Rockland Co., Hillburn (2; USNM); Tompkins Co., Groton (7; JNeg, UATA), Ithaca (28; CAS, CUNY, FDAG, USNM, VMKi); Ulster Co., Phoenician (1; CAS); Wyoming Co., Pike (2; MCZ). NORTH CAROLINA: (2; MCZ) Buncombe Co., Black Mountains (1; CAS). OHIO: Mohican Point (3; UMCG); Ashtabula Co., Ashtabula (2; MSUL), Conneaut (1; MSUL), Rock Creek (1; MSUL); Athens Co., Athens (1; UATA); Crawford Co., Plankton (1; CAS); Cuyahoga Co., Cleveland (1; FDAG); Knox Co., Gambier (1; UMCG); Preble Co., West Alexandria (1; RTBe); Warren Co., Twenty Mile Strand (19; DJLa). OKLAHOMA: Atoka Co., Atoka (6; CAS, MCZ, USNM), 5 mi. n. Stringtown (80; UASM); Carter Co., 10.7 mi. s. Drake (7; TLEr); Cherokee Co., 15 mi. sw. Talequah (1; BMNH); Comanche Co., Wichita National Forest (13, CAS); Cotton Co. (2; CAS); Craig Co., Grand Lake (6; DHKa); McCurtain Co., 7 mi. sw. Smithville (10; UASM); Murray Co., 10.3 mi. n. Drake (6; TLEr); Washita Co. (1; CAS). PENNSYLVANIA (15; AMNH, ANSP, CAS, MCZ, MSUL): Willow Mills (1; VMKi); Allegheny Co., Allegheny (1; MCZ); Bucks Co. (4; CAS, RUNB), Point Pleasant (1; CAS); Cumberland Co., Lemoyne (3; CAS), New Cumberland (12; CAS, CUNY, MCZ, VMKi), West Fairview (10; CAS); Monrow Co., Delaware Water Gap (12; AMNH, MCZ); Northampton Co., Bethlehem (4; CNHM), Easton (8; CAS, CNHM); Philadelphia Co., Frankford (3; USNM), Mount Airy (1; ANSP), Philadelphia (5; MCZ), Wyoming (1; USNM); Pike Co., Milford (6; USNM). SOUTH CAROLINA (1; MCZ). SOUTH DAKOTA: Mellette Co., White River (1; UASM). TENNESSEE: Carter Co., Elizabethton (1; CNHM); Davidson Co., Nashville (4; CAS, CUNY, LACM); Jackson Co., Cummins Mill (7; TCBa); Lincoln Co., 2 mi. n. Howell (5; UASM); Smith Co., Lancaster (2; TCBa); Warren Co., Cardwell Mountain (1; TCBa); White Co., Caney Fork River (2; TCBa), Sparta (1; TCBa).

TEXAS (21; ANSP, CAS, MCZ, RUNB, UKSM, USNM): Blanco Co., Cypress Mills (2; USNM), Johnson City (22; UASM); Colorado Co., Columbus (9; USNM); Cooke Co., 4 mi. sw. Era (1; CNC); Erath Co., Morgan Mill (2; INHS); Hamilton Co., 6 mi. n. Hamilton (6; ANSP); Kerr Co., Kerrville (1; CNC); Kinney Co., 23 mi. sw. Brackettville (3; DRWh); Lampasas Co., Adamsville (7; AMNH); McCulloch Co., 16 mi. s. Brady (2; CAS); Maverick Co., 8 mi. n. Quemado (5; UASM); Parker Co., 5 mi. sw. Weatherford (3; CNHM); Val Verde Co., 13 mi. nw. Del Rio (17; UASM). VERMONT: Clarendon (3; RTBe); South Alberg (1; RTBe); Addison Co., North Ferrisburg (5; RTBe); Bennington Co., Pownall (3; RTBe); Chittenden Co., Charlotte (2; RTBe), Shelburne (1; CAS); Franklin Co., East Georgia (13; RTBe); Rutland Co., Fair Haven (9; RTBe); Windham Co., Brattleboro (1; USNM), Newfane (1; RTBe), Townshend (4; RTBe); Windsor Co., Windsor (1; RTBe). VIRGINIA: Arlington Co., Rosslyn (4; MCZ, USNM); Fairfax Co. (1; USNM), Alexandria (13; AMNH, CAS, USNM), Black Pond (1; USNM), Glencarlyn (1; USNM), Great Falls (2; AMNH, USNM), Mount Vernon (4; USNM); Loudon Co. (2; AMNH); Roanoke Co., Buffalo Creek (6; CUNY), Roanoke (2; MZSP). WEST VIRGINIA: Greenbrier Co., White Sulphur Springs (1; CAS). WISCONSIN (6; CAS, CNHM, USNM): Milwaukee Co., Milwaukee (1; MCZ), Wauwatosa (1; CNHM). WYOMING: Niobrara Co., 37 mi. n. Lusk (8; UASM).

MEXICO

TAMAULIPAS: 34.9 mi. s. Nuevo Laredo (2; UASM).

Collecting notes. - Specimens of this abundant species have been collected from April to October, most of them in gravel bars along streams.

Taxonomic notes. - This species and *S. sulcifrons* were long confused in the literature, but Lindroth (1961) recognized their distinctness.

They are not closely related. As noted in my discussion on variation, there is a distinctive form of *S. lineolatus* in the Rio Grande Valley. It does not meet my criteria for recognition as a subspecies, but is no doubt geographically isolated.

3.52 The *longipennis* group

Diagnostic combination. - Members of this group are distinguished by the following combination of characters: body moderately to strongly flattened; paramedian clypeal carinae extended to median tooth; clypeal field narrow, no wider at base than apex of median frontal sulcus; submentum without accessory setae; pronotum without paralateral carinae; discal setae present on intervals three, five, and seven, total less than 20, average length less than 1.0 times maximum width of interval two; abdomen without extensive microsculpture, and without small lateral patches near coxal depressions of sternum three; endophallus with enlarged basal collar spines. Also: clypeal suture sharply impressed in most specimens; antennal articles five to ten filiform; front and middle tarsi broadened and with dense ventral pubescence, especially in males; sternum seven with paramedian ambulatory setae in males, not in females; paramedian carinae of sternum three not or weakly curved outward at apices; and pygidium crenulate or not at apex in females.

Distribution. - Members of this group range from the Colorado River system in Arizona and New Mexico in the west and from Tamaulipas and Nuevo Leon in the east south to Costa Rica. I examined 1382 specimens of the *longipennis* group.

Taxonomic notes. - I have not critically studied geographic variation in members of this group, as three species are neither widespread nor represented by sufficient material. Four species are distinguishable by male genitalic characteristics or by superficial characters. Variation in at least *S. longipennis* is extensive and no doubt is worthy of study, but such study is not required for species recognition.

3.521 *Schizogenius neovalidus* new species

Type material. - Holotype male and allotype female labelled "Gila River, nr. Cliff, Grant Co. NEW MEXICO 26.VIII.1964 Awram-Whitehead" (MCZ). An additional 97 specimens from various localities in Arizona and New Mexico are paratypes (AMNH, ANSP, BMNH, CAS, CNC, CNHM, CUNY, DJLa, DRWh, IRSB, JNeg, MGFT, TLEr, UASM, UATA, USNM).

Diagnostic combination. - Within the *longipennis* group, the following characteristics of the male genitalia are diagnostic of this species: apex of median lobe (Fig. 197) elongate, deflexed at sharp angle, right margin strongly flanged; basal collar spines of endophallus slender, elongate. In Arizona, most matured specimens may be distinguished from matured specimens of *S. longipennis* by rufopiceous rather than rufous femora, and by form of frontal carinae (Fig. 192). From matured specimens of *S. chiricahuanus* matured specimens of *S. neovalidus* are distinguished by piceous or dark rufopiceous rather than rufous or light rufopiceous elytra.

Description. - Body flattened. Color piceous, elytra not to weakly aeneous; femora in most specimens dark rufopiceous; tibiae, tarsi, and antennae rufous; palpi testaceous.

Integument. Conspicuous microsculpture on paramedian frontal sulci, mouthparts, genae, front legs except posterior surfaces of femora and trochanters, middle legs except anterior surfaces of trochanters, and hind tibiae and posterior surfaces of hind femora. Sternum three without conspicuous paralateral patches of microsculpture.

Head. Fig. 192, frontal carinae three abbreviated in most specimens. Paramedian clypeal carinae straight, not markedly elevated in basal half, extended to median tooth; median field triangular, narrow, no wider at base than apex of median frontal sulcus. Clypeal suture weakly to strongly engraved. Eye prominent, finely and uniformly faceted. Neck densely punctate. Gena coarsely punctate, rugose in front. Antennal articles four to ten elongate, article five about 1.6-1.7 times longer than wide.

Pronotum. Fig. 192. Sides bisetose; base not rugose; hind angles reduced. Paramedian longitudinal sulci moderately long, nearly straight to strongly bent near middle, strongly hooked basally. Anterior transverse impression not or weakly punctate; basal impression impunctate.

Legs. Front tarsus strongly dilated in males, moderately in females; middle tarsus moderately dilated inboth sexes; hind tarsus slender, short. Paronychia nearly as long as tarsal claws. Front tibia narrowed evenly to base. Front femur not strongly constricted near apex.

Elytra. Left elytron with about 6-8 setae on interval three, 5-8 on interval five, 3-5 on interval seven; total 14-19 in specimens examined. Striae deep and sharply engraved, finely punctate in basal three-fourths. Intervals one to seven broad and weakly convex, interval eight carinate at apex; intervals three, five, and seven broadly joined at apices. Humeral denticles moderately prominent.

Abdomen. Sternum three with paramedian carinae not or weakly curved outward at apices. Sternum seven with paramedian ambulatory setae in males only. Pygidium with apical margin entire in males and females.

Male genitalia. Median lobe, Fig. 197, apex elongate, deflexed at a 50-60 degree angle, right ventral margin strongly flanged; endophallus, Fig. 202, virga 0.42-0.48 length of median lobe, basal collar spines six to eight times longer than wide; 13 specimens examined.

Measurements and proportions. See Table 38. Of holotype: TL, 4.94 mm; LE, 3.09 mm; WH, 1.02 mm; WP, 1.32 mm; WE, 1.64 mm; WF/WH, 0.65; LP/WP, 0.87; DP/LP, 0.85; LP/WE, 0.70; Ta/Ti, 0.63; PS/LP, 0.64. Of allotype: TL, 5.29 mm; LE, 3.35 mm; WH, 1.02 mm; WP, 1.38 mm; WE, 1.78 mm; WF/WH, 0.65; LP/WP, 0.88; DP/LP, 0.86; LP/WE, 0.69; Ta/Ti, 0.64; PS/LP, 0.63.

Variation. - See Table 38. In some specimens, the front femora may be rufous or the third frontal carina not abbreviated basally; I otherwise observed no important variation.

Etymology. - Latin, *neo* = new, plus *validus* = strong. Since the Arizona form of *S. longipennis* was named *S. validus* by Fall, I here name this similar looking new species by the similar name, *S. neovalidus*.

Distribution. - The known range of this species, except for one female specimen collected recently by D. J. Larson on the Verde River, is restricted to upper reaches of the Gila River system in southeastern Arizona and southwestern New Mexico (Fig. 207). I examined 99 specimens from the following localities.

Table 38. Descriptive statistics for *S. neovalidus*, based on 16 males from Cliff, New Mexico.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	4.79-5.49	5.224	0.366	0.122	4.65
LE	3.00-3.41	3.248	0.212	0.071	4.34
WH	0.96-1.14	1.059	0.076	0.025	4.78
WP	1.22-1.50	1.401	0.128	0.043	6.09
WE	1.57-1.86	1.736	0.131	0.044	5.04
B. Setae on left elytron.					
Interval 3	6- 8	6.7			
Interval 5	6- 7	6.2			
Interval 7	3- 5	3.7			
Total	15-18	16.6	1.4	0.5	5.76
C. Proportions.					
WF/WH	0.61-0.65	0.632	0.019	0.006	1.96
LP/WP	0.84-0.92	0.881	0.037	0.012	2.80
DP/LP	0.82-0.89	0.848	0.026	0.009	2.03
LP/WE	0.69-0.73	0.711	0.015	0.005	1.40
Ta/Ti	0.61-0.69	0.654	0.033	0.011	3.40
PS/LP	0.58-0.67	0.614	0.033	0.011	3.56

UNITED STATES

ARIZONA: Gila Co., nr. Carrizo (3; UASM), 6 mi. n. Payson (1; DJLa); Graham Co., nr. Aravaipa (35; AMNH, ANSP, BMNH, CAS, CNC, CNHM, CUNY, DRWh, IRSB, JNeg, MGFT, UASM, UATA, USNM). NEW MEXICO: Catron Co., Glenwood (11; UASM); Grant Co., Cliff (33; MCZ, UASM), Gila (1; UASM), 26 mi. n. Silver City (15; TLEr).

Collecting notes. - Specimens of this species have been collected from late May through late August, in riparian gravel bars.

Taxonomic notes. - Until now, specimens of the *longipennis* group from Arizona have all been named *S. validus* Fall. But these specimens clearly represent three species, and, further, the name *S. validus* falls as a synonym of *S. longipennis* Putzeys. Males of all three species are well characterized by details of the male median lobe and endophallus, but females cannot be distinguished with certainty. Two females from Aravaipa are identified as *S. longipennis*, and a female of *S. neovalidus* from Payson is well within the range of *S. longipennis*. If these specimens are correctly identified, then the two species are sympatric; male specimens are required for confirmation.

3.522 *Schizogenius longipennis* Putzeys

Schizogenius tristriatus longipennis Putzeys 1866:227. *Type locality* "Mexique," here restricted to Fortin de las Flores, Veracruz; lectotype female labelled "longipennis. Chd. Mex. (C. Chd.)" on green paper in Putzeys' script, in IRSB (!), specimen labelled lectotype here designated. Bates 1881:37.

Schizogenius longipennis, Kult 1950:140.

Schizogenius validus Fall 1901:210. *Type locality* Rio Verde, central Arizona; type male in MCZ (!), specimen labelled "M.C.Z. Type 23860" here designated lectotype. Lindroth 1961:166. NEW SYNONYMY.

Diagnostic combination. - Males of this species are distinguished from males of other members of the *longipennis* group by the following combination of characters of the male genitalia: apex of median lobe short, deflected at weak angle, ventral margin in most specimens weakly swollen near angulation, not flanged (Fig. 198); endophallus with virga enlarged, about 0.42-0.48 length of median lobe; basal collar spines slender, elongate, about 10 times longer than wide. In Arizona, most matured specimens of *S. longipennis* are distinguished from matured specimens of *S. chiricahuanus* by darker body color, and from those of *S. neovalidus* by reddish front femora. In western Mexico, most specimens of *S. longipennis* are distinguished from most specimens of *S. pacificus* by larger body size, relatively larger eyes, less convex body, indistinct microsculpture on sternum two and basal margin of pronotum, pronotum proportionately smaller in relation to rest of body, elytra less strongly aeneous, and paramedian pronotal sulci shorter, less sharply terminated at apices.

Description. - As in *S. neovalidus* except as follows. Color of legs variable, front femora rufous to piceous. Form and sculpture of head and pronotum, Fig. 193; base of frontal carina three not abbreviated in most specimens; paramedian pronotal sulci in most specimens sharply terminated at apices. Left elytron with 13-21 discal setae in specimens examined. Pygidium with apical margin crenulate in some females.

Male genitalia. Median lobe, Fig. 198; apex short, deflexed at a 30-40 degree angle, right ventral margin not flanged, ventral margin in most specimens distinctly swollen near angulation; endophallus, Fig. 203, virga 0.42-0.48 length median lobe, basal collar spines about 10 times longer than wide; 34 specimens examined.

Measurements and proportions. See Table 39.

Variation. - Geographic variation not studied in detail. In general, there is a trend toward size reduction and reduced numbers of discal elytral setae from north to south. The frequency of crenulate pygidial margins in females is higher from Arizona to Sinaloa than elsewhere. The front femur tends to be reddish from Arizona to Sinaloa, reddish in the apical fourth from Jalisco to Guerrero, and piceous elsewhere. And the tibiae tend to be testaceous to rufous from Arizona to Guerrero, and dusky or piceous elsewhere.

Etymology. - Latin, *longus* = long, plus *penna* = wing, in reference to the elongate elytra.

Distribution. - The known range of this species extends from southern Arizona in the west and from Nuevo Leon and Tamaulipas in the east south at least to Costa Rica (Fig. 208). I studied 1115 specimens from the following localities.

UNITED STATES

ARIZONA (17; AMNH, ANSP, CAS, INHS, USNM): Hot Springs (2; CAS), Riverside (6; ANSP, CAS, USNM); Cochise Co., 2.8 mi. s. Portal (1; TLEr); Gila Co., 33 mi. s. Globe (1; DJLa), Pinal Mountains (1; CUNY), Roosevelt Lake (2; CAS, UKSM), Sierra Ancha Mountains (1; UASM); Graham Co., Aravaipa (2; CUNY, DRWh); Maricopa Co., Phoenix (1; MCZ); Santa Cruz Co., Pena Blanca (2; UASM), Sycamore Canyon (2; CAS); Yavapai Co., Bumble Bee

Table 39. Descriptive statistics for *S. longipennis*, based on 20 males from Paso de Ovejas, Veracruz, Mexico.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	4.87-5.54	5.270	0.305	0.091	3.85
LE	3.04-3.50	3.319	0.192	0.057	3.85
WH	0.97-1.10	1.046	0.058	0.017	3.72
WP	1.26-1.47	1.390	0.095	0.028	4.57
WE	1.61-1.82	1.742	0.098	0.029	3.76
B. Setae on left elytron.					
Interval 3	5- 7	6.1			
Interval 5	5- 7	5.6			
Interval 7	2- 4	3.3			
Total	12-17	15.0	1.5	0.4	6.49
C. Proportions.					
WF/WH	0.58-0.63	0.605	0.017	0.005	1.90
LP/WP	0.86-0.93	0.887	0.028	0.008	2.07
DP/LP	0.83-0.90	0.862	0.026	0.008	2.03
LP/WE	0.68-0.73	0.708	0.022	0.007	2.06
Ta/Ti	0.59-0.69	0.645	0.036	0.011	3.71
PS/LP	0.56-0.66	0.618	0.037	0.011	4.02

(1; CAS).

MEXICO

No locality (5; IRSB, MCZ); Matamoros (1; CAS). CHIAPAS: 3.2 mi. n. Arriaga (1; CNC), 18.4 mi. ne. Chiapa de Corzo (2; UASM), 32.5 mi. e. Comitan (1; UASM), Huehuetan (10; UASM), Huixtla (2; DRWh), 12.8 mi. nw. Huixtla (1; CNC), 38.2 mi. nw. Huixtla (1; CNC), Pijijiapan (18; UASM), Solosuchiapa (1; UASM), 4.0 mi. s. Solosuchiapa (4; UASM), 18.6 mi. se. Tonala (45; UASM). COLIMA: 3.4 mi. se. Colima (54; UASM), 8 mi. sw. Colima (3; UASM). GUERRERO: 41.4 mi. n. Acapulco (42; UASM). JALISCO: 4 mi. s. Atenquique (7; UASM), Cocula (3; IRSB), Ixtapa (34; UASM), 8.5 mi. n. Juchitlan (37; UASM), La Garita (1; CAS), 17.9 mi. w. Magdalena (8; UASM), Pitillal (48; UASM), Puerto Vallarta (1; UASM), Talpa de Allende (76; CNHM, CUNY, INHS, JNeg, MCZ, MZSP, UASM, UATA, USNM). MICHOACAN: 8.5 mi. n. Nueva Italia (10; UASM). MORELOS: Puente de Ixtla (1; CPBo), Tejalpa (1; FDAG), Tetecala (9; UASM). NAYARIT: Acaponeta (5; UASM), 2.4 mi. s. Acaponeta (9; UASM), 8 mi. nw. Acaponeta (11; CAS), 13.8 mi. e. San Blas (20; UASM). NUEVO LEON: Linares (1; DRWh), 32.9 mi. n. Montemorelos (2; UASM). OAXACA: 17.7 mi. w. El Camaron (1; BMNH), 25 mi. e. El Camaron (28; UASM), 29.4 mi. e. El Coyul (25; UASM), Juchatengo (3; AMNH), 11.1 mi. n. Matias Romero (1; BMNH), 9.9 mi. n. Pochutla (7; UASM), 18.6 mi. n. Pochutla (3; UASM), 19.1 mi. s. Suchixtepec (1; ANSP), 5 mi. e. Tapanatepec (1; ANSP), Tehuantepec (2; BMNH), Valle Nacional (50; UASM), 72.5 mi. s. Valle Nacional (16; UASM), 97.3 mi. s. Valle Nacional (1; CPBo), Zanatepec (20; UASM), 76 mi. w. Zanatepec (1; UASM), 18.4 mi. w. Zanatepec (4; UASM). PUEBLA: Tehuitzingo (2; CNHM), Tepexco (23; UASM). QUERETARO:

Escanelilla (9; UASM), Jalpan (6; UASM), 6.4 mi. e. Pinal de Amoles (1; JHeS). SAN LUIS POTOSI: 17 mi. n. Palitla (36; UASM), 2.7 mi. w. Santa Catarina (8; UASM), Tamazunchale (26; UASM). SINALOA: Alamosa (1; CAS), Choix (2; UCD), 5.5 mi. nw. Choix (1; UCD), Chupaderos (2; UCD), Concordia (19, UASM), 11.2 mi. ne. Concordia (1; JHeS), 30.6 mi. s. Culiacan (6; UASM), 8 mi. w. El Palmito (1; CNC), Mazatlan (2; MCZ), Rio Piaxtla (3; UASM), Rosario (11; UASM), 21-33 mi. e. Villa Union (11; CNC, UCB). SONORA: Alamos (1; CAS), 10 mi. s. Alamos (1; UCD). TABASCO: Teapa (54; MGFT, UASM). TAMAULIPAS: El Barretal (46; UASM), Encino (4; UASM), 15.2 mi. n. Ciudad Victoria (6; UASM), 21.3 mi. n. Ciudad Victoria (30; UASM), 39 mi. s. Ciudad Victoria (25; UASM). VERACRUZ: Coatzacoalcos (2; USNM), Cordova (4; CAS, USNM), Coyame (1; UASM), Fortin de las Flores (7; FDAG, UASM), 20 mi. nw. Huatusco (1; FDAG), Jalapa (3; MCZ, USNM), 21.8 mi. e. Jalapa (1; MCZ), Paso de Ovejas (52; UASM).

GUATEMALA

EL QUICHE: Sacapulas (1; AMNH).

COSTA RICA

CARTAGO: Turrialba (1; UAFA). LIMON: Guapiles (1; USNM). PUNTARENAS: Palmar Sur (2; UAFA), 6 mi. n. Palmar Sur (22; UAFA), 3 mi. s. Palmar Sur (1; UAFA).

Collecting notes. - Adult specimens of *S. longipennis* have been collected throughout the year, in riparian gravel bars or at lights. In material at hand, teneral adults are most abundant in the months just before and just after the wet season, which, in most of Mexico, extends from June through August.

Taxonomic notes. - Putzeys (1866) indicated that his specimens of *S. longipennis* were collected together with his specimens of *S. tristriatus*. As these must have come from Veracruz, and most likely from the Cordova area, and as I have seen specimens of both species from Fortin de las Flores, I have restricted the type locality to that locality. Despite the treatment of *S. longipennis* as a form of *S. tristriatus* by both Putzeys (1866) and Bates (1881), these names clearly refer to unrelated species.

The range of *S. longipennis* is sympatric with those of the other members of the *longipennis* group, and there hence is no question that *S. longipennis* is a distinct species. I have seen the types of both *S. longipennis* and *S. validus*. Specimens of *S. longipennis* from Arizona do differ in various ways from Veracruz specimens, as noted in my discussion of variation, but I have no evidence to suggest that variation in any characteristic is disjunct. Thus, I think the names *S. longipennis* and *S. validus* are synonyms.

3.523 *Schizogenius chiricahuanus* new species

Type material. - Holotype male and allotype female labelled "Cave Ck., Cochise Co. ChiricahuaMts. Ariz. ca.6000' Aug. 17, 1960" and "G.E. Ball family & R.B. Madge collectors" (MCZ). An additional 30 specimens from various localities in Arizona are paratypes (AMNH, CUNY, DJLa, DRWh, IRSB, KHSt, UASM, UKSM, USNM).

Diagnostic combination. - Within the *longipennis* group, matured specimens of this species are distinguished by rufous coloration. Also, characteristics of the male genitalia (Fig. 199) are diagnostic.

Description. - As in *S. neovalidus* except as follows. Average size smaller. Color light to dark rufous, not piceous or dark rufopiceous. Form and sculpture of head and pronotum, Fig. 194. Left elytron with about 6-8 setae on interval three, 6-8 on interval five, and 3-5 on interval seven; total 15-20 in specimens examined. Pygidium with apex crenulate in some females.

Male genitalia. Median lobe, Fig. 199, apex short, deflexed at 40-45 degree angle, right ventral margin not flanged, ventral margin not swollen near angulation; endophallus, Fig. 204, virga 0.32-0.38 length median lobe, basal collar spines about five times longer than wide or less; four specimens examined.

Measurements and proportions. See Table 40. Of holotype: TL, 4.52 mm; LE, 2.89 mm; WH, 0.90 mm; WP, 1.20 mm; WE, 1.53 mm; WF/WH, 0.64; LP/WP, 0.85; DP/LP, 0.89; LP/WE, 0.67; Ta/Ti, 0.61; PS/LP, 0.66. Of allotype: TL, 4.91 mm; LE, 3.12 mm; WH, 0.98 mm; WP, 1.30 mm; WE, 1.63 mm; WF/WH, 0.62; LP/WP, 0.86; DP/LP, 0.86; LP/WE, 0.69; Ta/Ti, 0.65; PS/LP, 0.67.

Etymology. - I name *S. chiricahuanus* after the Chiricahua Mountains of southern Arizona, since most specimens known to me were collected there.

Distribution. - Specimens of this species are known only from a few localities in southern Arizona (Fig. 209). I studied 33 specimens from the following localities.

UNITED STATES

ARIZONA: Cochise Co., Cave Creek (19; MCZ, UASM), Chiricahua Mountains

Table 40. Descriptive statistics for *S. chiricahuanus*, based on 16 males from Cochise County, Arizona.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	4.23-4.71	4.426	0.210	0.070	3.17
LE	2.68-2.97	2.812	0.119	0.040	2.83
WH	0.85-0.97	0.904	0.046	0.015	3.42
WP	1.08-1.26	1.164	0.068	0.023	3.92
WE	1.43-1.57	1.491	0.070	0.023	3.12
B. Setae on left elytron.					
Interval 3	6- 8	6.9			
Interval 5	6- 7	6.6			
Interval 7	3- 5	3.7			
Total	16-19	17.1	1.6	0.5	6.35
C. Proportions.					
WF/WH	0.59-0.65	0.617	0.026	0.009	2.78
LP/WP	0.83-0.90	0.866	0.030	0.010	2.35
DP/LP	0.84-0.89	0.868	0.028	0.009	2.16
LP/WE	0.63-0.71	0.678	0.030	0.010	2.91
Ta/Ti	0.58-0.69	0.642	0.040	0.013	4.19
PS/LP	0.62-0.69	0.654	0.026	0.009	2.67

(4; UKSM, USNM), Portal (2; KHSt), 5 mi. w. Portal (3; AMNH, CUNY), Rucker Lake (1; IRSB); Gila Co., Roosevelt Lake (1; DJLa), Sierra Ancha Mountains (3; DRWh, MCZ).

Collecting notes. - Specimens of this species have been collected in riparian gravel bars, from June through August.

Taxonomic notes. - *S. chiricahuanus* is sympatric with both *S. longipennis* and *S. neovalidus* in southern Arizona, or at least nearly so. This fact, and well marked differences in structures of male genitalia and in other features, indicate that *S. chiricahuanus* is reproductively isolated from those species. Known ranges of *S. chiricahuanus* and *S. pacificus* do not overlap, and differences in structures of male genitalia are smaller, but well marked differences in body form and in other characteristics indicate that these two forms are also reproductively isolated. Differences in habitus are clearly indicated in Tables 38-41 for the four species of the *longipennis* group.

3.524 *Schizogenius pacificus* new species

Type material. - Holotype male and allotype female labelled "Acapulco Gro., Mex. Aug.18,1938 Lipovsky" (MCZ). An additional 51 specimens from various localities in Guerrero, Jalisco, and Sinaloa are paratypes (CAS, DRWh, MCZ, UASM, USNM).

Diagnostic combination. - Within the *longipennis* group, specimens of *S. pacificus* are distinguished from those of *S. longipennis* and *S. neovalidus* by numerous details of male genitalia (Figs. 200), and from specimens of *S. chiricahuanus* by dark coloration. In addition, specimens of *S. pacificus* differ from specimens of the sympatric *S. longipennis* by distinct microsculpture on base of pronotum and on sternum two, and by a more convex body.

Description. - As in *S. neovalidus* except as follows. Body convex. Color piceous, elytra in most specimens distinctly aeneous; femora in most specimens partly or wholly piceous or dark rufopiceous; front tibia rufous to rufopiceous, hind tibiae rufotestaceous. Additional conspicuous microsculpture at base of pronotum and on sternum two in most specimens. Head and pronotum, Fig. 195. Left elytron with about 5-7 setae on interval three, 5-7 on interval five, 2-4 on interval seven; total 13-17 in specimens examined. Pygidium apex crenulate in females or not.

Male genitalia. Median lobe, Fig. 200, apex moderate, deflexed at a 40-45 degree angle, right ventral margin not flanged, ventral margin not swollen near angulation; endophallus, Fig. 205, virga 0.32-0.38 length median lobe, basal collar spines about five times longer than wide; five specimens examined.

Measurements and proportions. See Table 41. Of holotype: TL, 4.27 mm; LE, 2.62 mm; WH, 0.94 mm; WP, 1.25 mm; WE, 1.45 mm; WF/WH, 0.61; LP/WP, 0.84; DP/LP, 0.91; LP/WE, 0.72; Ta/Ti, 0.65; PS/LP, 0.57. Of allotype: TL, 4.67 mm; LE, 2.90 mm; WH, 0.99 mm; WP, 1.31 mm; WE, 1.57 mm; WF/WH, 0.62; LP/WP, 0.86; DP/LP, 0.93; LP/WE, 0.72; Ta/Ti, 0.71; PS/LP, 0.60.

Etymology. - I name this species after the Pacific Ocean, since most known specimens were collected along Pacific drainage systems.

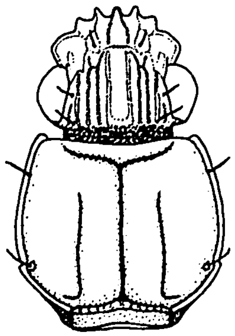
Distribution. - Specimens of *S. pacificus* have been collected along various rivers of the Pacific slope from southern Sinaloa to southern

Table 41. Descriptive statistics for *S. pacificus*, based on 16 males from San Juan Abajo, Jalisco, Mexico.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	4.01-4.92	4.327	0.415	0.138	6.32
LE	2.45-2.99	2.676	0.244	0.081	6.08
WH	0.89-1.02	0.995	0.068	0.023	4.56
WP	1.13-1.38	1.25	0.110	0.037	5.85
WE	1.39-1.63	1.491	0.121	0.040	5.41
B. Setae on left elytron.					
Interval 3	6- 7	6.2			
Interval 5	5- 7	5.8			
Interval 7	2- 4	3.0			
Total	14-17	15.0	1.1	0.4	4.87
C. Proportions.					
WF/WH	0.61-0.64	0.626	0.013	0.004	1.43
LP/WP	0.83-0.91	0.862	0.032	0.011	2.49
DP/LP	0.88-0.94	0.902	0.026	0.009	1.95
LP/WE	0.68-0.77	0.728	0.036	0.012	3.26
Ta/Ti	0.63-0.71	0.685	0.037	0.012	3.58
PS/LP	0.55-0.63	0.597	0.034	0.011	3.75

Fig. 191-195. Head and pronotum, dorsal aspect. 191. *S. lineolatus* Say, Frederick, Maryland. 192. *S. neovalidus* new species, Aravaipa, Arizona. 193. *S. longipennis* Putzeys, Linares, Nuevo Leon. 194. *S. chiricahuanus* new species, Portal, Arizona. 195. *S. pacificus* new species, Rosario, Sinaloa.

Fig. 196-200. Male median lobe, lateral aspect. 196. *S. lineolatus* Say, Edgewood, Maryland. 197. *S. neovalidus* new species, Glenwood, New Mexico. 198. *S. longipennis* Putzeys, Palitla, Veracruz. 199. *S. chiricahuanus* new species, Sierra Ancha Mountains, Arizona. 200. *S. pacificus* new species, Villa Union, Sinaloa.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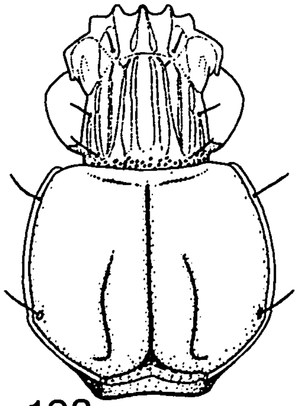
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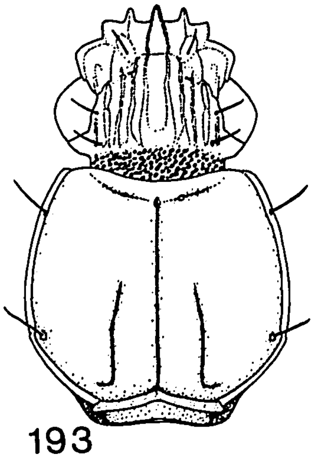
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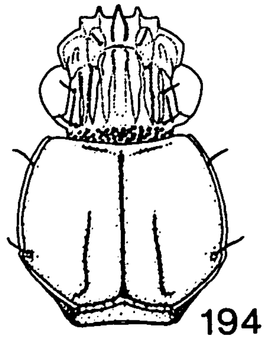
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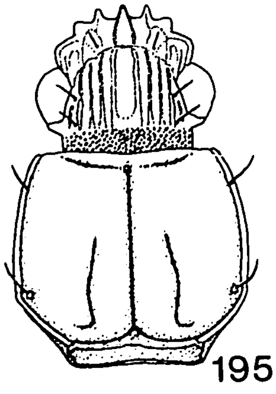
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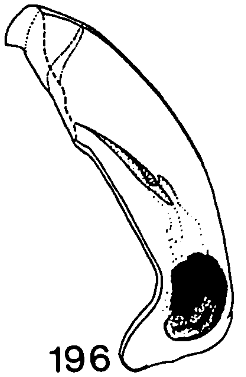
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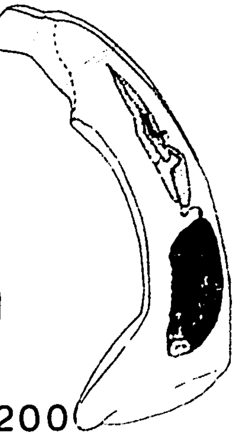
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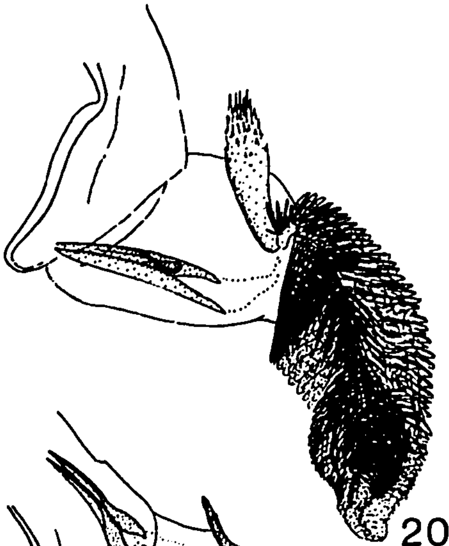
Fig. 201-205. Male endophallus. 201. *S. lineolatus* Say, Berryville, Arkansas. 202. *S. neovalidus* new species, Carrizo, Arizona. 203. *S. longipennis* Putzeys, Alamos, Sonora. 204. *S. chiricahuanus* new species, Portal, Arizona. 205. *S. pacificus* new species, Acapulco, Guerrero. Fig. 206-208. Known distributions. 206. *S. lineolatus* Say; open symbol represents state record only. 207. *S. neovalidus* new species. 208. *S. longipennis* Putzeys.



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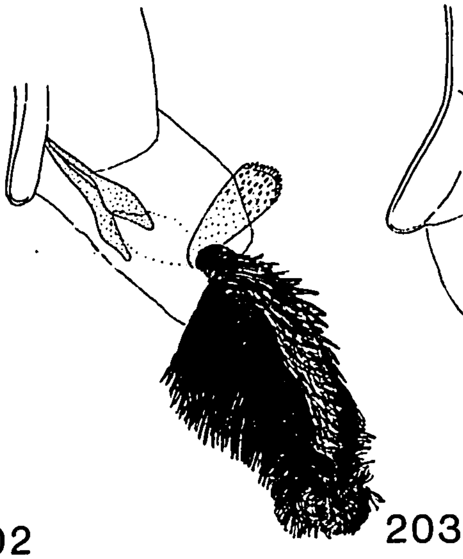

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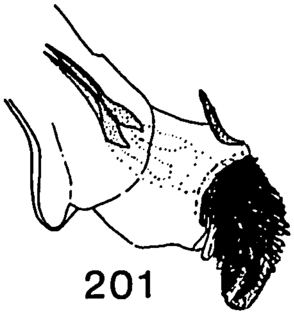

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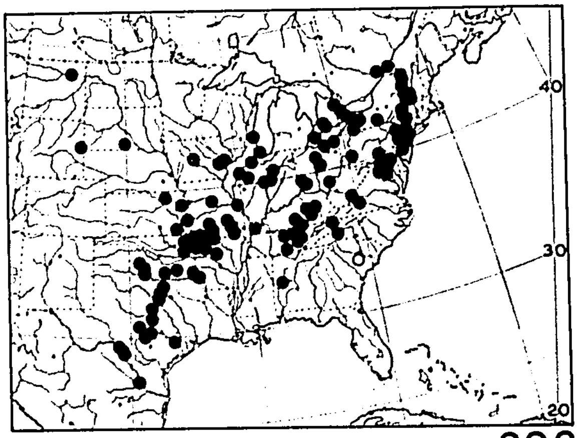

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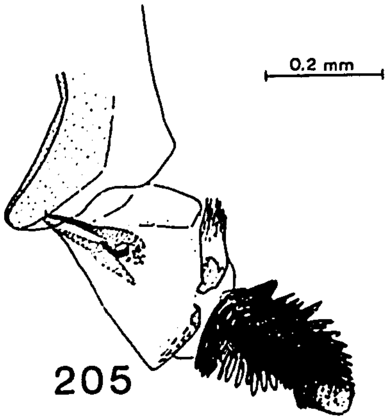

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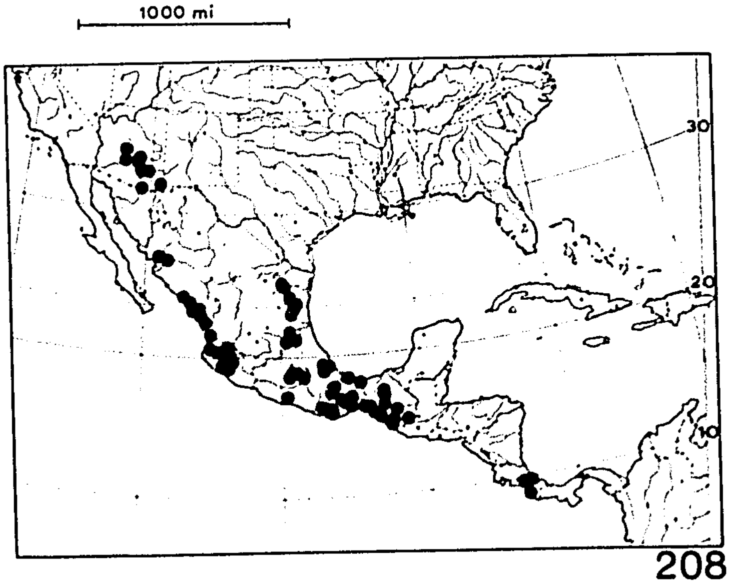

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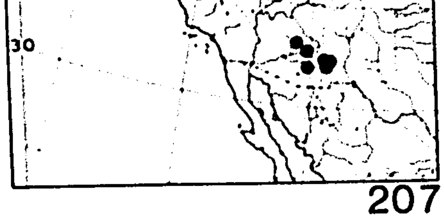

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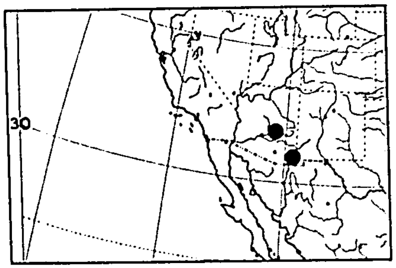
Fig. 209-210. Known distributions. 209. *S. chiricahuanus* new species. 210. *S. pacificus* new species. Fig. 211-214. Geographic variation in *S. lineolatus* Say. 211. Means of body size, Table 34. 212. Means of numbers of discal setae on left elytron, Table 35. 213. Means of relative eye size, Table 36. 214. Means of pronotal form, Table 37.



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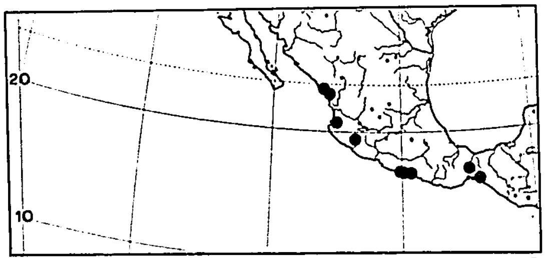

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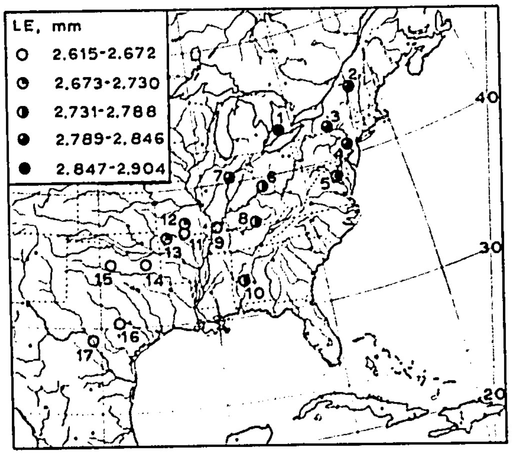

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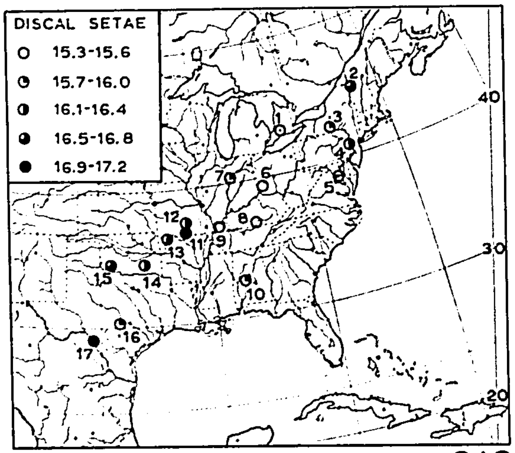

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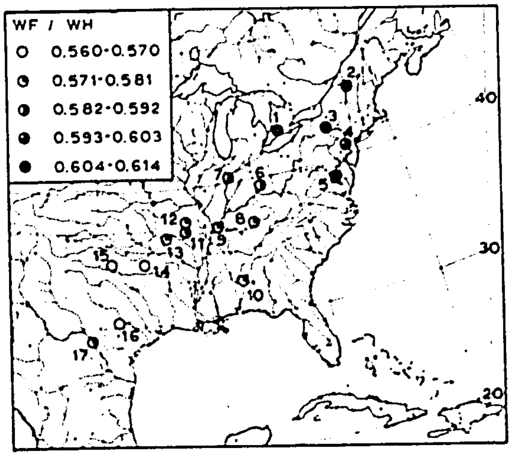

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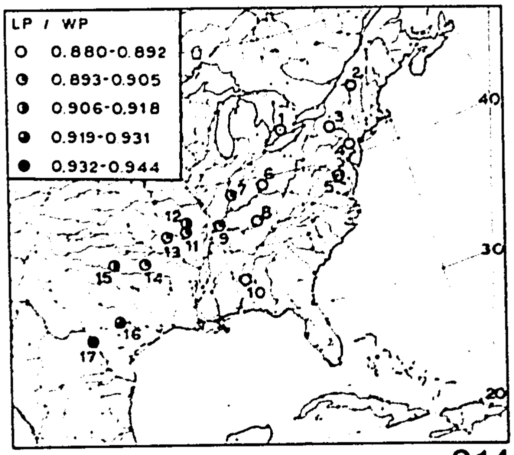


214

Oaxaca, and along one river of the Atlantic slope in the Isthmus of Tehuantepec in Oaxaca (Fig. 210). I studied 135 specimens from the following localities.

MEXICO

GUERRERO: Acapulco (7; MCZ), 24.8 mi. e. Acapulco (1; CAS), Coyuca (2; IRSB). JALISCO: 4 mi. s. Atenquique (4; UASM), San Juan Abajo (33; UASM). OAXACA: 11.1 mi. n. Matias Romero (12; UASM), 18.4 mi. w. Zanatepec (70; AMNH, ANSP, BMNH, CNC, CNHM, CUNY, JHeS, JNeg, MGFT, MZSP, UASM). SINALOA: Rosario (4; CAS, DRWh, USNM), Villa Union (2; UASM).

Collecting notes. - Specimens of this species have been collected in riparian gravel bars, or at lights, in January, March, June, August, and December. I suspect that its habitat differs somewhat from that of *S. longipennis*, since specimens of the two species have been taken together in only four places, and then in quite unequal samples. The more convex body form of *S. pacificus* suggests a sandier habitat than that of *S. longipennis*.

Taxonomic notes. - Specimens of this species are well differentiated from specimens of other members of the *longipennis* group in characters of male genitalia or habitus or both, and is unquestionably reproductively isolated from them.

3.53 The *depressus* group

Diagnostic combination. - Members of this group are distinguished by the following combination of characters: body moderately to strongly flattened; paramedian clypeal carinae extended to median tooth; clypeal field narrow, no wider at base than apex of median frontal sulcus; submentum without accessory setae; pronotum with paralateral carinae not or weakly developed; discal setae present on intervals three, five, and seven, total normally less than 30, average length less than 1.0 times maximum width of interval two; elytra concolorous with pronotum if aeneopiceous, not pale at apices if rufocastaneous; abdomen without extensive microsculpture except in small lateral patches near coxal depressions of sternum three, or, if extensively microsculptured than pronotal hind angles not prominent; endophallus with basal collar spines distinct but small. Also: clypeal suture sharply impressed in most species; antennal articles five to ten filiform; front and middle tarsi broadened and with dense ventral pubescence, especially in males; sternum seven with paramedian ambulatory setae in males, not in females; paramedian carinae of sternum three curved outward at apices; and pygidium crenulate or not at apex in females.

Distribution. - The composite range of members of this group is that of the whole genus. I examined 4953 specimens of the *depressus* group.

Taxonomic notes. - I made no attempt to classify the South American members of this large and difficult group, as I studied insufficient material to make a worthwhile contribution. The only species of the group known to extend into South America from Middle America is *S. pygmaeus*, which ranges at least to Colombia. Colombian specimens of that species may be distinguished from specimens of other Colombian species of the *depressus* group by details of the male genitalia. Also, they lack distinct microsculpture on the median field of the frons, have little or no microsculpture on the sides of the pronotum, and have a relatively convex pronotum with no indication of paralateral ridges.

In addition to the Colombian specimens of *S. pygmaeus*, I examined 511 specimens of one or perhaps several closely related South American species of the *depressus* group, from a few localities in Argentina, Bolivia, Brazil, and Colombia (AMNH, CAS, DRWh, IRSB, JNeg, MCZ, MGFT, MZSP, UASM). All of these have piceous body color, as do southern specimens of *S. pygmaeus* and the Middle American *S. emdeni*. I here refer to these specimens as a single taxon, *S. "apicalis."* Putzeys (1863:25) described *S. apicalis*, based on 12 specimens from the Amazon River. I have seen one male from the type series (IRSB) labelled "Amaz." and "S. apicalis Ptz." on green paper. As this specimen does not agree with the original description in various diagnostic characteristics, I prefer to make no lectotype designation until other type material has been seen. I have seen type material of no other described South American species of the *depressus* group, and am unable to place other species in that group from original or subsequent descriptions.

3.531 *Schizogenius arimao* Darlington

Schizogenius arimao Darlington 1934:71. *Type locality* Soledad, Cuba; holotype male in MCZ (1).

Diagnostic combination. - Specimens of this species differ from others of the *tristriatus* group by uniformly piceous elytra, abdomen microsculptured, and frontal carinae basally confused.

Description. - Body moderately flattened. Color piceous, not aeneous; front femora rufopiceous, legs otherwise rufous; palpi testaceous.

Integument. Strong microsculpture on paramedian frontal sulci, mouthparts, genae, front legs except posterior surfaces of femora and trochanters, middle legs except anterior surfaces of trochanters, hind tibiae and posterior surfaces of hind femora, elytral epipleura at base and on apical two-thirds, and abdomen.

Head. Fig. 215. Paramedian clypeal carinae straight, extended to median tooth, strongly elevated in basal half; median field triangular, no wider at base than apex of median frontal sulcus. Clypeal suture sharply defined. Eye prominent, finely and uniformly faceted. Neck densely punctate. Gena coarsely punctate, rugose in front. Antennal articles four to ten elongate, filiform, article five about 1.4 times longer than wide.

Pronotum. Fig. 215. Sides bisetose, hind angles obsolete, base not rugose. Paramedian longitudinal sulci elongate, hooked basally. Anterior transverse impression strongly punctate.

Legs. Front and middle tarsi slightly dilated and pubescent ventrally in both sexes; hind tarsus slender. Paronychia conspicuous, nearly as long as tarsal claws. Front tibia narrowed evenly to base. Front femur not strongly constricted near apex.

Elytra. Left elytron with about 7 setae each on intervals three and five, and about 4 on interval seven (Darlington, 1934). Striae deep, sharply engraved, strongly punctate in basal two-thirds. Intervals one to seven broad and flat, interval eight carinate at apex; apices of intervals three, five, and seven broadly joined. Humeral denticles prominent.

Abdomen. Sternum three with paramedian carinae curved outward at apices. Sternum seven with a pair of paramedian ambulatory setae in males only (Darlington, 1934). Pygidium not examined.

Male genitalia. Median lobe, Fig. 222; 1 specimen studied.

Measurements and proportions. Based on one male from the type locality. TL, 3.61 mm; LE, 2.23 mm; WH, 0.74 mm; WP, 0.94 mm; WE, 1.19 mm; WF/WH, 0.61; LP/WP, 0.94; DP/LP, 0.81; LP/WE, 0.75; Ta/Ti, 0.65; PS/LP, 0.66.

Etymology. - *S. arimao* was named after the Arimao River.

Distribution. - *S. arimao* is known only from two localities in Cuba (Darlington, 1934) (Fig. 235). Although I saw type material in the Museum of Comparative Zoology, my description is based on just one topotypic male given to me by Darlington.

Taxonomic notes. - This species has no known close relatives. Darlington suggested a relationship with *S. tristriatus*, but I think it most closely related to the South American *S. "apicalis"* and the Middle American *S. emdeni*. In particular, the weak but evident paralateral pronotal carinae suggest a relationship with *S. "apicalis"*, a suggestion supported by zoogeographic considerations, reduced hind angles, short antennae, small size, dark color, and comparatively elongate tarsi. Abdominal microsculpture of this species is a characteristic convergent in the taxon *S. ochthocephalus* and in members of the *tristriatus* group.

3.532 *Schizogenius emdeni* new species

Type material. - Holotype female labelled "S. Geronimo. Guatemala.

Champion.", "B.C.A. Col. I. 1. Schizogenius tristriatus, Putz.", "TYPE", and "Schizogenius Emdeni Kt. 57 det. K. Kult" (BMNH). Four males and two females from Palmar Sur, Costa Rica are paratypes (DRWh, UAFA, UASM).

Diagnostic combination. - Best distinguished from *S. pygmaeus*, the only other known piceous Middle American member of the *depressus* group without abdominal microsculpture, by details of male genitalia. Also, most specimens have fewer than 15 elytral setae, and reduced paralateral patches of microsculpture on sternum three.

Description. - As in *S. pygmaeus* except as follows. Body color piceous, elytra distinctly aeneous. Patches of microsculpture in coxal depressions of sternum three smaller, less distinct. Head and pronotum, Fig. 216. Left elytron with five or six setae on interval three, five on interval five, and two or three on interval seven; total 12-14 in specimens examined. Male genitalia with median lobe, Fig. 223; one specimen examined.

Measurements and proportions. Of holotype: TL, 4.04 mm; LE, 2.48 mm; WH, 0.80 mm; WP, 1.11 mm; WE, 1.29 mm; WF/WH, 0.61; LP/WP, 0.92; DP/LP, 0.83; LP/WE, 0.79; Ta/Ti, 0.62; PS/LP, 0.66. Of type series: TL, 3.31-3.751-4.04 mm; LE, 2.05-2.316-2.48 mm; WH, 0.65-0.739-0.80 mm; WP, 0.86-1.009-1.11 mm; WE, 1.06-1.196-1.29 mm; WF/WH, 0.60-0.616-0.64; LP/WP, 0.90-0.941-0.98; DP/LP, 0.79-0.814-0.84; LP/WE, 0.76-0.784-0.80; Ta/Ti, 0.62-0.657-0.68; PS/LP, 0.62-0.651-0.70.

Etymology. - K. Kult recognized this species as distinct, and planned to name it after the well known coleopterist Fritz van Emden. As he never published the name, I do so here.

Distribution. - *S. emdeni* is so far known only from two localities in Middle America (Fig. 235). I studied seven specimens from the following localities.

GUATEMALA

BAJA VERAPAZ: San Geronimo (1; BMNH).

COSTA RICA

PUNTARENAS: Palmar Sur (6; DRWh, UAFA, UASM).

Collecting notes. - In Costa Rica, specimens of *S. emdeni* were collected at black lights by R. T. Allen, in August.

Taxonomic notes. - I selected as holotype the specimen earlier selected by Kult, in order to avoid future confusion. There is no doubt that the Costa Rican specimens are conspecific with it.

Reduced numbers of elytral setae and reduced paralateral patches of microsculpture on sternum three superficially suggest placement in the *longipennis* group. I place *S. emdeni* in the *depressus* group because the patches of microsculpture are present, and because of similarities in some statistical characteristics with *S.arimao* and *S. "apicalis"*.

3.533 *Schizogenius sulcifrons* Putzeys

Schizogenius sulcifrons Putzeys 1846:652. *Type locality* "Amerique boreale," restricted to Rumney, New Hampshire by Lindroth (1961); lectotype female designated by Lindroth (1961), in Hope Museum at Oxford, not seen by me. Lindroth 1961:167.

Schizogenius lineolatus, LeConte 1857:83. Putzeys 1863:24. Putzeys

1866:228. Gemminger and Harold 1868:206. LeConte 1879:34. Leng 1920:48. Csiki 1927:551.

Diagnostic combination. - Specimens of *S. sulcifrons* are distinguished from those of other piceous species of *Schizogenius* found in eastern North America by having in combination: more than 20 discal setae per elytron in most specimens: weakly developed pronotal hind angles; and uniformly piceous pronotum and elytra. Most specimens differ from most of the western *S. litigiosus* by abdomen paler than elytra.

Description. - Body flattened. Color piceous above, rufopiceous below; legs and antennae rufous; palpi testaceous; elytra in most specimens strongly aeneous.

Integument. Conspicuous microsculpture on paramedian frontal sulci, mouthparts, genae, front legs except posterior surfaces of femora and trochanters, middle legs except anterior surfaces of trochanters, hind tibiae and posterior surfaces of hind femora, elytral epipleura on apical two-thirds, and sternum three in coxal depressions and small paralateral patches.

Head. Fig. 217. Paramedian clypeal carinae straight, moderately elevated in basal half, extended to median tooth; median field triangular, narrow, no wider at base than apex of median frontal sulcus. Clypeal suture sharply defined. Eye prominent, finely and uniformly faceted. Neck densely punctate. Gena coarsely punctate, rugose in front. Antennal articles four to ten elongate, article five about 1.6-1.8 times longer than wide.

Pronotum. Fig. 217. Sides bisetose; base not rugose; hind angles weakly developed. Paramedian longitudinal moderately elongate, nearly straight, strongly hooked basally. Paralateral carinae absent. Anterior transverse impression not or weakly punctate.

Legs. Front and middle tarsi moderately dilated and pubescent ventrally, less so in females; hind tarsus slender, short. Paronychia nearly as long as tarsal claws. Front tibia narrowed evenly to base. Front femur not strongly constricted near apex.

Elytra. Left elytron with about seven to eleven setae each on intervals three and five, five to eight on interval seven; total 19-30 in specimens examined. Striae deep and sharply engraved, finely punctate in basal two-thirds. Intervals one to seven broad and flat, interval eight carinate at apex; intervals three, five, and seven broadly joined at apices. Humeral denticles moderate.

Abdomen. Sternum three with paramedian carinae curved outward at apices. Sternum seven with paramedian ambulatory setae in males only. Pygidium with apical margin normally crenulate in females, entire in males.

Male genitalia. Median lobe, Fig. 224; six specimens examined.

Measurements and proportions. See Table 42. As this sample includes males and females, these data are not directly comparable with data given for other members of the *depressus* group. Males tend to be smaller than females; the mean LE of six males from Rumney, New Hampshire, is 2.505 mm.

Variation. - I had insufficient material of this species for a useful statistical analysis of variation. I noticed no important geographic variation in either pronotal form or in numbers of elytral setae. But, from the midwestern states, through the Washington, D. C. area, through

Table 42. Descriptive statistics for *S. sulcifrons*, based on 6 males and 6 females from Rumney, New Hampshire.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.69-4.50	4.128	0.314	0.121	5.08
LE	2.32-2.85	2.601	0.215	0.083	5.50
WH	0.75-0.85	0.808	0.039	0.015	3.20
WP	0.97-1.17	1.086	0.087	0.033	5.33
WE	1.19-1.43	1.329	0.104	0.040	5.24
B. Setae on left elytron.					
Interval 3	8- 9	8.5			
Interval 5	7-10	8.4			
Interval 7	5- 7	6.0			
Total	20-25	22.9	2.8	1.1	8.00
C. Proportions.					
WF/WH	0.62-0.68	0.658	0.026	0.010	2.58
LP/WP	0.85-0.91	0.892	0.023	0.009	1.73
DP/LP	0.80-0.85	0.828	0.024	0.009	1.91
LP/WE	0.70-0.75	0.727	0.021	0.008	1.97
Ta/Ti	0.59-0.66	0.621	0.035	0.013	3.73
PS/LP	0.68-0.76	0.707	0.039	0.015	3.68

New York state, to New Hampshire, there are definite trends toward larger body size and reduced eyes. These trends agree with those observed for *S. lineolatus* in the same general areas.

Etymology. - Latin, *sulcus* = groove + *frons* = front, in reference to the plurisulcate frons.

Distribution. - The known range of *S. sulcifrons* includes much of North America east of the Mississippi River, from New Brunswick (Lindroth, 1961) to Georgia in the east, and from Wisconsin to Mississippi in the west (Fig. 236). I studied 131 specimens from the following localities.

CANADA

No locality (1; ANSP). ONTARIO: London (6; CNHM, UASM), Saint Augustine (1; USNM), Toronto (3; CUNY, MCZ). See Lindroth (1961) for additional Canadian records.

UNITED STATES

No locality (9; ANSP, CAS, PSUU, UKSM). ALABAMA: Jackson Co., Big Coon Creek (1; TCBa). DISTRICT OF COLUMBIA: Washington (7; CAS, USNM). GEORGIA (1; ANSP). ILLINOIS: Vermilion Co., Kickapoo State Park (2; RTBe). INDIANA (1; CNHM): Parke Co., The Shades State Park (1; RTBe); Tippecanoe Co. (3; CNC, MCZ, UATA). KENTUCKY: Metcalfe Co., 8 mi. e. Edmonton (2; DRWh). MAINE: Oxford Co., Paris (1; MCZ). MARYLAND: Frederick Co., Frederick (1; RTBe); Harford Co., Edgewood (3; CUNY); Prince Georges Co., Bladensburg (1; USNM). MASSACHUSETTS: Franklin Co., Northfield (2; MCZ). MISSISSIPPI: Ireland (1; UKSM). NEW HAMPSHIRE: Carroll Co., North Conway (2; MCZ); Grafton Co., Rumney (15; CNHM, CNC, MCZ, UASM). NEW JERSEY (1; CAS); Warren Co., Phillipsburg (1; CAS). NEW YORK (7; CAS, UKSM, USNM): New Windsor (2; USNM); Erie Co., Lancaster

(1; CAS); Schuyler Co., Watkins Glen (3; AMNH, MCZ); Suffolk Co., Riverhead (1; CUNY); Tompkins Co., Groton (5; JNeg), Ithaca (15; CAS, CUNY, USNM); Ulster Co., Esopus (5; CUNY, MCZ). NORTH CAROLINA: Buncombe Co., Black Mountains (1; CAS). OHIO: Knox Co., Gambier (3; UMCG). PENNSYLVANIA (2; CAS); Allegheny Co., Allegheny (1; MCZ); Monroe Co., Delaware Water Gap (2; AMNH); Philadelphia Co., Philadelphia (2; MCZ); Pike Co., Milford (1; USNM). SOUTH CAROLINA (1; MCZ). TENNESSEE: Davidson Co., Nashville (2; CAS, USNM); Monroe Co., Sweetwater (3; AMNH). VERMONT (1; MCZ): Chittenden Co., Milton (1; RTBe); Rutland Co., Poultney (1; RTBe). VIRGINIA: Loudon Co. (4; AMNH). WISCONSIN (1; CUNY).

Collecting notes. - Specimens of *S. sulcifrons* have been collected from late March through September, generally in riparian gravel bars. I found specimens of this species, *S. lineolatus*, *S. amphibius*, and *S. planulatus* along a small stream near Edmonton, Kentucky.

Taxonomic notes. - See discussion by Lindroth (1961). As I did not see the lectotype, I accept Lindroth's concept of the species. Though *S. sulcifrons* and *S. lineolatus* have been confused in the past, they are not really closely related. *S. sulcifrons* is closely related to *S. litigiosus*, but ranges of the two forms are widely separated and there is no evidence of intergradation between them.

3.534 *Schizogenius litigiosus* Fall

Schizogenius litigiosus Fall 1901:210. *Type locality* Sylvania, California; holotype female in MCZ (!). Lindroth 1961:168.

Schizogenius depressus, Hatch 1949:118. Hatch 1953:69.

Diagnostic combination. - Fully colored specimens of this species are distinguished from other members of the *depressus* group in western North America by their piceous coloration. Most specimens are distinguished from most specimens of the eastern *S. sulcifrons* by having concolorous abdomen and elytra.

Description. - Body flat. Color piceous; front femora rufous to rufopiceous; antennae, tibiae, tarsi, and middle and hind femora rufous; palpi testaceous; elytra not or weakly aeneous, rufescent toward apices in many specimens.

Integument, head, pronotum, legs, elytra, and abdomen as in *S. sulcifrons* except as follows. Head and pronotum, Fig. 218. Left elytron with about six to nine setae each on intervals three and five, three to five on interval seven; total 16-22 in specimens examined. Apex of pygidium normally entire in females and males.

Male genitalia. Median lobe, Fig. 225; six specimens examined.

Measurements and proportions. See Table 43.

Variation. - There is a definite trend toward reduced eye size from northern California to southern British Columbia, and there may also be a trend toward increased body size from south to north. I otherwise found no conspicuous geographic variation. I had insufficient material from most areas for any useful statistical analysis of geographic variation.

Etymology. - Latin, *litigiosus* = contentious or quarrelsome; Fall probably suggested this name because this species had previously been confused with *S. pluripunctatus* and *S. depressus*.

Distribution. - The known range of *S. litigiosus* extends from southern

Table 43. Descriptive statistics for *S. litigiosus*, based on 18 males from Clear Lake, California.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.43-4.34	4.033	0.315	0.099	5.21
LE	2.13-2.70	2.495	0.191	0.060	5.11
WH	0.71-0.88	0.822	0.061	0.019	4.92
WP	0.87-1.15	1.054	0.107	0.034	6.76
WE	1.10-1.38	1.284	0.098	0.031	5.08
B. Setae on left elytron.					
Interval 3	6- 8	7.2			
Interval 5	6- 8	7.0			
Interval 7	3- 5	4.4			
Total	16-21	18.6	2.1	0.6	7.40
C. Proportions.					
WF/WH	0.60-0.65	0.617	0.022	0.007	2.35
LP/WP	0.90-0.97	0.935	0.024	0.007	1.69
DP/LP	0.78-0.82	0.801	0.020	0.006	1.63
LP/WE	0.74-0.79	0.768	0.022	0.007	1.92
Ta/Ti	0.60-0.70	0.648	0.040	0.013	4.12
PS/LP	0.65-0.73	0.688	0.034	0.011	3.25

British Columbia to southern California, west of the Rocky Mountains (Fig. 237). I studied 605 specimens from the following localities.

CANADA

BRITISH COLUMBIA: Duncan (12; CAS, MCZ), Keremeos (8; BMNH, DRWh, IRSB, MGFT). For other Canadian records, see Lindroth (1961).

UNITED STATES

CALIFORNIA (11; AMNH, CAS, MCZ, USNM): La Panza (1; CAS); Alameda Co., Alameda Creek (1; CAS), 20 mi. s. Livermore (1; UCB); Butte Co., Oroville (7; CAS), Paradise (2; CAS); Calaveras Co., Mokelumne Hill (23; CAS, MCZ); Colusa Co., Cooks Springs (2; CAS); Del Norte Co. (3; CNHM); Eldorado Co. (7; CNHM, MGFT); Fresno Co., Camp Greeley (1; CAS); Glenn Co., Elk Creek (1; CAS), 25 mi. w. Elk Creek (1; CAS), Hamilton City (2; UCD); Humboldt Co. (2; CAS), 6 mi. e. Bridgeville (1; TLEr), Garberville (2; CAS), Hoopa (2; CAS, UASM), Larabee Creek (2; CAS), Mad River (1; CAS), North Dobbyn Creek (1; CAS), Redwood Creek (1; UASM), Shively (3; UCD), Willow Creek (2; CAS); Kings Co., Stratford (2; CAS); Lake Co. (2; CAS), Clear Lake (28; CAS), Grossford (1; CAS), Kelseyville (3; CAS), Middle Creek (23; CAS), Middletown (5; CAS), North Fork Cache Creek (10; UCD), Scott Creek (1; CAS); Los Angeles Co., Cole (1; CAS), Pomona (1; USNM); Madera Co., North fork (1; CUNY); Marin Co. (1; CAS), Fairfax (15; CAS); Mendocino Co. (3; CNHM), Black Butte River (18; CAS), Bloody Run Creek (1; CAS), Dry Creek (4; CAS), Eel River (3; CAS), Longvale (13; CAS), Mailliard (2; CAS), 8 mi. w. Navarro (1; CAS), 2 mi. nw. Philo (1; CAS), Twin Rocks (1; CAS), Williams Creek (13; CAS), 2 mi. s. Yorkville (3; CAS); Modoc Co., 9.5 mi. s. Cedarville (35; CAS), Lake City (2; CAS); Napa Co. (6; CAS, USNM), Monticello (10; CAS, UCD, MCZ), Pope Valley

(6; CAS), Saint Helena (5; CAS, MCZ, UASM); Placer Co., Auburn (3; UCD), Penryn (1; UCB); Plumas Co., Clio (4; CAS); Sacramento Co., Cosumnes River (2; CAS), Fair Oaks (2; UCD); San Bernadino Co., Hesperia (1; CAS), Mojave River (1; TLEr); San Diego Co. (2; LACM); San Francisco Co. (3; CAS); Santa Clara Co., Anderson Reservoir (1; DHKa), Gilroy Hot Springs (11; CAS, DJLa, TLEr), Los Gatos (1; CAS), Mount Hamilton (3; CAS); Shasta Co., Redding (9; CAS); Siskiyou Co. (1; USNM), 2.3 mi. nw. Callahan (9; CAS), Dillon Creek (6; UASM), Scott River (1; CAS), Yreka (1; MCZ); Sonoma Co. (6; CAS, CUNY, LACM, MCZ), Agua Caliente (2; CNHM), Annapolis (2; CAS), Cloverdale (1; CAS), Duncan Mills (3; CAS), Guerneville (12; CAS), Healdsburg (2; CAS), Preston (1; CAS), Rio Nido (1; CAS), Russian River (6; CAS, MCZ), Santa Rosa (10; CAS, MCZ, MSUL), 2.5 mi. w. Skaggs Springs (2; CAS), Sylvania (5; CAS, MCZ, LACM); Stanislaus Co., 22 mi. w. Patterson (4; CAS); Tehama Co., Red Bluff (29; CNHM); Trinity Co., 2 mi. e. Burnt Ranch (6; CAS, RTBe), Canyon City (1; CAS); Clear Creek (1; TLEr), Douglas City (3; UASM), Hayfork Creek (9; CAS), Hyampton (3; CAS), Mad River (3; CAS, UASM), 4 mi. se. Ruth (22; CAS), 6 mi. s. Ruth (5; CAS), Ruth Dam (1; TLEr), Trinity Center (2; CAS), Weaverville (1; CAS); Tulare Co., Fairview (1; UCB), Kaweah (1; CAS); Yolo Co., Davis (13; UCD), Putah Canyon (2; UCD), Rumsey (1; UCD). IDAHO: Nez Perce Co., 6 mi. n. Lenore (1; DHKa); Owahee Co., Hot Creek Falls (3; CNHM). NEVADA (2; ANSP): Lyon Co., Weeks (3; UASM); Washoe Co., Pyramid Lake (1; UCD). OREGON (1; ANSP): Jackson Co., Cow Creek (3; CAS, MCZ), Eagle Point (1; CNHM), Medford (17; CAS, MCZ, UCD, USNM), Talent (2; UCD); Josephine Co. (7; CNHM); Lane Co., Eugene (3; CNHM), Middle Fork of Willamette River (1; CNHM); Malhuer Co., Sucker Creek Canyon (3; CNHM); Umatilla Co., McKay Reservoir (1; CNHM); Wasco Co., The Dalles (1; USNM); Wheeler Co., John Day Gorge (1; CNHM); Yamhill Co., Dayton (2; MCZ). WASHINGTON: Yakima Co., Toppenish (8; MCZ, USNM).

Collecting notes. - In the north, specimens of this species have been collected from May to September. In central California, adults may be found throughout the year. Adults are found in riparian gravel bars.

Taxonomic notes. - This species was confused with *S. depressus* by Hatch (1949, 1953), but well distinguished by Lindroth (1961). The range of *S. litigiosus* is entirely included within that of *S. depressus*, and specimens of both species have often been found at the same locality.

3.535 *Schizogenius pygmaeus* Van Dyke

Schizogenius pygmaeus Van Dyke 1925:12. *Type locality* Clear Lake, California; holotype in CAS, not seen by me.

Schizogenius championi Kult 1950:142. *Type locality* Pantaleon, Escuintla, Guatemala; holotype in BMNH, not studied. NEW SYNONYMY.

Diagnostic combination. - Within the *depressus* group, all dark or bicolored specimens seen from Mexico belong to *S. pygmaeus*, and none from the United States or Canada do. In Middle America south of Mexico, dark forms of this species are best distinguished from specimens of *S. emdeni* by characteristics given in the key. In South America, specimens of *S. pygmaeus* are distinguished from other members of the *depressus* group by details of male genitalia. Specimens of pale forms of *S. pygmaeus* are best distinguished from specimens of pale forms of *S. falli*, *S. ochthocephalus*, and *S. depressus* by characteristics given in the key. Ranges of *S. pygmaeus* and *S. scopaeus* are largely allopatric. The latter species is distributed along Atlantic drainage systems; its range extends south of the Rio Grande only in Nuevo Leon and Tamaulipas where it is sympatric with black forms of *S. pygmaeus*. The range of *S. pygmaeus* reaches the Rio Grande drainage basin only in southern Chihuahua, where *S. scopaeus* is not known to occur. Where the two species approach one another or overlap in range, specimens are distinguishable by conspicuous differences in the male genitalia and, in northeastern Mexico, by color.

Description. - Body weakly convex. Color testaceous or ferrugineous to brunneous to piceous, some specimens distinctly bicolored with head and pronotum darker than elytra; some dark specimens slightly aeneous; legs and antennae ferrugineous or testaceous; palpi testaceous.

Integument. Distinct microsculpture on paramedian frontal sulci, mouthparts, genae, front legs except posterior surfaces of femora and trochanters, middle legs except anterior surfaces of trochanters, hind tibiae and posterior surfaces of hind femora, shoulders and apical two-thirds of elytral epipleura, and small areas in coxal depressions of sternum three.

Head. Fig. 219. Clypeus with paramedian carinae straight, extended to median tooth, strongly elevated in basal half; median field narrow, no wider at base than apex of median frontal sulcus. Clypeal suture sharply defined. Eye prominent, finely and uniformly faceted. Neck finely, densely punctate. Gena coarsely punctate, rugose in front. Antennal articles four to ten elongate, article five about 1.4-1.5 times longer than wide.

Pronotum. Fig. 219. Sides bisetose; base not rugose; hind angles weakly developed. Paramedian longitudinal sulci moderately long, nearly straight, strongly hooked basally. Anterior transverse impression weakly to strongly punctate.

Legs. Front and middle tarsi moderately dilated and pubescent ventrally, less so in females; hind tarsus slender, short. Paronychia nearly as long as tarsal claws. Front tibia narrowed evenly to base. Front femur not strongly constricted near apex.

Elytra. Left elytron with about six to ten setae on interval three, five to nine on interval five, three to six on interval seven; total 14-24 in specimens examined. Striae sharply engraved, finely punctate in basal two-thirds. Intervals one to seven broad and flat, interval eight carinate at apex; intervals three, five, and seven broadly joined at apices. Humeral denticles weakly developed.

Abdomen. Sternum three with paramedian carinae curved outward at apices. Sternum seven with paramedian ambulatory setae in males only. Pygidium with apical margin finely crenulate in some females.

Male genitalia. Median lobe, Fig. 226, 227, form of apex variable (Fig. 234); 20 specimens examined.

Measurements and proportions. See Table 44.

Variation. - As shown in Fig. 242, specimens from interior and Pacific drainage basins south to and including the Rio Balsas are reddish, without conspicuous variation. Mature specimens from coastal lowland Atlantic drainage basins in Mexico, and from all localities south of Mexico, are dark piceous. In Pacific drainage systems in Chiapas and Oaxaca, most specimens are strongly bicolored, but others are

Table 44. Descriptive statistics for *S. pygmaeus*, based on 20 males from Clear Lake, California.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	2.80-3.22	3.032	0.152	0.045	3.35
LE	1.72-1.98	1.861	0.091	0.027	3.25
WH	0.57-0.66	0.629	0.038	0.011	4.03
WP	0.72-0.84	0.792	0.045	0.013	3.79
WE	0.89-1.02	0.958	0.043	0.013	2.98
B. Setae on left elytron.					
Interval 3	7- 9	8.0			
Interval 5	7- 9	7.6			
Interval 7	3- 6	4.6			
Total	17-23	20.2	2.3	0.7	7.46
C. Proportions.					
WF/WH	0.64-0.70	0.660	0.021	0.006	2.11
LP/WP	0.91-0.98	0.936	0.023	0.007	1.67
DP/LP	0.77-0.83	0.802	0.023	0.007	1.91
LP/WE	0.74-0.80	0.771	0.022	0.006	1.88
Ta/Ti	0.55-0.70	0.646	0.052	0.016	5.40
PS/LP	0.66-0.73	0.690	0.027	0.008	2.57

piceous or intermediate. In upland areas in Atlantic drainage systems in both Oaxaca and Chiapas, dark and bicolored forms are commonly found together. In Guerrero south of the Rio Balsas, and in upland Atlantic drainage areas in San Luis Potosi, most specimens are dark red and many are slightly bicolored. Specimens from 5000' on the Rio Tula in Hidalgo are brown. In short, there is a gradation from red forms (*S. pygmaeus*) to dark forms (*S. championi*) in Mexico, both eastward and southward.

Statistical data on variation in body size, numbers of elytral setae, relative eye size, and pronotal form are given in Tables 45-48. Major discontinuities, representing strong statistically significant differences, are shown in Fig. 243-246 by heavy broken lines. Two or more such gaps are found in central California (setae, LP/WP), between southern California and Arizona (setae, WF/WH), along the Sierra Madre Occidental (LE, setae, WF/WH), and along the Sierra Madre del Sur (LE, setae, LP/WP). These gaps strongly suggest that gene flow is impeded across these regions.

Fig. 234 portrays observed variation in form of male genitalia in *S. pygmaeus*. Because of considerable individual variation, analysis of geographic variation is difficult. I found no important clinal variation except for a sudden increase in size of apex toward northern California. Specimens from this area cannot be distinguished by form of apex of male genitalia from specimens of *S. scopaeus* from northeastern Mexico and the lower Rio Grande in Texas.

I conclude that some gene flow exists between narrow bodied form of *S. pygmaeus* in central and northern California and wider bodied forms further south, and between small eyed forms in California and large eyed forms in Arizona. There is little or no gene flow across the higher

Table 45. Variation in body size (LE, in mm) in selected samples of *S. pygmaeus*; see Fig. 243. Males and females each 50% in samples 1-28.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	22	1.77-2.00	1.878	0.091	0.029	3.58
2	16	1.70-2.00	1.907	0.130	0.044	4.56
3	14	1.71-2.16	1.907	0.152	0.054	5.32
4	16	1.62-2.03	1.841	0.197	0.066	7.14
5	24	1.87-2.15	2.028	0.128	0.035	4.20
6	12	1.75-2.15	1.970	0.170	0.065	5.74
7	18	1.80-2.16	1.988	0.142	0.047	4.76
8	24	1.81-2.12	1.954	0.125	0.034	4.26
9	12	1.83-2.13	1.962	0.164	0.063	5.57
10	18	1.88-2.20	2.019	0.126	0.040	4.16
11	26	1.80-2.23	1.984	0.164	0.043	5.51
12	16	1.87-2.30	2.078	0.158	0.053	5.08
13	18	1.68-1.95	1.839	0.106	0.033	3.83
14	10	1.70-1.93	1.817	0.115	0.050	4.32
15	12	1.75-2.07	1.957	0.140	0.054	4.77
16	20	1.69-2.02	1.860	0.143	0.043	5.13
17	16	1.82-2.12	1.938	0.115	0.038	3.96
18	12	1.90-2.24	2.027	0.139	0.054	4.58
19	12	1.73-1.95	1.818	0.101	0.039	3.70
20	10	1.80-2.03	1.910	0.132	0.055	4.57
21	12	1.75-2.08	1.951	0.153	0.059	5.24
22	26	1.91-2.25	2.114	0.127	0.033	4.01

Table 45. (Continued.)

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
23	20	1.86-2.14	2.002	0.114	0.034	3.78
24	16	1.98-2.26	2.103	0.131	0.044	4.14
25	22	1.88-2.25	2.090	0.154	0.044	4.91
26	12	1.99-2.30	2.113	0.149	0.057	4.70
27	12	1.99-2.29	2.170	0.132	0.051	4.04
28	24	1.95-2.28	2.092	0.142	0.039	4.53
29	9	1.96-2.21	2.101			
30	6	2.00-2.21	2.135			
31	6	1.99-2.12	2.038			

Table 46. Variation in numbers of elytral setae in selected samples of *S. pygmaeus*; see Fig. 244. Males and females each 50% in samples 1-28.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	22	18-23	20.6	1.7	0.6	6.30
2	16	19-22	20.5	1.5	0.5	4.94
3	14	16-19	18.4	1.3	0.5	4.62
4	16	19-22	20.2	1.3	0.4	4.23
5	24	17-23	19.6	2.0	0.5	6.85
6	12	18-23	19.4	2.3	0.9	8.06
7	18	15-22	19.2	2.6	0.8	9.02
8	24	17-22	19.0	2.1	0.6	7.54
9	12	17-21	19.0	1.6	0.6	5.50
10	18	16-20	18.6	1.7	0.5	6.19
11	26	15-21	18.7	2.1	0.6	7.68
12	16	17-21	19.2	2.1	0.7	7.18
13	18	14-18	16.3	1.5	0.5	6.30
14	10	15-17	16.2	0.9	0.4	3.90
15	12	15-19	16.8	1.7	0.6	6.62
16	20	15-18	16.8	1.5	0.4	5.44
17	16	14-18	16.1	2.0	0.7	8.44
18	12	16-20	17.5	1.5	0.6	5.71
19	12	14-18	16.0	1.7	0.7	7.05
20	10	15-18	16.9	1.7	0.7	6.51
21	12	16-20	17.5	1.8	0.7	6.67
22	26	16-20	17.4	1.6	0.4	6.11

Table 46. (Continued.)

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
23	20	16-20	17.8	1.6	0.5	5.93
24	16	18-21	19.1	1.6	0.5	5.57
25	22	16-22	18.6	2.3	0.6	8.07
26	12	18-21	19.5	1.5	0.6	5.13
27	12	19-24	21.9	2.1	0.8	6.29
28	24	19-25	21.8	2.0	0.6	6.20
29	9	19-24	21.4			
30	6	18-21	19.5			
31	6	17-19	18.5			

Table 47. Variation in relative eye size (WF/WH) in selected samples of *S. pygmaeus*; see Fig. 245. Males and females each 50% in samples 1-28.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	22	0.65-0.67	0.658	0.013	0.004	1.30
2	16	0.64-0.67	0.655	0.017	0.006	1.76
3	14	0.64-0.68	0.659	0.017	0.006	1.73
4	16	0.60-0.66	0.637	0.022	0.007	2.27
5	24	0.60-0.65	0.628	0.018	0.005	1.97
6	12	0.61-0.65	0.631	0.017	0.007	1.85
7	18	0.60-0.64	0.624	0.015	0.005	1.58
8	24	0.60-0.65	0.622	0.019	0.005	2.08
9	12	0.60-0.62	0.610	0.011	0.004	1.21
10	18	0.60-0.64	0.618	0.016	0.005	1.72
11	26	0.59-0.65	0.619	0.024	0.006	2.60
12	16	0.60-0.64	0.623	0.015	0.005	1.63
13	18	0.59-0.63	0.604	0.016	0.005	1.81
14	10	0.59-0.64	0.616	0.025	0.010	2.67
15	12	0.59-0.63	0.608	0.021	0.008	2.31
16	20	0.58-0.62	0.604	0.020	0.006	2.23
17	16	0.59-0.63	0.615	0.015	0.005	1.68
18	12	0.59-0.62	0.603	0.016	0.006	1.78
19	12	0.58-0.62	0.598	0.020	0.008	2.23
20	10	0.58-0.62	0.599	0.019	0.008	2.15
21	12	0.57-0.61	0.595	0.022	0.008	2.43

Table 47. (Continued.)

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
22	26	0.58-0.61	0.599	0.015	0.004	1.52
23	20	0.58-0.62	0.598	0.018	0.005	1.90
24	16	0.58-0.63	0.606	0.020	0.007	2.16
25	22	0.60-0.64	0.619	0.018	0.005	1.92
26	12	0.62-0.65	0.638	0.016	0.006	1.66
27	12	0.61-0.65	0.634	0.020	0.008	2.07
28	24	0.60-0.66	0.633	0.023	0.006	2.40
29	9	0.60-0.65	0.628			
30	6	0.60-0.63	0.615			
31	6	0.58-0.63	0.600			

Table 48. Variation in pronotal form (LP/WP) in selected samples of *S. pygmaeus*; see Fig. 246. Males and females each 50% in samples 1-28.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	22	0.90-0.98	0.934	0.026	0.007	1.86
2	16	0.92-0.97	0.941	0.020	0.007	1.42
3	14	0.89-0.94	0.913	0.022	0.008	1.63
4	16	0.89-0.95	0.922	0.025	0.008	1.84
5	24	0.86-0.94	0.907	0.030	0.008	2.15
6	12	0.87-0.95	0.913	0.036	0.014	2.61
7	18	0.88-0.94	0.909	0.025	0.008	1.83
8	24	0.88-0.93	0.908	0.023	0.006	1.71
9	12	0.88-0.93	0.899	0.022	0.008	1.61
10	18	0.88-0.93	0.906	0.021	0.007	1.53
11	26	0.88-0.91	0.919	0.022	0.006	1.61
12	16	0.89-0.95	0.910	0.028	0.009	2.08
13	18	0.88-0.93	0.904	0.019	0.006	1.38
14	10	0.87-0.94	0.898	0.032	0.014	2.39
15	12	0.88-0.94	0.916	0.023	0.009	1.64
16	20	0.88-0.94	0.906	0.021	0.006	1.54
17	16	0.88-0.93	0.897	0.023	0.008	1.71
18	12	0.89-0.93	0.910	0.019	0.007	1.41
19	12	0.88-0.93	0.908	0.023	0.009	1.70
20	10	0.88-0.91	0.901	0.016	0.007	1.22
21	12	0.87-0.94	0.914	0.027	0.011	2.00
22	26	0.87-0.93	0.902	0.023	0.006	1.73

Table 48. (Continued.)

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
23	20	0.88-0.93	0.905	0.023	0.007	1.70
24	16	0.88-0.93	0.908	0.023	0.008	1.67
25	22	0.88-0.93	0.904	0.022	0.006	1.66
26	12	0.89-0.95	0.919	0.030	0.012	2.20
27	12	0.88-0.95	0.912	0.031	0.012	2.24
28	24	0.89-0.94	0.920	0.022	0.006	1.60
29	9	0.90-0.96	0.927			
30	6	0.88-0.92	0.905			
31	6	0.88-0.93	0.910			

parts of the Sierra Madre Occidental, but gene flow is unrestricted from north to south on both sides of this mountain range. South of the Rio Balsas, and across the Sierra Madre del Sur, gene flow is limited. Across northern Mexico from the eastern side of the Sierra Madre Occidental to the Atlantic coast, there is no evidence that gene flow is restricted. Nor is gene flow restricted along the Atlantic coast to Middle America, across to the Pacific in Chiapas, and west from there to the southern side of the Sierra Madre del Sur. No geographically proximate forms are reproductively isolated, and no forms warrant formal recognition as subspecies.

Etymology. - Latin, *pygmaeus* = dwarf, a reference to the small size of these beetles.

Distribution. - Specimens of *S. pygmaeus* have been found at elevations ranging from near sea level to about 6500'. *S. pygmaeus* ranges from northern California, Arizona, extreme western New Mexico, southern Chihuahua, Durango, Zacatecas, San Luis Potosi, Nuevo Leon, and Tamaulipas, southward at least to Colombia (Fig. 239). I studied 1112 specimens of this species from the following localities.

UNITED STATES

ARIZONA (9; ANSP, CUNY, MCZ, UKSM, USNM): 10 mi. e. Continental (1; UATA), Hot Springs (2; USNM), Riverside (3; CAS, USNM); Cochise Co., Chiricahua Mountains (1; UKSM), Cochise Stronghold (4; TLEr, UATA), Palominas (1; UASM), 5 mi. w. Portal (4; AMNH, CNC), Rucker Lake (1; UASM); Coconino Co., Bill Williams Fork (1; UKSM); Gila Co., Globe (3; MCZ, UASM), 33 mi. s. Globe (1; DJLa), Pinal Mountains (2; UASM), Rice (3; MCZ, UASM), Salt River (2; USNM), San Carlos Lake (1; UASM);

Graham Co., Aravaipa (18; UASM), Galiuro Mountains (2; USNM); Graham Mountains (2; UATA), Power's Garden (2; UASM), Thatcher (1; UCD); Pima Co., Ajo Mountains (1; CAS), Arivaca (11; CAS, MCZ), Baboquivari Mountains (6; CAS, MCZ), Organ Pipe National Monument (1; CAS), Quitobaquito (17; UASM), Sabino Canyon (38; AMNH, CNC, TCBa, TLEr, UATA, UCD, UKSM), Sahuarita (1; MCZ), Santa Catalina Mountains (1; CAS), Tanque Verde (14; UATA), Tucson (6; CAS, MCZ, UATA, USNM); Pinal Co., 14 mi. e. Oracle (1; CAS), Superior (1; CAS); Santa Cruz Co., Madera Canyon (4; UATA, UCD), Nogales (6; CAS, CNHM), Patagonia (10; CAS, CNHM, CUNY, TLEr, UATA), Pena Blanca (9; CNC, UASM, UATA), Tumacacori Mountains (17; CAS); Yuma Co., Fort Yuma (2; USNM). CALIFORNIA (12; ANSP, CAS, MCZ): Alameda Co., 20 mi. s. Livermore (1; TLEr); Butte Co., Oroville (1; CAS); Calaveras Co., Mokelumne Hill (6; CAS), El Dorado Co. (1; CNHM); Fresno Co., La Fevre Creek (3; CAS), 11.6 mi. s. Tollhouse (5; TLEr); Lake Co. (3; CAS), Clear Lake (59; CAS), North Fork Cache Creek (2; UCD); Los Angeles Co., Pasadena (1; CAS), Pomona (1; RUNB), San Gabriel Canyon (2; TCBa), Tujunga Canyon (4; LACM, MSUL); Mendocino Co., Longvale (1; CAS); Riverside Co., Palm Springs (15; AMNH, CAS, CNC); San Bernadino Co. (1; MCZ), Mojave River (1; TLEr), San Bernadino Mountains (1; MGFT); San Diego Co., Elsinore Lake (4; CAS), Poway (4; CAS), Warners Hot Springs (1; MSUL); Santa Barbara Co., Santa Barbara (1; CAS); Santa Clara Co., Gilroy Hot Springs (3; TLEr), Mount Hamilton (29; CAS); Sonoma Co., Rio Nido (1; CAS); Stanislaus Co., Del Puerto Creek (1; DHKa), Patterson (2; CAS), 20 mi. w. Patterson (1; TLEr); Yolo Co., Davis (9; UCD). NEW MEXICO: Grant Co., Cliff (3; DRWh), 21.9 mi. ne. Pinos Altos (1; UASM).

MEXICO

AGUASCALIENTES: 2.8 mi. s. Aguascalientes (1; UASM). BAJA CALIFORNIA (4; CAS): Catavinia (4; CAS), 20 mi. n. Comondu (1; CAS), Ensenada (1; UKSM), 12.4 mi. e. La Paz (1; CAS), Las Cruces (7; CAS), 5 mi. nw. Miraflores (1; CAS), 5 mi. s. Miraflores (1; CAS), 5 mi. w. San Bartolo (11; CAS), Santa Rosa (2; CNHM, MCZ), Santiago (1; CAS), 6 mi. sw. Santiago (4; UATA), Triunfo (8; CAS). CHIAPAS: 3.2 mi. n. Arriaga (15; UASM), 20.9 mi. n. Arriaga (19; UASM), 5.9 mi. e. Chiapa de Corza (1; UASM), 12.2 mi. ne. Chiapa de Corzo (12; UASM), 32.5 mi. e. Comitan (3; BMNH), Huehuetan (2; IRSB), Huixtla (12; UASM), Macuilapa (6; FDAG), San Quintin (38; UASM), Tonala (2; UASM), 18.6 mi. se. Tonala (9; UASM). CHIHUAHUA: Catarinas (7; AMNH), Parral (1; AMNH), 15 mi. e. Parral (1; AMNH). COLIMA: 3.4 mi. se. Colima (5; UASM), 8 mi. sw. Colima (1; UASM). DURANGO: 12.2 mi. s. El Banco (30; UASM), 4.2 mi. w. Vicente Guerrero (8; UASM). GUANAJUATO: 9.8 mi. s. Silao (2; UASM). GUERRERO: Acapulco (4; MCZ), 24.8 mi. e. Acapulco (3; UASM), 41.4 mi. n. Acapulco (8; UASM), Coyuca (4; UASM), 23.7 mi. n. Zumpango del Rio (1; UASM), 30.8 mi. n. Zumpango del Rio (1; UASM). HIDALGO: Tasquillo (6; UASM). JALISCO: Ajijic (1; CAS), Cocula (19; UASM), 9.7 mi. e. Encarnacion de Diaz (8; UASM), 8.5 mi. n. Juchitlan (10; UASM), 10.6 mi. s. La Huerta (1; UASM), 17.7 mi. nw. Los Volcanes (1; UASM), 17.9 mi. w. Magdalena (2; UASM), Pitallal (31; UASM), Puerto Vallarta (5; UASM), Talpa de Allende (4; UASM). MEXICO: Tejupilco (3; MCZ). MICHOACAN: 8.5 mi. n. Nueva Italia (32; UASM), 20 mi. n. Nueva Italia (3; UASM). MORELOS: Tetecala (2; UASM). NAYARIT: 2.4 mi. s. Acaponeta (1; UASM), 14 mi. e. San Blas (3; UASM). NUEVO LEON: 14.8 mi. w. Linares (3; UASM). OAXACA: 17.7 mi. w. El

Camaron (2; UASM), 25 mi. w. El Camaron (11; UASM), 29.4 mi. e. El Coyul (1; UASM), Huitzo (2; BMNH), 11.1 mi. n. Matias Romero (7; UASM), 19 mi. s. Matias Romero (3; CNC), 22.5 mi. w. Oaxaca (2; MGFT), 9.9 mi. n. Pochutla (15; UASM), Rio Jalpan (1; FDAG), Salina Cruz (3; AMNH), Tehuantepec (2; BMNH), Totolapan (1; UKSM), Valle Nacional (1; UASM), Zanatepec (25; UASM), 18.4 mi. w. Zanatepec (17; UASM). PUEBLA: Acatlan (2; UCB), 9 mi. n. Amatitlan (2; CAS), Petlalcingo (17; UASM), Tehuitzingo (4; UASM), Tepexco (13; UASM). QUERETARO: Escanelilla (1; UASM), Jalpan (3; UASM). SAN LUIS POTOSI: 14 mi. e. Ciudad del Maiz (1; CAS), Ciudad del Valles (1; CPBo), El Naranjo (1; CAS), Huichihuayan (1; UKSM), 7.5 mi. nw. Mexquitic (1; UASM), 2.7 mi. w. Santa Catarina (23; UASM), Tamazunchale (1; UASM), 19.3 mi. nw. Tamazunchale (1; UASM), Vergel (1; CPBo). SINALOA: Concordia (18; UASM), 11.2 mi. ne. Concordia (1; UASM), 12 mi. s. Mazatlan (3; TLEr, UCB), Rosario (1; UASM), 28 mi. e. Villa Union. SONORA: (4; CNC), Alamos (16; CAS), 7 mi. s. Alamos (10; UCB, UCD), 10 mi. s. Alamos (1; UCD), 10 mi. w. Alamos (5; AMNH), 5 mi. w. Alamos (1; UATA), 16 mi. ne. Ciudad Obregon (1; CNC), Hermosillo (4; CAS), 10 mi. e. Navajoa (4; UATA), San Carlos Bay (2; CAS). TAMAULIPAS: Ciudad Victoria (1; USNM), 15.2 mi. n. Ciudad Victoria (1; UASM), 21.3 mi. n. Ciudad Victoria (13; UASM), Encino (2; UASM). VERACRUZ: Bobo (1; BMNH), Catemaco (2; JNeg), Fortin de las Flores (1; FDAG), 20 mi. nw. Huatusco (5; FDAG), 21.8 mi. e. Jalapa (9; UASM), Paso de Ovejas (12; UASM). ZACATECAS: Jalpa (6; UASM), Sain Alto (4; UASM).

GUATEMALA

ALTA VERAPAZ: Trece Aguas (1; USNM). CHIQUIMULA: Chiquimula (5; AMNH).

GUATEMALA: Chinautla (1; BMNH). QUICHE: Sacapulas (1; AMNH).

EL SALVADOR

LA PAZ: La Herradura (4; JNeg). SAN SALVADOR: Guzapa (4; JNeg), San Salvador (4; JNeg).

HONDURAS

COMAYAGUA: Rancho Chiquito (4; FDAG). El Zamarano (1; OSUC).

NICARAGUA

RIVAS: 10 km. nw. Sapoa (1; FDAG).

COSTA RICA

GUANACASTE: 5 km. n. Canas (1; LACM). LIMON: Los Diamantes (1; FDAG). PUNTARENAS: Palmar Sur (1; UAFA), 6 mi. n. Palmar Sur (12; UAFA). 7 mi. nw. Palmar Sur (1; UAFA), Villa Neilly (1; FDAG).

COLOMBIA

MAGDALENA: Aracataca (1; MCZ), Rio Frio (7; MCZ).

Collecting notes. - Specimens of this species have been taken throughout the year, at lights or in riparian gravel bars. At most localities where specimens of *S. pygmaeus* and *S. falli* have been collected together, one of the two species was strongly numerically dominant.

Taxonomic notes. - Although I studied holotypes of neither *S. pygmaeus* nor *S. championi*, I did study paratypes of both and have no doubt that my association of the names is correct. As shown in my analysis of geographic variation above, these two names clearly refer to a single species. Lindroth (1961) suggested that the form in southern California might be a distinct species, but though most specimens are distinguishable from topotypic specimens of *S. pygmaeus*, there is no evidence for reproductive isolation.

3.536 *Schizogenius scopaeus* new species

Type material. - Holotype male and allotype female labelled "Limpia Canyon, 2 mi. n.w. Fort Davis, Texas. 3.VIII.63 D.R.Whitehead" (MCZ). An additional 98 specimens from Jeff Davis County, Texas are paratypes (AMNH, ANSP, BMNH, CAS, CNC, CNHM, DJLa, DRWh, IRSB, MGFT, UASM, UCD, USNM).

Diagnostic combination. - Specimens of this species are reliably distinguished from red specimens of *S. pygmaeus* only by form of apex of male median lobe, and by geographic distribution.

Description. - As in *S. pygmaeus* except as follows. Body color testaceous to ferrugineous, not brunneous, piceous, bicolored, or aeneous. Left elytron with about eight to eleven setae on interval three, seven to ten on interval five, four to seven on interval seven; total 18-27 in specimens examined. Male genitalia with median lobe, Fig. 228-229, apex in most specimens, particularly western specimens, broader than in specimens of *S. pygmaeus* (Fig. 234); 20 specimens examined.

Measurements and proportions. See Table 49. Of holotype: TL, 3.25 mm; LE, 2.00 mm; WH, 0.66 mm; WP, 0.84 mm; WE, 1.04 mm; WF/WH, 0.64; LP/WP, 0.93; DP/LP, 0.81; LP/WE, 0.75; Ta/Ti, 0.60; PS/LP, 0.68. Of allotype: TL, 3.50 mm; LE, 2.18 mm; WH, 0.71 mm; WP, 0.92 mm; WE, 1.12 mm; WF/WH, 0.63; LP/WP, 0.90; DP/LP, 0.78; LP/WE, 0.74; Ta/Ti, 0.64; PS/LP, 0.72.

Table 49. Descriptive statistics for *S. scopaeus*, based on 20 males from Limpia Canyon, Texas.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.04-3.60	3.265	0.199	0.059	4.07
LE	1.86-2.22	2.010	0.144	0.043	4.78
WH	0.64-0.75	0.685	0.040	0.012	3.89
WP	0.79-0.93	0.848	0.050	0.015	3.91
WE	0.97-1.18	1.054	0.078	0.023	4.93
B. Setae on left elytron.					
Interval 3	9-11	9.6			
Interval 5	7-10	8.6			
Interval 7	4- 7	5.4			
Total	20-26	23.5	2.3	0.7	6.55
C. Proportions.					
WF/WH	0.60-0.66	0.628	0.023	0.007	2.47
LP/WP	0.88-0.95	0.924	0.026	0.008	1.86
DP/LP	0.78-0.84	0.804	0.022	0.007	1.86
LP/WE	0.72-0.77	0.747	0.023	0.007	2.04
Ta/Ti	0.60-0.70	0.658	0.044	0.013	4.48
PS/LP	0.64-0.77	0.694	0.038	0.011	3.67

Variation. - Statistical data on variation in body size, numbers of elytral setae, relative eye size, and pronotal form are given in Tables 50-53 and summarized in Fig. 243-246. From north to south, numbers of elytral setae increase, eyes increase in size, and pronota narrow. Specimens from central Texas tend to be smaller than specimens from the Rio Grande Valley to the South and from Arkansas and Missouri to the north. The form of apex of median lobe of male genitalia (Fig. 234) shows considerable variation; in particular, the apex is much larger in specimens from Colorado and western Texas.

Etymology. - Greek, *skopaios* = dwarf. This word is an etymological synonym of the Latin *pygmaeus*, chosen to indicate the great similarity of these two species.

Distribution. - *S. scopaeus* ranges over an area limited in the north by the Missouri River, in the east by the Mississippi River, in the west by the Rocky Mountains, and in the south by the Rio Grande except for a small area in northeastern Mexico (Fig. 238). I studied 357 specimens of this species from the following localities.

UNITED STATES

No locality (1; ANSP). ARKANSAS: Carroll Co., 5 mi. w. Berryville (15; UASM); Washington Co., 7 mi. s. Fayetteville (7; UASM). COLORADO: Baca Co., Regnier (1; AMNH); Pueblo Co., 38 mi. e. Walsenburg (6; UASM). MISSOURI: Butler Co., 12 mi. se. Elsinore (5; CAS); Crawford Co., Meremac River (1; USNM); McDonald Co., 3 mi. n. Noel (1; CAS); Reynolds Co., Ellington (2; USNM); Ripley Co., 5.5 mi. n. Briar (8; CAS); Wayne Co., Williamsville (1; CNC). OKLAHOMA: Atoka Co., 5 mi. n. Stringtown (4; UASM); Carter Co., 10.7 mi. s. Drake (1; TLEr); Cimarron Co., Black

Table 50. Variation in body size (LE, in mm) in selected samples of *S. scopaeus*; see Fig. 243. Males and females each 50%.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	22	1.77-2.10	1.940	0.122	0.035	4.19
2	26	1.83-2.15	1.975	0.122	0.032	4.10
3	14	1.82-2.05	1.964	0.096	0.034	3.24
4	22	1.89-2.28	2.068	0.151	0.043	4.86
5	22	1.71-2.01	1.879	0.122	0.035	4.34
6	20	1.71-2.02	1.888	0.140	0.042	4.95
7	20	1.85-2.14	1.971	0.139	0.041	4.71
8	12	1.87-2.18	1.975	0.121	0.047	4.09

Table 51. Variation in numbers of elytral setae in selected samples of *S. scopaeus*; see Fig. 244. Males and females each 50%.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	22	21-27	23.0	2.6	0.7	7.51
2	26	20-27	23.2	2.4	0.6	7.01
3	14	21-27	22.9	2.8	1.0	8.20
4	22	20-28	23.6	2.4	0.7	6.85
5	22	18-26	21.6	2.6	0.7	8.01
6	20	19-25	21.6	2.0	0.6	6.27
7	20	18-23	20.6	1.7	0.5	5.50
8	12	19-24	21.0	1.9	0.7	6.09

Table 52. Variation in relative eye size (WF/WH) in selected samples of *S. scopaeus*; see Fig. 245. Males and females each 50%.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	22	0.59-0.65	0.616	0.019	0.005	2.05
2	26	0.60-0.65	0.624	0.020	0.005	2.18
3	14	0.61-0.64	0.629	0.015	0.005	1.58
4	22	0.60-0.65	0.629	0.023	0.006	2.42
5	22	0.63-0.66	0.640	0.012	0.003	1.23
6	20	0.62-0.67	0.643	0.025	0.008	2.63
7	20	0.63-0.68	0.650	0.020	0.006	2.09
8	12	0.64-0.68	0.654	0.020	0.008	2.00

Table 53. Variation in pronotal form (LP/WP) in selected samples of *S. scopaeus*; see Fig. 246. Males and females each 50%.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	22	0.89-0.96	0.922	0.030	0.009	2.19
2	26	0.88-0.97	0.925	0.028	0.007	1.99
3	14	0.90-0.96	0.931	0.031	0.011	2.22
4	22	0.89-0.96	0.922	0.026	0.007	1.88
5	22	0.87-0.95	0.911	0.030	0.009	2.23
6	20	0.87-0.94	0.914	0.025	0.007	1.82
7	20	0.89-0.93	0.904	0.015	0.004	1.10
8	12	0.87-0.93	0.902	0.026	0.010	1.96

Mesa State Park (1; CAS); Comanche Co., Wichita National Forest (13; CAS); Cotton Co. (1; CAS); Murray Co., 10.3 mi. n. Drake (4; TLEr). TEXAS (11; AMNH, CAS, CNHM, INHS, MCZ, MSUL, UKSM, USNM): Austin Co., Austin (8; CAS, USNM). Bexar Co., San Antonio (1; CAS); Blanco Co., Cypress Mills (2; USNM), Johnson City (12; UASM), Twin Sisters (2; UASM); Brewster Co., Alpine (1; MCZ), Big Bend National Park (1; CNC), Green Valley (1; CAS), 22 mi. s. Marathon (3; UCD); Culberson Co., 2.5 mi. e. Nickle Creek Station (1; CNHM); Jeff Davis Co., Barrel Springs Creek (8; BMNH, DRWh, IRSB, MGFT), Davis Mountains State Park (4; CAS, DJLa), Fort Davis (21; AMNH, ANSP, CAS, CNC, MCZ, UCD), 4 mi. w. Fort Davis (4; CNC), Limpia Canyon (64; AMNH, CNC, CNHM, MCZ, UASM, USNM); Kinney Co., 23 mi. sw. Brackettville (6; UASM); Lampasas Co., Adamsville (2; JNeg); Llano Co., Enchanted Rock (13; CNC); Maverick Co., 8 mi. n. Quemado (9; UASM); McCulloch Co., 16 mi. s. Brady (26; CAS); Terrell Co., Chandler Ranch (6; UASM), Independence Creek (14; UASM); Val Verde Co., Del Rio (4; CNC, USNM), 13 mi. nw. Del Rio (17; UASM).

MEXICO

NUEVO LEON: Cienega de Flores (8; UASM), Linares (1; JHeS), Montemorelos (11; UASM), 32.9 mi. n. Montemorelos (1; UASM), 5 mi. s. Monterrey (8; CNC), 6 mi. s. Monterrey (1; FDAG), 4.8 mi. e. Sabinas Hidalgo (1; UASM). TAMAULIPAS: 39 mi. s. Ciudad Victoria (1; CBoP), Villagran (11; UASM).

Collecting notes. - Specimens of *S. scopaeus* are abundant in gravel bars along both permanent and intermittent streams. In northeastern Mexico they are found in less protected places than are specimens of *S. pygmaeus*, such as along the intermittent Arroyo Villagran in Tamaulipas.

All specimens were collected between April and October. On repeated occasions, specimens have been taken at lights in the vicinity of Fort Davis and Limpia Canyon, Texas.

Taxonomic notes. - I recognize *S. scopaeus* as a new species distinct from *S. pygmaeus* because these taxa overlap in range in northeastern Mexico and because I cannot show that they form a continuous circle of races through Durango, Chihuahua, and western Texas. Such a circle of races is quite possible, and is strongly suggested in statistical comparisons summarized in Fig. 243-246. But male genitalia in this area are divergent (Fig. 234); western forms of *S. scopaeus*, so far as studied, have broad apices while those of *S. pygmaeus* in Durango and Chihuahua have narrow apices. A detailed study of material from the Rio Conchos system in Chihuahua will be required to finally decide whether the forms here separated as *S. scopaeus* and *S. pygmaeus* are conspecific or not. A stepped cline in the genitalic characteristic is surely a possibility. However, *S. scopaeus* is largely replaced by the related *S. falli* in the Big Bend region of Texas, and Chihuahua *S. pygmaeus* and Texas *S. scopaeus* may therefore be geographically isolated along the lower parts of the Rio Conchos.

3.537 *Schizogenius falli* new species

Type material. - Holotype male and allotype female labelled "MEX. Nuevo Leon Rio Sabinas Hidalgo, 4.8 mi. e. Sabinas Hidalgo 800' X.22-23. 65" and "George E. Ball D. R. Whitehead collectors" (MCZ). An additional 34 specimens from various localities in Nuevo Leon are paratypes (BMNH, CAS, CNC, CNHM, DRWh, IRSB, MGFT, UASM, USNM).

Diagnostic combination. - Within the *depressus* group, specimens of this species are recognized by the following combination of characters: pale color; small size; abdomen without extensive microsculpture; and frontal carinae strongly fused basally.

Description. - As in *S. pygmaeus* except as follows. Body color testaceous to ferrugineous, not brunneous, piceous, bicolored, or aeneous. Head and pronotum, Fig. 220; frontal carinae confused basally; pronotal hind angles more prominent. Left elytron with about seven to eleven setae on interval three, six to ten on interval five, four to six on interval seven; total 17-27 in specimens examined. Male genitalia with median lobe, Fig. 230; 10 specimens examined.

Measurements and proportions. See Table 54. Of holotype: TL, 3.80 mm; LE, 2.30 mm; WH, 0.80 mm; WP, 1.02 mm; WE, 1.20 mm; WF/WH, 0.66; LP/WP, 0.94; DP/LP, 0.76; LP/WE, 0.79; Ta/Ti, 0.59; PS/LP, 0.71. Of allotype: TL, 3.78 mm; LE, 2.34 mm; WH, 0.80 mm; WP, 0.99 mm; WE, 1.18 mm; WF/WH, 0.66; LP/WP, 0.93; DP/LP, 0.77; LP/WE, 0.78; Ta/Ti, 0.56; PS/LP, 0.70.

Variation. - Data on variation in body size, numbers of elytral setae, relative eye size, and pronotal form are given in Tables 55-58, and summarized in Fig. 247-250. In general, body size increases from west to east, with no important gaps between geographically proximate samples (Fig. 247). Specimens from interior parts of the range tend to have more setae than do those from peripheral areas, and there is a statistically significant difference between the Chihuahua and Durango samples (16 and 17) (Fig. 248). Relative eye size (Fig. 249) tends

Table 54. Descriptive statistics for *S. falli*, based on 20 males from 4.8 miles east of Sabinas Hidalgo, Nuevo Leon.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.52-4.18	3.858	0.237	0.071	4.10
LE	2.15-2.58	2.358	0.150	0.045	4.25
WH	0.74-0.85	0.794	0.041	0.012	3.40
WP	0.93-1.09	1.019	0.065	0.019	4.27
WE	1.10-1.29	1.203	0.071	0.021	3.91
B. Setae on left elytron.					
Interval 3	7- 9	8.2			
Interval 5	6- 9	7.5			
Interval 7	4- 6	5.3			
Total	19-24	21.0	1.7	0.5	5.44
C. Proportions.					
WF/WH	0.65-0.70	0.671	0.020	0.006	1.99
LP/WP	0.92-0.97	0.942	0.020	0.006	1.40
DP/LP	0.75-0.78	0.762	0.013	0.004	1.09
LP/WE	0.78-0.83	0.801	0.022	0.007	1.85
Ta/Ti	0.56-0.62	0.594	0.024	0.007	2.75
PS/LP	0.67-0.76	0.709	0.032	0.009	3.00

Table 55. Variation in body size (LE, in mm) in selected samples of *S. falli* and *S. ochthocephalus* (sample one from Davis, California); see Fig. 247. Males and females each 50%.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	12	2.19-2.50	2.292	0.136	0.053	3.97
2	12	2.09-2.47	2.247	0.167	0.064	4.95
3	24	2.08-2.42	2.211	0.166	0.045	4.99
4	20	2.00-2.38	2.182	0.136	0.041	4.16
5	20	2.05-2.45	2.208	0.145	0.043	4.38
6	14	2.00-2.40	2.229	0.155	0.055	4.64
7	14	2.14-2.40	2.281	0.096	0.042	3.43
8	14	2.17-2.52	2.340	0.136	0.048	3.87
9	20	2.00-2.59	2.309	0.234	0.070	6.75
10	20	2.17-2.47	2.320	0.158	0.047	4.54
11	10	2.10-2.50	2.295	0.192	0.081	5.57
12	18	2.20-2.58	2.368	0.165	0.052	4.64
13	20	1.95-2.35	2.186	0.198	0.059	6.05
14	20	1.87-2.39	2.080	0.201	0.060	6.44
15	20	1.90-2.33	2.170	0.195	0.058	5.97
16	20	2.04-2.55	2.304	0.215	0.064	6.23
17	18	2.15-2.50	2.326	0.140	0.044	4.02
18	20	2.20-2.58	2.396	0.183	0.055	5.09

Table 56. Variation in numbers of elytral setae in selected samples of *S. falli* and *S. ochthocephalus* (sample one from Davis, California); see Fig. 248. Males and females each 50%.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	12	18-22	19.9	1.7	0.7	5.85
2	12	19-23	21.0	1.8	0.7	5.74
3	24	19-25	21.2	2.0	0.6	6.37
4	20	19-24	21.0	2.0	0.6	6.29
5	20	19-25	21.5	2.3	0.7	7.16
6	14	20-25	21.9	1.8	0.6	5.50
7	14	20-25	21.7	2.2	0.8	6.62
8	14	20-23	21.6	1.5	0.5	4.71
9	20	19-24	21.8	2.1	0.6	6.48
10	20	19-24	21.1	2.4	0.7	7.52
11	10	20-24	21.3	2.0	0.8	6.28
12	18	18-25	21.2	2.3	0.7	7.29
13	20	18-24	21.4	2.6	0.8	8.08
14	20	17-26	21.0	3.4	1.0	10.73
15	20	18-24	21.1	2.2	0.6	6.86
16	20	17-25	20.4	2.8	0.8	9.06
17	18	19-27	22.1	2.6	0.8	7.85
18	20	19-24	21.4	2.1	0.6	6.68

Table 57. Variation in relative eye size (WF/WH) in selected samples of *S. falli* and *S. ochthocephalus* (sample one from Davis, California); see Fig. 249. Males and females each 50%.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	12	0.65-0.69	0.671	0.017	0.007	1.74
2	12	0.62-0.66	0.636	0.016	0.006	1.70
3	24	0.62-0.66	0.645	0.015	0.004	1.58
4	20	0.63-0.67	0.651	0.015	0.004	1.49
5	20	0.63-0.66	0.644	0.014	0.004	1.47
6	14	0.62-0.66	0.641	0.017	0.006	1.78
7	14	0.63-0.68	0.654	0.025	0.009	2.52
8	14	0.63-0.68	0.653	0.019	0.007	1.94
9	20	0.63-0.68	0.666	0.021	0.006	2.14
10	20	0.63-0.66	0.648	0.019	0.006	1.91
11	10	0.65-0.69	0.669	0.024	0.010	2.38
12	18	0.64-0.68	0.661	0.014	0.004	1.42
13	20	0.62-0.66	0.647	0.016	0.005	1.67
14	20	0.61-0.67	0.650	0.022	0.007	2.26
15	20	0.63-0.67	0.652	0.019	0.006	1.98
16	20	0.65-0.70	0.669	0.026	0.008	2.61
17	18	0.64-0.68	0.662	0.021	0.007	2.09
18	20	0.65-0.70	0.673	0.026	0.008	2.56

Table 58. Variation in pronotal form (LP/WP) in selected samples of *S. falli* and *S. ochthocephalus* (sample one from Davis, California); see Fig. 250. Males and females each 50%.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	12	0.93-0.96	0.952	0.014	0.005	0.98
2	12	0.94-0.98	0.958	0.017	0.006	1.16
3	24	0.90-0.99	0.950	0.035	0.010	2.47
4	20	0.92-0.98	0.952	0.024	0.007	1.71
5	20	0.93-0.98	0.956	0.028	0.008	1.96
6	14	0.90-0.97	0.937	0.025	0.009	1.80
7	14	0.92-0.98	0.944	0.023	0.008	1.65
8	14	0.92-0.99	0.950	0.030	0.011	2.11
9	20	0.90-1.00	0.950	0.030	0.009	2.11
10	20	0.94-0.98	0.952	0.015	0.004	1.06
11	10	0.90-0.96	0.936	0.030	0.013	2.15
12	18	0.90-0.96	0.931	0.024	0.008	1.72
13	20	0.93-0.98	0.935	0.017	0.005	1.18
14	20	0.92-0.99	0.947	0.032	0.010	2.25
15	20	0.92-0.97	0.946	0.018	0.006	1.31
16	20	0.91-0.98	0.944	0.025	0.008	1.80
17	18	0.90-0.99	0.944	0.036	0.011	2.57
18	20	0.92-0.98	0.948	0.022	0.007	1.56

to decrease from west to east, and there is a statistically significant difference between the Boquillas and Marathon samples (9 and 10). Specimens from the northeast and southwest of the range (Fig. 250) tend to have wider pronota than those from elsewhere, and the samples from Cochise Stronghold and Portal (5 and 6) are statistically significantly different in this characteristic. For a more extended discussion, see the taxonomic notes section under *S. ochthocephalus*.

Etymology. - I dedicate the name *S. falli* in recognition of the many important contributions to our knowledge of North American Coleoptera made by the late H. C. Fall.

Distribution. - The known range of *S. falli* extends west from southern Illinois to extreme southern California and south to Colima (Fig. 240). I studied 1032 specimens from the following localities.

UNITED STATES

No locality (2; ANSP). ARIZONA (13; AMNH, ANSP, INHS, MCZ, USNM): Cochise Co., Bear Canyon (1; CUNY), Benson (1; UATA), Carr Canyon (1; CAS), Cave Creek (4; UASM), Chiricahua Mountains (2; CAS, USNM), Cochise Stronghold (42; DJLa, TLEr, UATA), Douglas (1; CNHM), Portal (4; UCB), 5 mi. w. Portal (6; AMNH, CUNY, FDAG, UCD), Texas Pass (15; CUNY), Whetstone Mountains (2; CAS), Wilcox (1; CAS); Gila Co., Globe (32; CAS, CNC, MCZ, UASM, USNM), 33 mi. s. Globe (2; DJLa), Rice (4; MCZ, UASM), San Carlos Lake (16; CUNY, MCZ, UASM); Graham Co., Aravaipa (2; CAS, UASM), Galiuro Mountains (1; USNM), Marijilda Canyon (2; CAS, UATA), Power's Garden (8; UASM), Thatcher (5; UCD); Maricopa Co., Haslampa District (1; CAS), Phoenix (6; MCZ, USNM), Salt River (2; MCZ), Tempe (1; USNM), Verde River (4; LACM, MCZ), Wickenburg (1; LACM); Mojave Co., Kingman (1; UKSM); Pima Co., Alamo Canyon (3; CAS), Arivaca (8; CAS, MCZ, UKSM), Azo (3; CAS), Baboquivari Canyon (6; CAS), Brown's Canyon (4; CAS, UATA), Catalina Springs (2; USNM), Elkhorn Ranch (1; CAS), Kits Peak Rincon (2; AMNH), Organ Pipe National Monument (10; UATA, UCD), Pantano (3; CUNY), Pepper Sauce Canyon (1; CAS), 17 mi. w. Quijotoa (1; UASM), Quitobaquito (3; AMNH, UASM), Robles Ranch (3; UCD), Sabino Canyon (15; CAS, RTBe, TCBa, TLEr, UCD, UKSM, USNM), Santa Catalina Mountains (6; CAS, UATA), Staghorn Ranch (1; CNC), Tanque Verde (4; UATA), Tucson (97; ANSP, CAS, JNeg, UATA, UCB, USNM); Pinal Co., 10 mi. w. Casa Grande (1; CAS), Oracle (2; USNM), 14 mi. e. Oracle (1; CAS), Superior (3; UATA); Santa Cruz Co., Black Dike Prospect (2; AMNH), Calabasas Canyon (3; UASM), Canelo (6; UATA), Madera Canyon (30; DHKa, UATA, UCD), Nogales (32; AMNH, CAS, CNHM, UASM, UCD), Patagonia (10; CAS, CNHM, TLEr, UASM, UATA), Pena Blanca (30; CNC, CUNY, UASM); Santa Rita Mountains (9; UKSM, USNM), Sycamore Canyon (11; CAS, UATA); Yavapai Co., Bumble Bee (3; CAS), Congress (1; UATA), Jerome (4; CAS); Yuma Co., Yuma (10; UKSM, USNM). ARKANSAS: Carroll Co., Berrytown (7; UKSM), Eureka Springs (7; UKSM); Madison Co., Patrick (1; UKSM); Washington Co. (1; INHS), 7 mi. s. Fayetteville (5; UASM). CALIFORNIA (2; MCZ, USNM): Imperial Co., Potholes (2; CAS); Riverside Co., Palm Springs (1; USNM). COLORADO: Montrose Co., Cimarron (1; CUNY). ILLINOIS: Pike Co., Pittsfield (1; UCD). MISSOURI: Crawford Co., Meremac River (1; USNM); Ripley Co., 5.5 mi. n. Briar (1; CAS); Wright Co., Mountain Grove (1; TCBa). NEBRASKA: Douglas Co., Omaha (1; CAS). NEW MEXICO: Dona Ana Co., Agustin Pass (2; CAS), Las Cruces (1; CNC), White Sands (1; UKSM); Grant Co., Cliff (1; DRWh), Silver City (1; CNC); Hidalgo Co., Lordsburg (1; CNC); Luna Co., Deming (1; UCD), 7.5 mi. nw. Florida (7; CAS); Rio Arriba Co., San Juan Pueblo (1; DRWh). OKLAHOMA: Cimarron Co., Black Mesa State Park (1; CAS). TEXAS (20; AMNH, ANSP, CAS, INHS, MCZ, USNM): Blanco Co., Cypress Mills (3; USNM), Round Mountain (1; MCZ); Brewster Co. (1; MCZ), Black Gap Refuge (1; CNC), Boquillas (62; AMNH, CNC, UCB), Green Valley (1; CAS), Hot Springs (21; AMNH, CNC), Lajitas (2; CNC), 22 mi. s. Marathon (39; UCD), Maverick (3; CNC), Nine Point Draw (1; CNC), Panther Junction (1; CNC), Rio Grande Village (4; CAS, UASM), Terlingua (2; CNC), Tornillo Flat (3; CNC); Jeff Davis Co., Davis Mountains State Park (10; CAS, DHKa, DJLa), Fort Davis (7; CAS, CNC); Llano Co., Enchanted Rock (7; CNC); Presidio Co., 4 mi. w. Lajitas (1; JHeS), 6 mi. e. Presidio (21; UASM); Terrell Co., 10 mi. e. Dryden (1; DJLa), Lozier Canyon (1; MCZ); Val Verde Co., Del Rio (3; CAS, USNM). UTAH: San Juan Co., 8 mi. e. Bluff (1; UATA).

MEXICO

BAJA CALIFORNIA: 10 mi. sw. Canipole (3; UATA), 20 mi. n. Comondu (5; CAS), Conception Bay (1; CAS), 8 mi. nw. El Progreso (1; CAS), La Paz (2; CAS), 25 mi. w. La Paz (1; CAS), Purissima (2; UASM), 5 mi. w. San Bartolo (7; CAS), 12 mi. nw. San Bartolo (3; CAS), 10 mi. sw. San Jose del Cabo (8; UATA), 25 mi. s. Santa Rosalia (1; CAS), 6 mi. sw. Santiago (12; UATA), Triunfo (7; CAS). CHIHUAHUA: 25 mi. sw. Camargo (2; AMNH), Catarinas (5; AMNH), 70 mi. n. Chihuahua (1; UCB), 33 mi. s. Ciudad Jimenez (3; DJLa), Parral (1; UCB), 15 mi. e. Parral (3; AMNH), 40 mi. ne. Parral (3; UASM), 5 mi. w. Parrita (3; UCB), 63 mi. w. Santa Barbara (4; AMNH), Valle de Olivos (2; AMNH). COAHUILLA: Boquillas del Carmen (3; CNC), 15 mi. n. Saltillo (1; UASM). COLIMA: 8 mi. sw.

Colima (1; UASM). DURANGO: 12.2 mi. s. El Banco (25; UASM), Las Nieves (3; UASM), 4.2 mi. w. Vicente Guerrero (1; UASM). NAYARIT: Acaponeta (1; CAS), 2.4 mi. s. Acaponeta (2; UASM). NUEVO LEON: Cienega de Flores (2; CAS), 14.8 mi. w. Linares (2; BMNH), 5 mi. s. Monterrey (2; CNC), 4.8 mi. e. Sabinas Hidalgo (30; CNHM, DRWh, IRSB, MCZ, MGFT, UASM, USNM). SINALOA: 30.6 mi. s. Culiacan (1; UASM), 26 mi. n. Pericos (1; CAS), 4 mi. s. Villa Union (1; UCB). SONORA (2; BMNH): Alamos (6; CAS), 5 mi. w. Alamos (3; UATA), 10 mi. w. Alamos (5; AMNH), Hermosillo (40; CAS, UATA), 40 mi. n. Hermosillo (13; CAS), 10 mi. e. Navajoa (21; UATA), San Bernadino (1; CAS), San Carlos Bay (1; CAS), San Lorenzo (1; CNHM). TAMAULIPAS: Nuevo Laredo (1; USNM). ZACATECAS: 25 mi. w. Fresnillo (1; CAS), 1.3 mi. se. Sain Alto (1; UASM).

Collecting notes. - Within the *depressus* group, *S. falli* is similar to *S. pygmaeus*, *S. scopaeus*, and *S. depressus*, and has in the past been confused with them. But these species are sympatric, and specimens are constantly distinguishable by form of frontal carinae and by details of male genitalia. That *S. falli* is specifically distinct is further confirmed by the fact that sympatric population samples of these species are statistically significantly different in various ways.

My reasons for distinguishing the related *S. ochthocephalus* from *S. falli* are discussed in my treatment of that species.

3.538 *Schizogenius ochthocephalus* new species

Type material. - Holotype male and allotype female labelled "Davis Cal I.17 1956," "Taken in flood debris," and "E. A. Kurtz Collector" (UCD). An additional 16 specimens from various localities in central and northern California are paratypes (CAS, DRWh, UASM, UCD).

Diagnostic combination. - Within the *depressus* group, this is the only known pale species with extensive abdominal microsculpture.

Description. - As in *S. falli* except as follows. Left elytron with about seven to eight setae on interval three, six to eight on interval five, four to six on interval seven; total 18-21 in specimens examined. Abdomen extensively microsculptured. Male genitalia with median lobe, Fig. 231; four specimens examined.

Measurements and proportions. See Table 59. Of holotype: TL, 3.64 mm; LE, 2.25 mm; WH, 0.75 mm; WP, 0.93 mm; WE, 1.12 mm; WF/WH, 0.65; LP/WP, 0.96; DP/LP, 0.78; LP/WE, 0.79; Ta/Ti, 0.56; PS/LP, 0.70. Of allotype: TL, 3.88 mm; LE, 2.40 mm; WH, 0.80 mm; WP, 1.02 mm; WE, 1.25 mm; WF/WH, 0.67; LP/WP, 0.94; DP/LP, 0.78; LP/WE, 0.77; Ta/Ti, 0.61; PS/LP, 0.71.

Variation. - See Table 59. I have seen insufficient material to analyze geographic variation, and no such variation is evident.

Etymology. - Greek, *ochthos* = mound, plus *kephalos* = head, in reference to lumpy appearance of head caused by basal coalescence of frontal sulci.

Distribution. - *S. ochthocephalus* is known from only a few localities in central and northern California (Fig. 240). I studied the following 18 specimens.

Table 59. Descriptive statistics for *S. ochthocephalus*, based on 11 males from various localities in California.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.51-3.77	3.633	0.122	0.049	2.23
LE	2.18-2.34	2.247	0.074	0.030	2.18
WH	0.71-0.77	0.743	0.026	0.010	2.33
WP	0.89-0.97	0.928	0.035	0.014	2.54
WE	1.10-1.17	1.127	0.034	0.014	2.03
B. Setae on left elytron.					
Interval 3	7- 8	7.4			
Interval 5	6- 8	7.1			
Interval 7	5- 6	5.2			
Total	18-21	19.6	1.8	0.7	6.14
C. Proportions.					
WF/WH	0.65-0.69	0.670	0.020	0.008	2.00
LP/WP	0.94-0.97	0.955	0.021	0.009	1.49
DP/LP	0.76-0.81	0.784	0.020	0.008	1.73
LP/WE	0.77-0.80	0.784	0.013	0.005	1.11
Ta/Ti	0.55-0.60	0.580	0.034	0.014	3.93
PS/LP	0.69-0.73	0.706	0.019	0.008	1.78

UNITED STATES

CALIFORNIA: Calaveras Co., Mokelumne Hill (1; CAS); Humboldt Co., Fernbridge (1; UASM); Lake Co., Clear Lake (1; CAS); Sacramento Co., Fair Oaks (1; UCD); Sonoma Co., Guerneville (1; CAS); Yolo Co., Davis (13; DRWh, UCD).

Collecting notes. - I have not collected specimens of this species, but presume they live in riparian gravel bars. Available specimens were collected in January, March, April, and June.

Taxonomic notes. - This species is sympatric with *S. pygmaeus* and *S. depressus*, and differs constantly from them by having abdominal microsculpture and basally confused frontal carinae. *S. ochthocephalus* clearly shares a common ancestry with *S. falli*, and may be only a geographic isolate of that species, but I think it is reproductively isolated for the following reasons. There is evidently at least one complete morphological discontinuity between the two taxa, as all specimens of the former have the abdomen completely microsculptured, while none of the latter do. Mean eye size in *S. ochthocephalus* (sample one) is taxonomically significantly smaller (Table 57) than in the geographically nearest sample of *S. falli* (sample two, Yuma), and in this characteristic an otherwise continuous cline is interrupted (Fig. 249). These discontinuities indicate that *S. ochthocephalus* is more likely reproductively isolated from *S. falli* than not, and justify my recognition of them as distinct species. The *S. ochthocephalus* sample is further characterized by fewer elytral setae than the Yuma sample of *S. falli* (Table 56, Fig. 248), but the difference is not statistically significant.

Since no related species in the *depressus* group have extensive abdominal microsculpture, presence of such microsculpture in *S. ochthocephalus* must be a specialization. The four characteristics studied by statistical analysis exemplify central-peripheral patterns of variation (Brown, 1958; Ball, 1960), in which peripheral character states are best regarded as ancestral. I judge that large body size (Fig. 247) and small numbers of elytral setae (Fig. 248) are peripheral character states, and hence probably ancestral. The small body size character state is evidently spreading outward from the Sonoran Region, but has reached neither the *S. ochthocephalus* sample nor eastern samples of *S. falli*. Increased numbers of elytral setae may be a character state now spreading outward from the Chihuahuan Region, with impeded gene flow between the Chihuahua and Durango samples, and no gene flow between *S. falli* and *S. ochthocephalus*. The evidence for central-peripheral variation in relative eye size (Fig. 249) is stronger; the small eye character state is definitely peripheral, and hence most probably is ancestral. The enlarged eye character state apparently is spreading outward from the Sonoran Region, but does not affect *S. ochthocephalus*, and, curiously, is only weakly evident in the Big Bend part of Texas.

Even more interesting is the pattern of variation in pronotal form (Fig. 250). The wide pronotum, as in samples 12 and 13, is a peripheral character state which I think must be ancestral. Further support for this notion comes from a comparison of two samples from the Dragoon Mountains in Arizona. One sample from Texas Pass, not tabulated or figured, was collected in 1917; the second sample, collected in 1965, is from Cochise Stronghold (sample five). Data for the Texas Pass sample are as follows: N, 12; Range, 0.89-0.98; Mean, 0.936; 1.5SD, 0.030;

2SE, 0.011; CV(%), 2.11. If the statistical data for these two samples properly reflect their respective populations, there must have been a shift in time from broad to narrow pronotal form. The difference is statistically significant, and I therefore interpret it as biologically significant; there has, in the region of the Dragoon Mountains, been a shift from the ancestral to derived character state within a period of less than 50 years. I suggest that in *S. falli* the narrow pronotum character state is spreading from two foci, in the Sonoran Region and along the Rio Grande. If this assertion is correct, then the narrow pronotum in *S. ochthocephalus* must be an independently acquired specialization. However, my interpretation may be overly simplified, in view of the complex pattern of variation in pronotal form. A test of my hypothesis of central-peripheral variation may be made by searching for other shifts in time, from narrow to broad or broad to narrow pronotal form.

3.539 *Schizogenius depressus* LeConte

Schizogenius depressus LeConte 1852:197. *Type locality* Colorado River, California; type in MCZ, male labelled MCZ 5843 here designated lectotype (!). LeConte 1857:83. Putzeys 1863:24. Putzeys 1866: 223. LeConte 1879:34. Hatch 1949:118. Hatch 1953:69. Lindroth 1961:168.

Diagnostic combination. - Among pale members of the *depressus* group without ventral microsculpture, specimens of *S. depressus* are distinguished by prominent pronotal hind angles, frontal sulci not or weakly confused basally, and elytral length over 2.0 mm.

Description. - As in *S. pygmaeus* except as follows. Larger, elytral length 2.05 mm or more. Body color testaceous to ferrugineous or castaneous, not piceous, bicolored, or aeneous. Head and pronotum, Fig. 221; eyes uniformly faceted except in some Mexican specimens, where inner facets enlarged; neck densely to sparsely punctate; antennal article five about 1.4 to 1.6 times longer than wide; pronotal hind angles prominent in most specimens; anterior transverse impression finely punctate. Left elytron with six to twelve setae on interval three, six to 11 on interval five, four to seven on interval seven; total 16-30 in specimens examined; humeral denticles moderately sharp and prominent. Male genitalia with median lobe, Fig. 232; endophallus, Fig. 233; 20 specimens examined.

Measurements and proportions. See Table 60.

Variation. - Specimens from the Rio Balsas drainage in the state of Mexico have much larger inner than outer eye facets. Specimens from Zacatecas also have large inner eye facets, though less pronouncedly so. Eyes in all other specimens are uniformly faceted, including those from the Rio Tula drainage in the state of Mexico. The Zacatecas locality is, in a sense, geographically intermediate between the two state of Mexico localities, as it is from an interior drainage system, while the Rio Balsas drains to the Pacific and the Rio Tula to the Atlantic.

Statistical data on variation in body size, numbers of elytral setae, relative eye size, and pronotal form are given in Tables 61-64, and summarized in Fig. 251-254. The main features of variation in body

Table 60. Descriptive statistics for *S. depressus*, based on 20 males from Clear Lake, California.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.39-3.92	3.706	0.194	0.058	3.49
LE	2.06-2.40	2.263	0.123	0.037	3.61
WH	0.70-0.81	0.764	0.039	0.012	3.41
WP	0.91-1.05	0.990	0.052	0.016	3.50
WE	1.06-1.24	1.165	0.069	0.020	3.92
B. Setae on left elytron.					
Interval 3	6- 9	7.0			
Interval 5	6- 8	7.2			
Interval 7	4- 6	4.6			
Total	16-22	18.8	2.0	0.6	7.15
C. Proportions.					
WF/WH	0.63-0.68	0.650	0.020	0.006	2.08
LP/WP	0.90-0.96	0.930	0.024	0.007	1.69
DP/LP	0.76-0.81	0.788	0.023	0.007	1.98
LP/WE	0.77-0.83	0.790	0.024	0.007	1.99
Ta/Ti	0.59-0.68	0.634	0.041	0.012	4.31
PS/LP	0.70-0.78	0.735	0.032	0.009	2.88

Table 61. Variation in body size (LE, in mm) in selected samples of *S. depressus* (Fig. 251). Males and females each 50%.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	4	2.22-2.50	2.378			
2	14	2.32-2.92	2.563	0.221	0.079	5.74
3	20	2.16-2.71	2.442	0.226	0.067	6.17
4	12	2.22-2.58	2.432	0.184	0.071	5.09
5	30	2.25-2.78	2.560	0.183	0.044	4.76
6	16	2.32-2.66	2.487	0.165	0.055	4.43
7	4	2.39-2.58	2.482			
8	40	2.05-2.60	2.321	0.154	0.035	4.71
9	16	2.31-2.69	2.501	0.152	0.050	4.04
10	16	2.12-2.56	2.325	0.203	0.068	5.82
11	12	2.29-2.69	2.514	0.181	0.070	4.80
12	14	2.26-2.72	2.461	0.166	0.059	4.50
13	14	2.35-2.75	2.520	0.213	0.076	5.62
14	20	2.28-2.72	2.502	0.169	0.050	4.50
15	6	2.32-2.70	2.558			
16	18	2.30-2.70	2.529	0.167	0.053	4.41
17	16	2.15-2.78	2.530	0.241	0.080	6.34
18	26	2.35-2.69	2.494	0.143	0.037	3.83
19	24	2.25-2.75	2.508	0.200	0.054	5.31
20	48	2.19-2.72	2.449	0.187	0.036	5.10
21	40	2.25-2.78	2.520	0.164	0.035	4.36

Table 61. (Continued.)

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
22	4	2.65-2.85	2.775			
23	24	2.50-2.92	2.676	0.161	0.044	4.01

Table 62. Variation in numbers of elytral setae in selected samples of *S. depressus* (Fig. 252). Males and females each 50%.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	4	18-21	19.5			
2	14	18-22	20.4	1.7	0.6	5.65
3	20	17-22	19.8	2.3	0.7	7.61
4	12	18-21	19.5	1.3	0.5	4.09
5	30	18-23	20.4	1.9	0.5	6.12
6	16	18-23	20.1	1.9	0.6	6.43
7	4	17-21	18.8			
8	40	16-22	19.2	1.8	0.4	6.15
9	16	17-21	19.2	1.6	0.5	5.53
10	16	18-23	19.9	1.9	0.6	6.33
11	12	18-22	19.8	1.7	0.7	6.02
12	14	18-22	19.8	1.6	0.6	5.31
13	14	19-22	20.3	1.8	0.6	5.94
14	20	17-22	19.8	2.0	0.6	6.68
15	6	20-23	21.8			
16	18	21-25	23.0	2.3	0.7	6.67
17	16	20-25	22.1	2.1	0.7	6.37
18	26	20-24	22.0	1.7	0.4	5.05
19	24	20-28	23.0	3.2	0.9	9.16
20	48	20-30	22.2	2.9	0.6	8.66
21	40	19-25	22.6	2.0	0.5	6.93

Table 62. (Continued.)

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
22	4	24-27	25.5			
23	24	19-23	20.5	2.0	0.5	6.44

Table 63. Variation in relative eye size (WF/WH) in selected samples of *S. depressus* (Fig. 253). Males and females each 50%.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	4	0.66-0.69	0.675			
2	14	0.63-0.68	0.658	0.021	0.008	2.13
3	20	0.63-0.69	0.670	0.023	0.007	2.24
4	12	0.66-0.69	0.676	0.016	0.006	1.47
5	30	0.63-0.67	0.654	0.017	0.004	1.73
6	16	0.66-0.70	0.674	0.015	0.005	1.63
7	4	0.65-0.68	0.670			
8	24	0.62-0.68	0.655	0.020	0.005	2.01
9	16	0.63-0.68	0.659	0.017	0.006	1.70
10	16	0.65-0.69	0.666	0.016	0.005	1.63
11	12	0.63-0.67	0.650	0.022	0.009	2.27
12	14	0.63-0.67	0.652	0.020	0.007	2.01
13	14	0.65-0.67	0.663	0.012	0.004	1.25
14	20	0.63-0.68	0.657	0.018	0.005	1.79
15	6	0.64-0.67	0.657			
16	18	0.64-0.68	0.661	0.016	0.005	1.63
17	16	0.64-0.69	0.659	0.024	0.008	2.44
18	26	0.62-0.70	0.654	0.026	0.007	2.67
19	24	0.63-0.68	0.664	0.022	0.006	2.26
20	48	0.62-0.68	0.653	0.025	0.005	2.51
21	24	0.63-0.68	0.655	0.022	0.006	2.70

Table 63. (Continued.)

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
22	4	0.62-0.67	0.642			
23	24	0.62-0.66	0.640	0.018	0.005	1.93

Table 64. Variation in pronotal form (LP/WP) in selected samples of *S. depressus* (Fig. 254). Males and females each 50%.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	4	0.91-0.94	0.925			
2	14	0.91-0.96	0.939	0.023	0.008	1.64
3	20	0.90-0.95	0.932	0.019	0.006	1.76
4	12	0.91-0.96	0.932	0.026	0.010	1.84
5	30	0.89-0.95	0.928	0.021	0.005	1.53
6	16	0.90-0.96	0.927	0.025	0.008	1.79
7	4	0.93-0.97	0.948			
8	24	0.89-0.98	0.933	0.032	0.009	2.29
9	16	0.89-0.96	0.928	0.029	0.010	2.10
10	16	0.89-0.96	0.929	0.032	0.011	2.27
11	12	0.91-0.98	0.938	0.034	0.013	2.40
12	14	0.92-0.96	0.941	0.017	0.006	1.21
13	14	0.87-0.96	0.936	0.038	0.013	2.67
14	20	0.91-0.95	0.932	0.020	0.006	1.46
15	6	0.88-0.94	0.915			
16	18	0.89-0.95	0.923	0.025	0.008	1.82
17	16	0.89-0.95	0.923	0.022	0.007	1.62
18	26	0.89-0.95	0.923	0.024	0.006	1.76
19	24	0.88-0.96	0.930	0.028	0.008	2.04
20	48	0.89-0.98	0.928	0.024	0.005	1.75
21	24	0.89-0.98	0.939	0.028	0.008	2.06

Table 64. (Continued.)

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
22	4	0.90-0.97	0.942			
23	24	0.88-0.96	0.928	0.031	0.008	2.23

size (Fig. 251) are the following. Western samples are varied, but all show clear evidence of clinal relationships with geographically related samples. Eastern samples decrease in mean body size south to the Colorado River, and increase from there south into Mexico. Northern samples are not statistically significantly different from one another, but seem not to be clinally continuous across the Rocky Mountains.

Variation in numbers of elytral setae (Fig. 252) may be summzrized as follows. In the United States, samples from the Rio Papigochic, Colorado River, Great Basin, Rio Grande, Canadian River, and Missouri River drainage basins have statistically significantly more elytral setae than any of the western samples. Samples within each of these two areas are evidently clinally related to one another. Northern samples do not appear to be clinally continuous across the Rocky Mountains. The Chihuahua sample (number 22) is probably related with the Arizona sample (number 21) via a steep cline. Additional collections are needed to determine relationships between the quite different Chihuahua and Zacatecas samples (22 and 23).

Variation in relative eye size (Fig. 253) has the following main features. In both east and west, there is a general trend toward increased eye size from north to south, with particularly large eyes characteristic of Mexican samples. In the United States, eye size in eastern samples is quite uniform but in the west a discordant pattern of variation is evident in the north. Northern samples do not appear to be clinally continuous across the Rocky Mountains.

The chief features of variation in pronotal form (Fig. 254) are as follows. The pattern of variation in western samples is complex, and no definte trends are evident, but geographically related samples are probably clinally continuous. Among eastern samples there is a definite cline toward narrower pronotal form from north to south. Across the Rocky Mountains in the north, there is strong evidence of clinal discontinuity in this characteristic.

Among Mexican specimens, only those from Zacatecas were numerous enough to form a good sample for statistical analysis; thus, no detailed account of variation is yet possible. The Chihuahua specimens are evidently related by steep character clines to specimens from the Chiricahua Mountains of Arizona. Specimens from Zacatecas differ markedly from those from Chihuahua, particularly in numbers of elytral setae, but the differences probably reflect mainly a lack of intermediate collections. Specimens from Atlantic and Pacific drainages in the state of Mexico are strongly differentiated. Rio Tula and Guanajuato specimens differ from Rio Balsas specimens by narrower pronota, and by uniformly faceted and much smaller eyes. Zacatecas specimens are intermediate in these characteristics, and may also be considered geographically intermediate since they are from an interior drainage system. I suspect that the Rio Balsas and Rio Tula populations are geographically quite isolated from one another despite their proximity, and that they may even be reproductively isolated.

In America north of Mexico, sample means for numbers of elytral setae in eastern samples of *S. depressus* are statistically significantly greater than in western samples. Eastern samples are similar in all ways measured, and are linked to one another by definite character clines. Western samples are more varied, but are similarly related by character clines. There is no evidence of reproductive isolation between eastern and western forms in the south, but differences in mean numbers of elytral setae do indicate geographic isolation. In the north, the Montana sample (sample 15) is similar in most ways to some of the more distant western samples, especially samples two and five, but is divergent from them in pronotal form. Western samples geographically closer to the Montana sample, particularly samples three and four, are more differentiated in most or all characteristics measured. In the Pacific Northwest, these characteristics vary in definite geographic patterns, apparently independently of one another but not randomly. Most notably, small eyed forms extend southwest from the Snake River to northern California, thus separating large eyed forms to the north and south (Fig. 253). These facts suggest that the northern populations were once clinally continuous across the Rocky Mountains, but later became geographically and perhaps even reproductively isolated. The eastern form may relatively recently have crossed the mountain barrier to interact with the western form, resulting in character displacement (Brown and Wilson, 1956). This hypothesis of character displacement may be tested by searching for bimodal character state distributions in large samples collected along the western slopes of the Rocky Mountains. Insufficient material is available at present for such an analysis.

Although I have no direct evidence of character displacement in the northwest, I cannot otherwise explain how such a complex pattern of variation and differentiation may have originated. I assume that my hypotheses are correct, and postulate the following sequence of events. *S. depressus* was once widespread in western North America, with clinal continuity in the south via the Colorado River, in the north via the Columbia and Missouri Rivers, and perhaps also across the Great Basin. With deteriorating climatic conditions in the Pleistocene, and particularly with advances of glaciation southward along the Rocky Mountains, clinal continuity in the north was repeatedly broken by geographic isolation. During subsequent interglaciation, geographic isolation may have been partially maintained. Much later, the retreat of the Wisconsin glaciation was accompanied by a rapid spread of desert conditions in the south (Martin and Mehringer, 1965), and resulted in a break in clinal continuity there. As climates in the north moderated, renewed contact between eastern and western forms was established, but too late for renewed clinal continuity. Possible datings for Late Pleistocene events (Martin and Mehringer, 1965) are: glacial advance, 70,000 years ago; glacial retreat, 12,000 years ago; and reestablishment of contact between eastern and western forms in the north, less than 12,000 years ago.

Etymology. - Latin, *depressus* = flattened, in reference to the flattened body form.

Distribution. - *S. depressus* ranges further north, and reaches higher elevations, than any other species in the genus (Fig. 241). It ranges in the east along upper reaches of the Rocky Mountain drainage systems as far north as Montana, and in the west it occurs in coastal and montane regions north to southern British Columbia. To the south, *S. depressus* extends to both Atlantic and Pacific drainage basins in the state of Mexico, where specimens have been found as high as 8000' above sea level. One specimen labelled "D. C." belongs to this species and is no doubt incorrectly labelled. I examined 1179 additional specimens of this species from the following localities.

CANADA

BRITISH COLUMBIA: Salmon Arm (2; CAS, MCZ), Vaseaux Lake (1; UASM), Vernon (3; CAS); see Lindroth (1961) for additional Canadian records.

UNITED STATES

No locality (4; IRSB, MGFT, USNM). ARIZONA (29: AMNH, ANSP, CAS, CUNY, INHS, USNM): Cochise Co., Bear Canyon (1; CUNY), Bisbee (1; CAS), Cave Creek (22; AMNH, CAS, TCBa, UASM), Chiricahua Mountains (12; CAS, UKSM, USNM), Cochise Stronghold (2; TLEr, UATA), Montezuma Pass (1; CNC), Palmerlee (1; USNM), Pinery Creek (2; CNHM), 5 mi. w. Portal (30; AMNH, CNC, CUNY, MSUL, TLEr, UCD), Ramsey Canyon (1; UATA), Rucker Lake (1; UASM), Sierra Vista (1; CNC), South Fork Forest Camp (1; UATA), Texas Pass (1; CAS), Turkey Creek (1; UATA); Coconino Co. (1; CNHM), Flagstaff (6; CAS, UKSM), Oak Creek Canyon (1; UASM); Gila Co., Globe (3; CAS,CNC), 6 mi. n. Payson (1; DJLa), Rice (1; UASM), Roosevelt Lake (1; UASM), San Carlos Lake (1; CUNY); Graham Co., Arcadia Forest Camp (1; UATA), Camp Geronimo (1; UATA), Noon Creek (2; UATA), Power's Garden (1; UASM); Greenlee Co., Clifton (1; CAS), Diamond Creek (3; UASM); Pima Co., Rincon Mountains (4; UASM),Sahuarita (3; MCZ); Santa Cruz Co., Madera Canyon (6; DHKa, UATA, UCD), Nogales (2; CAS, MGFT), Santa Rita Mountains (3; UKSM), Sycamore Canyon (1; CAS); Yavapai Co., Crown King (3; CAS), Prescott (12; CAS, MCZ, UASM). CALIFORNIA (26; AMNH, ANSP, CNHM, INHS, MCZ, RUNB, UKSM, USNM): Alameda Co., Arroyo Mocho (4; TLEr, UCB), Berkeley (2; CUNY), Livermore (1; CAS), Sunol (1; UCB); Alpine Co., Markleville (1; CAS); Calaveras Co., Mokelumne Hill (3; CAS); Colusa Co., Cooks Springs (2; CAS); Contra Costa Co., March Springs Creek (3; CAS, MCZ), Moraga (1; CAS), Mount Diablo (2; CAS), San Pablo Valley (1; UCB); Del Norte Co. (2; CNHM); El Dorado Co.

(11; CNHM), Pollock Pines (1; UCD); Fresno Co., Kings River (1; CAS), Stevenson Creek (3; CAS), Trimmer (6; CAS); Humboldt Co., Fernbridge (1; UASM), Frenchman Creek (2; CAS); Inyo Co., Panamint Mountains (1; USNM); Kern Co. (4; USNM); Lake Co., Adams Springs (1; CAS), Clear Lake (90; CAS), Lower Lake (2; CAS), North Fork Cache Creek (33; UCD), Middletown (1; CAS); Los Angeles Co., Arroyo del Valle (1; CAS), Crystal Lake (9; TCBa), Pasadena (4; CAS), Santa Monica (3; CAS, INHS), Tanbark Flat (1; UCD), Tapia Park (1; LACM), Tujunga Canyon (7; LACM); Marin Co., Camp Taylor (2; CAS, CNHM), Fairfax (5; CAS), Lake Lagunitas (1; CAS), San Anselmo (1; CAS); Mariposa Co. (1; CNHM), Miami Ranger Station (1; CAS), Yosemite Valley (1; INHS); Mendocino Co. (2; CNHM, MCZ), Bloody Run Creek (1; CAS), 8 mi. w. Navarro (3; CAS), 2 mi. nw. Philo (1; CAS); Modoc Co. (9; CNHM, MGFT), Davis Creek (2; CAS), 4.5 mi. n. Fort Bidwell (3; CAS), 3 mi. s. Lake City (1; CAS); Mono Co., Fales Hot Springs (1; CAS); Napa Co. (1; CNHM), Mount Saint Helena (1; CAS), Rutherford (5; TLEr); Nevada Co. (4; CNHM, MGFT), Truckee (9; CAS, MCZ, USNM); Placer Co. (1; USNM), Bear Valley (2; CAS), Lake Tahoe (20; CAS, MCZ, UASM, UCD), Tahoe City (3; CAS); Riverside Co., Banning (1; CAS), Idyllwild (2; CAS, UCB), Pinon Flat (1; UCB), Riverside (2; CAS), San Jacinto Mountains (1; CAS); San Benito Co., Pinnacles National Monument (1; CAS); San Bernadino Co., 9 mi. nw. Fawnskin (1; TLEr), San Bernadino Mountains (1; CAS), South Fork Santa Ana River (1; CAS); San Diego Co., Poway (1; CAS), Warners Springs (2; CAS); San Luis Obispo Co., La Panza (2; CAS), San Luis Obispo (2; CAS); San Mateo Co. (2; CAS, MCZ); Santa Barbara Co., Santa Cruz Island (3; CAS, UCD), Santa Inez Mountains (1; CAS); Santa Clara Co., Alum Rock Park (1; TLEr), Arroyo Bayo (1; TLEr), Gilroy Hot

Springs (11; CAS, TLEr), Los Gatos (2; CAS), San Martin (23; CAS), Stanford (1; CAS); Siskiyou Co. (2; CAS, USNM), 2.3 mi. nw. Callahan (1; CAS), Dunsmuir (1; USNM), 1.3 mi. e. Grenada (1; CAS), McCloud (1; CAS); Sonoma Co. (4; CAS, CUNY, LACM), Cazadero (1; CAS), Guerneville (1; CAS), Healdsburg (1; CAS), Santa Rosa (1; MSUL); Stanislaus Co., Del Puerto Creek (1; TLEr); Trinity Co., 10 mi. sw. Big Bar (3; CAS), Hyampon (1; CAS), 4 mi. se. Ruth (2; CAS); Tulare Co., Gray Meadow (1; CAS), Kaweah (1; CAS), Sequoia National Park (2; CAS, UCD); Tuolumne Co., Hardin Flat (1; CAS). COLORADO (4; USNM): Baca Co., Regnier (1; AMNH); Boulder Co., 6.9 mi. n. Golden (14; TLEr), Lyons (2; UASM), South Boulder Creek (3; DHKa), 2 mi. e. Wonderview (1; DHKa); El Paso Co., Colorado Springs (1; USNM); Fremont Co., Canon City (7; ANSP, CAS, MCZ, USNM); Jefferson Co., Coal Creek Canyon (1; CAS), Golden (3; DHKa), 2 mi. n. Golden (3; TLEr), 2 mi. e. Morrison (10; DHKa), Waterton (5; DHKa); Huerfane Co., La Veta (1; MCZ); La Plata Co., Durango (1; MCZ); Larimer Co., Fort Collins (2; CAS). IDAHO: Idaho Co., 39 mi. e. Lowell (1; HGou); Kootenai Co., Hayden's Lake (1; CAS); Nez Perce Co., Juliaetta (2; CUNY, USNM), 6 mi. w. Lenore (12; DHKa, HGou), Waha Lake (17; AMNH, CAS, MCZ, USNM). MONTANA: Blaine Co., Bear Paw Mountains (2; USNM); Cascade Co., Armington (3; DJLa, UASM); Lewis and Clark Co., Helena (1; UASM), 4 mi. s. Wolf Creek (1; UASM). NEW MEXICO (3; UKSM): Bernalillo Co., Albuquerque (1; USNM); Catron Co., 3 mi. s. Beaverhead (28; TLEr), 12.3 mi. n. Glenwood (4; UASM); Grant Co., 4 mi. e. Hillsboro (1; CNHM), 23 mi. n. Mimbres (5; TLEr), Silver City (1; MCZ), 14 mi. n. Silver City (1; MSUL), 26 mi. n. Silver City (16; TLEr); Rio Arriba Co., San Juan Pueblo (1; DRWh); Sandoval Co., Jemez Mountains (5; CAS), Jemez Springs

(2; TCBa); San Miguel Co., Las Vegas (2; INHS), Porvenir (1; CAS), Sapello (15; UASM); Taos Co., Taos (2; CAS). OREGON: Columbia Co., Portland (1; CUNY); Grant Co., Blue Mountains (2; CAS); John Day Gorge (2; CNHM); Jackson Co., Medford (14; CAS, UCD), Talent (48; UCD), Tolo (1; UCD); Lake Co., Crooked Creek (5; MSUL), Lakeview (1; CNHM), Paisley (2; CNHM); Malhuer Co., Sucker Creek (5; CAS, CNHM); Marion Co., Detroit (1; CAS); Yamhill Co., Dayton (1; MCZ). SOUTH DAKOTA: Lawrence Co., Spearfish (1; DRWh). TEXAS: Randall Co., Canyon (5; MSUL). UTAH (2; JNeg): Beaver Co., Beaver Creek Hills (2; USNM), South Creek (1; USNM); Juab Co., Nephi (1; USNM); San Juan Co., Arch Canyon (2; MCZ); Utah Co., American Fork (30; ANSP, CAS, USNM), Provo (30; CAS, MCZ, USNM); Weber Co., Ogden (23; CNHM, MCZ, USNM); Chad's Ranch (2; MCZ, USNM). WASHINGTON: Franklin Co., Kahlotus (1; USNM); Walla Walla Co., College Place (1; CNC), Walla Walla (21; CAS). WYOMING: Laramie Co., 11 mi. n. Cheyenne (22; UASM).

MEXICO

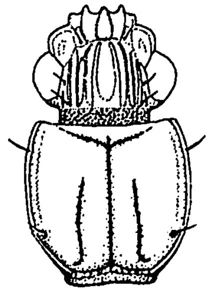
CHIHUAHUA: Catarinas (2; AMNH), 23.0 mi. s. Minaca (1; UASM), Santa Barbara (3; AMNH), 63 mi. w. Santa Barbara (1; AMNH). GUANAJUATO (1; BMNH). MEXICO: Temescaltepec (3; MCZ), Villa Carbon (3; JHen). ZACATECAS: General Enrique Estrada (69; UASM, IRSB, BMNH).

Collecting notes. - I have collected specimens of this species at several localities, all at comparatively high altitudes or latitudes, in gravel bars along unshaded streams. The only locality where I collected a good series was near Laramie, Wyoming, where I found specimens of no other species of the genus. At lower elevations elsewhere, however, specimens have been taken together with specimens of one or more other species. Specimens of *S. depressus* have been taken throughout the year in the more southern parts of the United States.

Taxonomic notes. - *S. depressus* is closely related to *S. pygmaeus*, *S. scopaeus*, *S. ochthocephalus*, and *S. falli*, but is sympatric with all of them and clearly is reproductively isolated. As noted by Lindroth (1961), Hatch (1949, 1953) erred in placing *S. litigiosus* as a synonym of *S. depressus*.

As I suggested in my disucssion on variation, eastern and western populations of *S. depressus*, in both the northern and southern extremes of its range, may be reproductively isolated. Here, then, is a fertile field for future investigations at the population level.

Fig. 215-221. Head and pronotum, dorsal aspect. 215. *S. arimao* Darlington, Soledad, Cuba. 216. *S. emdeni* new species, San Geronimo, Guatemala. 217. *S. sulcifrons* Putzeys, Edmonton, Kentucky. 218. *S. litigiosus* Fall, Gilroy, California. 219. *S. pygmaeus* Van Dyke, Cliff, New Mexico. 220. *S. falli* new species, Sabinas Hidalgo, Nuevo Leon. 221. *S. depressus* LeConte, San Juan Pueblo, New Mexico. Fig. 222-232. Male median lobe, lateral aspect. 222. *S. arimao* Darlington, Soledad, Cuba. 223. *S. emdeni* new species, Palmar Sur, Costa Rica. 224. *S. sulcifrons* Putzeys, Rumney, New Hampshire. 225. *S. litigiosus* Fall, Willow Creek, California. 226. *S. pygmaeus* Van Dyke, Tollhouse, California. 227. Same, Linares, Nuevo Leon. 228. *S. scopaeus* new species, Montemorelos, Nuevo Leon. 229. Same, Brackettville, Texas. 230. *S. falli* new species, Power's Garden, Arizona. 231. *S. ochthocephalus* new species, Fernbridge, California. 232. *S. depressus* LeConte, Power's Garden, Arizona. Fig. 233. Male endophallus, *S. depressus* LeConte, Oliver, British Columbia.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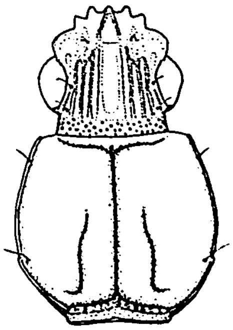
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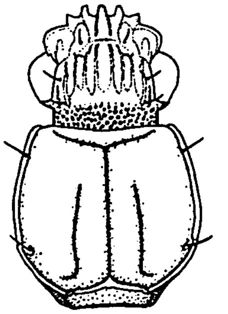
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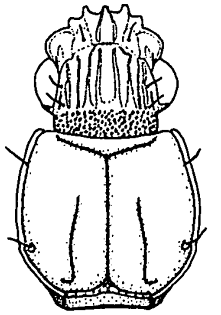
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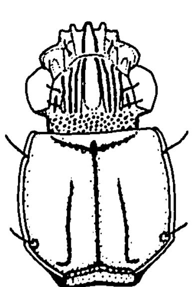
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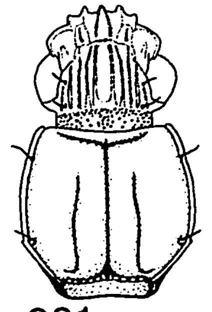
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0.2 mm


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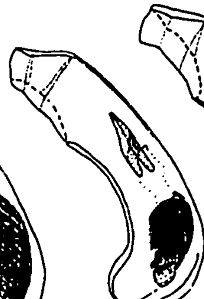
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Fig. 234. Geographic variation in form of apex of male median lobe in *S. pygmaeus* Van Dyke, circles, and *S. scopaeus* new species, squares.

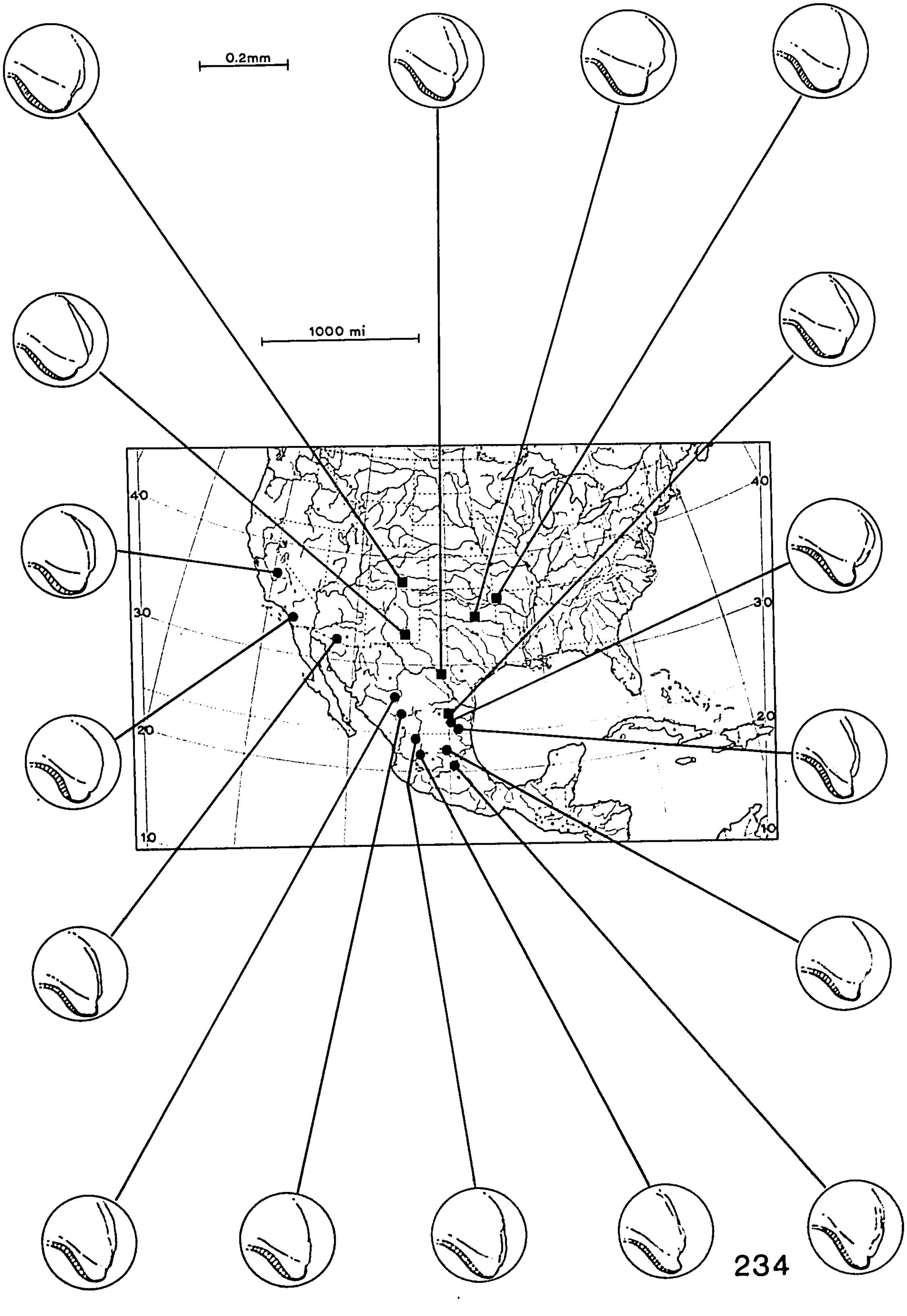
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Fig. 235-239. Known distributions. 235. *S. arimao* Darlington, circles, and *S. emdeni* new species, triangles. 236. *S. sulcifrons* Putzeys; open symbols represent state records only. 237. *S. litigiosus* Fall. 238. *S. scopaeus* new species. 239. *S. pygmaeus* Van Dyke.

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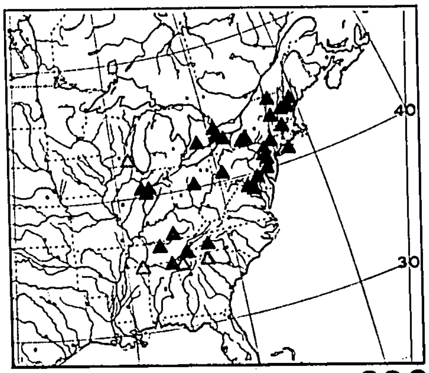

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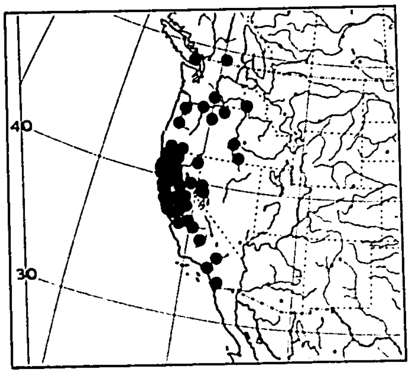
1000 mi



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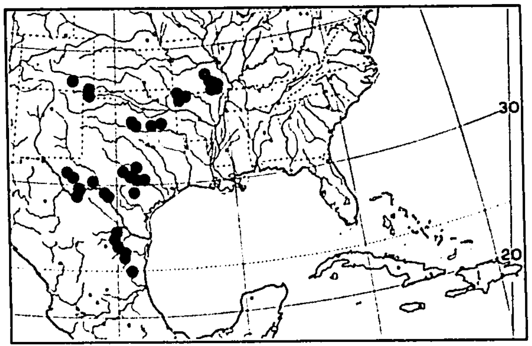

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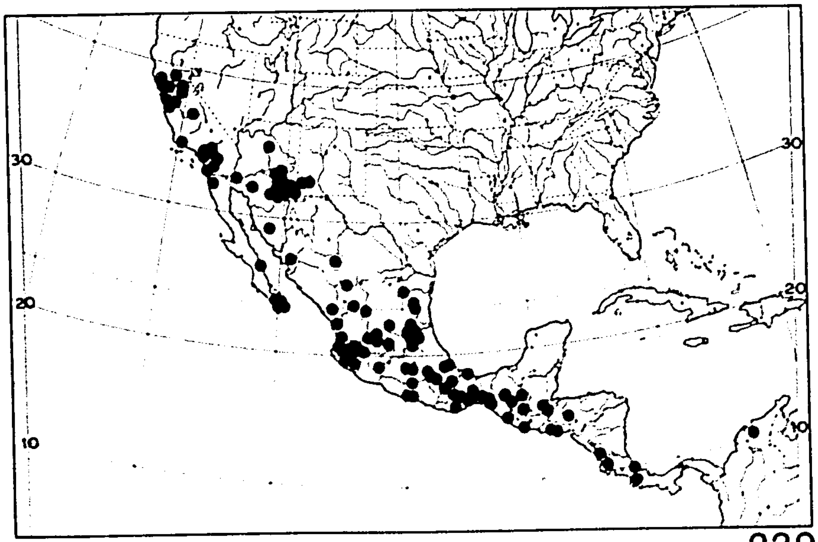
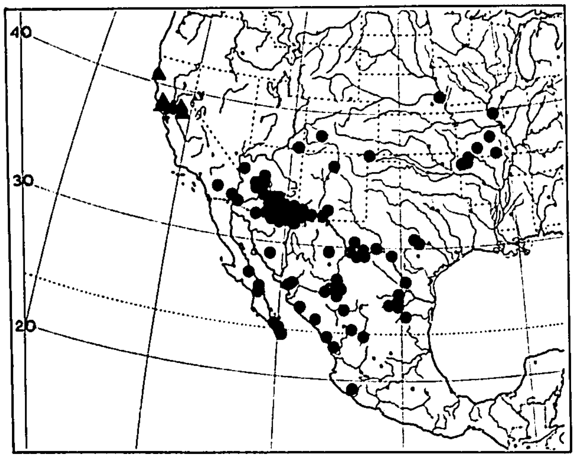


239

Fig. 240-241. Known distributions. 240. *S. falli* new species, circles, and *S. ochthocephalus* new species, triangles. 241. *S. depressus* LeConte. Fig. 242. Geographic variation in body color of *S. pygmaeus* Van Dyke, circles, and *S. scopaeus* new species, squares; legend applies to both taxa.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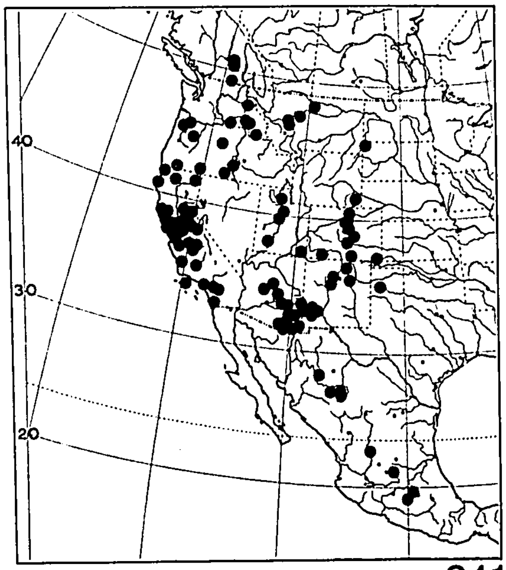
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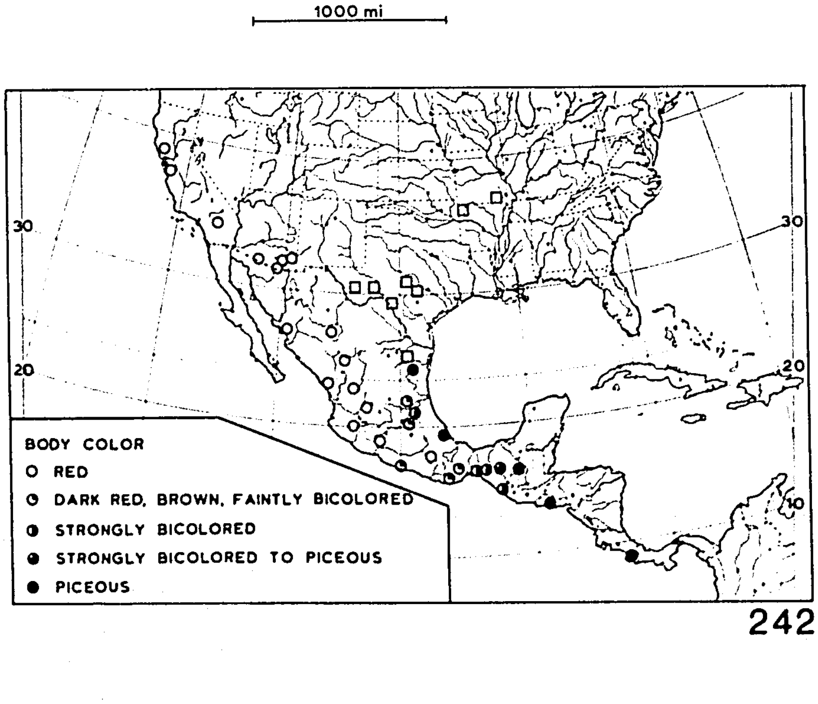
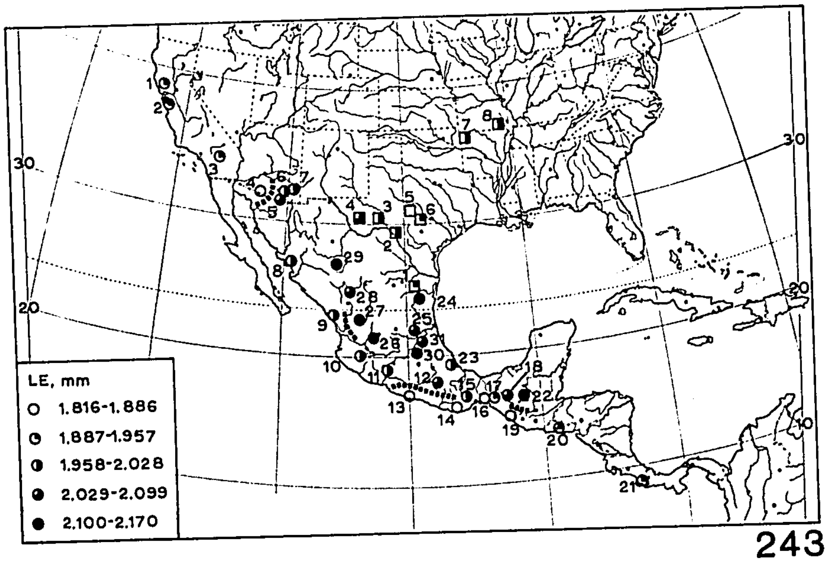
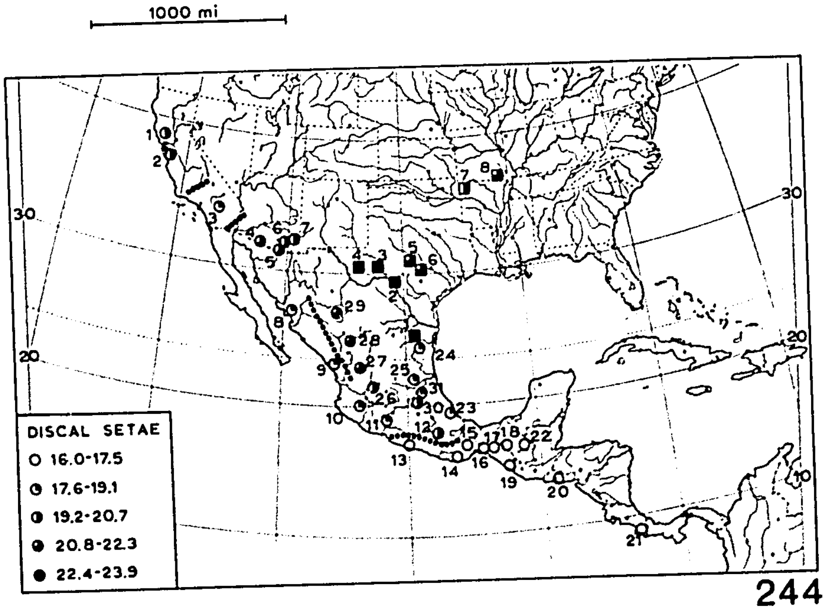

1000 mi
30
20
30
20
10
BODY COLOR
○ RED
◔ DARK RED, BROWN, FAINTLY BICOLORED
◑ STRONGLY BICOLORED
◕ STRONGLY BICOLORED TO PICEOUS
● PICEOUS

242

Fig. 243-244. Geographic variation in *S. pygmaeus* Van Dyke, circles, and *S. scopaeus* new species, squares; broken lines indicate probable major barriers to gene flow. 243. Means of body size, Tables 45 and 50. 244. Means of numbers of discal setae on left elytron, Tables 46 and 51.

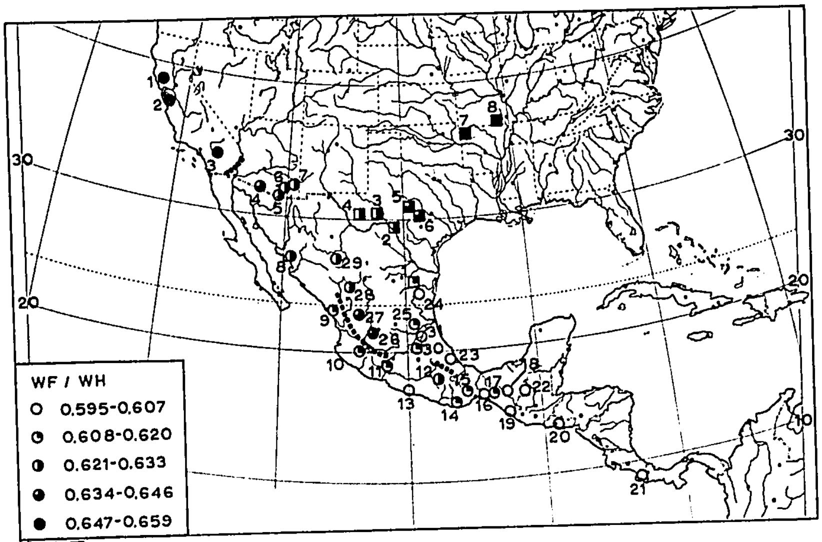

LE, mm
○ 1.816-1.886
◔ 1.887-1.957
◑ 1.958-2.028
◕ 2.029-2.099
● 2.100-2.170
30
20
10

243


1000 mi
DISCAL SETAE
○ 16.0-17.5
◔ 17.6-19.1
◑ 19.2-20.7
◕ 20.8-22.3
● 22.4-23.9
30
20
10

244

Fig. 245-246. Geographic variation in *S. pygmaeus* Van Dyke, circles, and *S. scopaeus* new species, squares; broken lines indicate probable major barriers to gene flow. 245. Means of relative eye size, Tables 47 and 52. 246. Means of pronotal form, Tables 48 and 53. Fig. 247-248. Geographic variation in *S. ochthocephalus* new species, Sample 1, and *S. falli* new species, Samples 2-18. 247. Means of body size, Table 55. 248. Means of numbers of discal setae on left elytron, Table 56.



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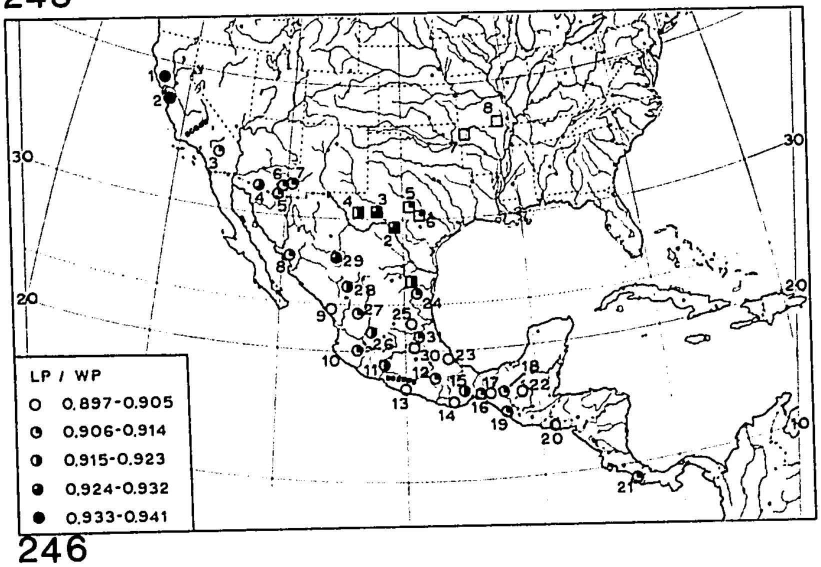

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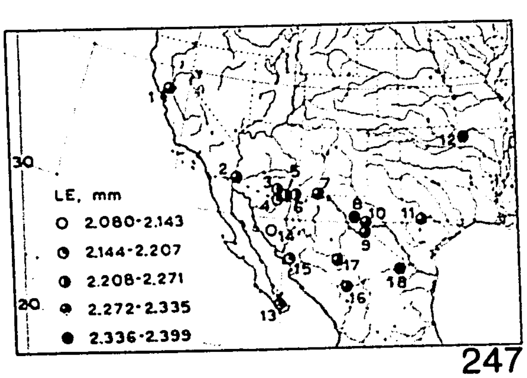

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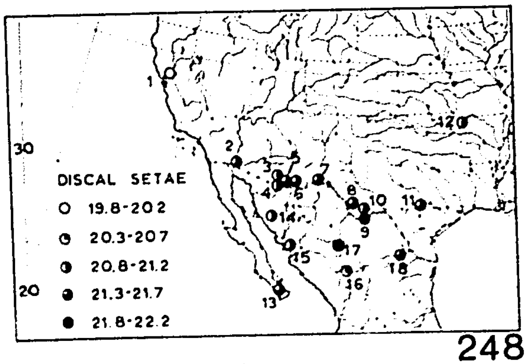

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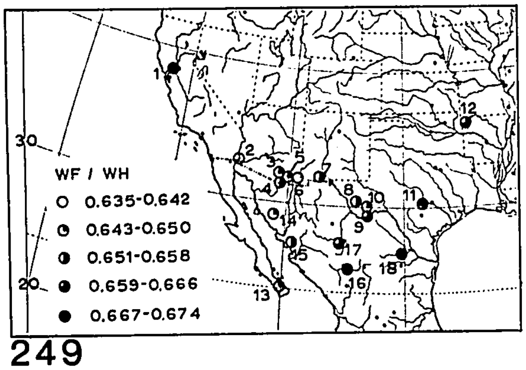
Fig. 249-250. Geographic variation in *S. ochthocephalus* new species, Sample 1, and *S. falli* new species, Samples 2-18. 249. Means of relative eye size, Table 57. 250. Means of pronotal form, Table 58. Fig. 251-254. Geographic variation in *S. depressus* LeConte. 251. Means of body size, Table 61. 252. Means of numbers of discal setae on left elytron, Table 62. 253. Means of relative eye size, Table 63. 254. Means of pronotal form, Table 64.



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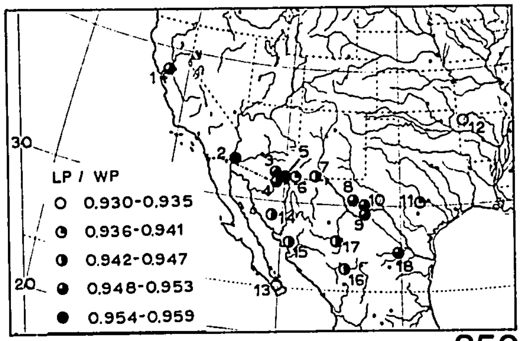
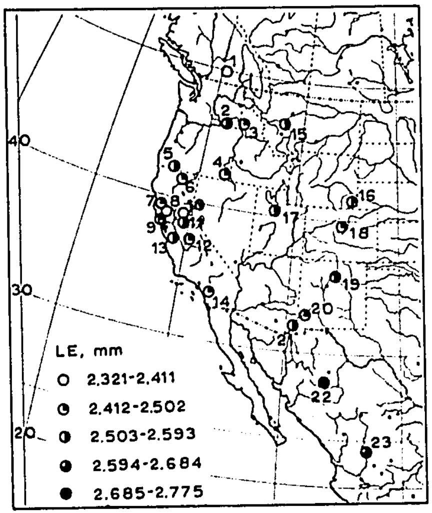


250

1000 mi



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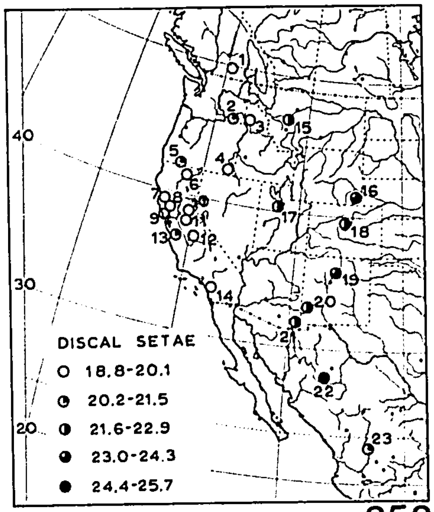

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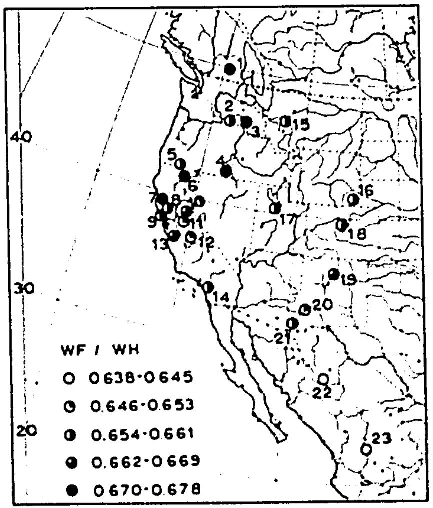

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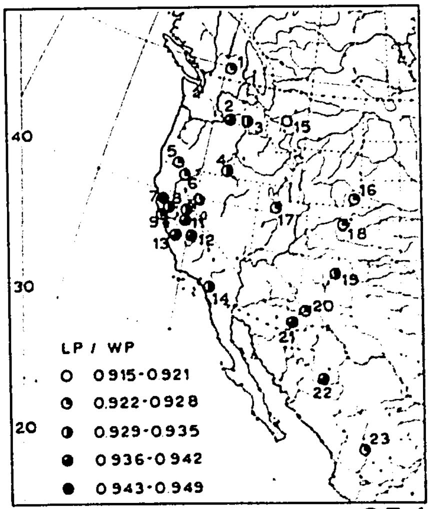

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4.0 PHYLOGENY

4.1 Introduction

A taxonomic study normally includes aids for identification of specimens, and organizes information for storage and retrieval. I believe it should do much more than this. It should be based on evolutionary theory, and thus furnish sufficient background to predict relationships or similarities in characteristics not yet studied, and to make whatever critical comparisons are needed to test those predictions. Therefore, phylogenetic and biogeographic analyses are important adjuncts to taxonomic work.

In this preface to my analysis of *Schizogenius* phylogeny I wish to provide the reader with a general summary of my philosophical and procedural approaches, which derive from a blending of patristic, cladistic, and even some phenetic philosophies and procedures. I do not claim originality for ideas aired in this section. All have at least been touched upon, and most have been explored in detail, by one or more of the following: Blackwelder (1962); Brundin (1966); Crowson (1970); Darlington (1970); Ehrlich and Raven (1969); Hennig (1966); Hull (1964, 1970); Mayr (1969); Sokal and Crovello (1970); and Tuomokoski (1967). Among these authors, only Darlington and Mayr are "evolutionary" taxonomists (Hull, 1970). The following discussion is given mainly to amplify those of my ideas about phylogeny that do not completely agree with theirs; it closes with a series of examples, some from the literature and some from my own work, chosen to illustrate these ideas.

4.11 Classification, phylogeny, and zoogeography

The evolutionary history of a taxon relates closely to its past and present distribution patterns and to environmental factors responsible for those patterns. Thus, to classify taxa in accordance both with evolutionary theory and with all of the facts known about the organisms, one must determine probable evolutionary pathways and correlate these with probable historical zoogeography. The phylogeny, zoogeography, and classification of a group must be compatible with one another, and a classification is therefore likely to be most useful if completed after a careful consideration of phylogenetic and zoogeographic evidence.

Discussions on phylogeny and zoogeography provide indications of the taxonomist's logic, and may even suggest compatibility tests for evaluating the integrity of his work. Without these discussions, only experience permits users to evaluate a taxonomic work. Thus, the user is entitled not only to know something about the taxonomist's philosophical and procedural approaches, but also to know where compatibility tests may most appropriately be made. In this study of *Schizogenius* I did my best to ensure compatibility. Phylogeny was a major consideration in developing the entire classification, and my original classification was modified repeatedly until all incompatibilities obvious to me were eliminated. Zoogeography was considered in working out relationships at the species level, and among many of the species groups. Relationships among the *truquii, lineolatus, longipennis, depressus, brevisetosus, pluripunctatus, sallei, tristriatus, capitalis,* *lindrothi*, *darlingtoni*, *ocellatus*, and *quadripunctatus* groups were analyzed with zoogeographic considerations in mind. But relationships of all other species groups to these groups and to one another were analyzed independently of zoogeographic considerations, so the user may, if he so desires, test for compatibility between zoogeography and phylogeny among these groups. Given in section 4.14 are compatibility between phylogeny and zoogeography in the carabid genus *Evarthrus* and the carabid division Brachinida, and an example of noncompatibility in the milliped genus *Cleptoria*.

4.12 Phylogenetic methods

In general, my methods for reconstructing a phylogeny conform with Hennig's (1966) holomorphological and chorological methods. No data are available to permit use of paleontological and parasitological methods, so these require no further discussion here. Hennig's principles for working out phylogenetic relationships may be summarized as follows: recognize and define a monophyletic group; determine its sister group; and repeat these processes until the phylogeny of a group is completely reconstructed. I apply these principles by using four closely related procedures. I first develop from morphological data a probable phylogeny which best fits these data. Then I compare this phylogeny with chorological data, and modify as required. From the modified phylogeny, I estimate the most probable morphological and chorological characteristics of the common ancestors of sister groups, and if necessary modify the phylogeny accordingly. Finally, the revised phylogeny is correlated with major paleogeological events, and again revised if necessary.

In general, the simplest system for explanation of all available morphological and chorological data is the system of choice. I believe further that a phylogeny should be reconstructed as completely as possible, so long as sufficient data are available and so long as these data are not to be overruled by rigid *a priori* decisions. Darlington (1970) rightly criticizes Hennig (1966) and Brundin (1966) for gross oversimplifications in certain of their phylogenetic and zoogeographic procedures and interpretations. But I do not think these criticisms constitute grounds for rejection of cladistic methods; they are useful as analytical tools, even if only as generalizations.

Monophyly, paraphyly, and polyphyly. - According to Darlington (1970), "the central thesis of cladism is that taxonomic categories [i.e., taxa] must be monophyletic in a special, rigid sense, and that their rank must be determined by time of origin rather than by degree of difference or extent of diversification." Tuomikoski (1967), who otherwise basically agrees with Hennig (1966) and Brundin (1966), suggests that paraphyletic taxa may be acceptable under certain conditions. I (1966b) treated the genus *Halocoryza* as a paraphyletic taxon in disregard of the sister group rule, the rule of monophyly, and the rule of ranking by time of origin. This was done to account for the relative divergence of *Schizogenius* from New World *Halocoryza*; all species of *Halocoryza* are more similar to one another than to any species of *Schizogenius* in known characteristics, and probably also in characteristics not yet studied. This is consistent with my premise that a classification should be based on hypotheses about patristic relationships, rather than cladistic relationships alone. My treatment of the genera *Halocoryza* and *Schizogenius* parallels classifications in which birds are segregated from crocodiles and other reptiles (Darlington, 1970; Hennig, 1966).

Taxa are not always monophyletic in the "special, rigid sense" of Hennig (1966), Brundin (1966), and Tuomikoski (1967). This is clear in botanical diploid-tetraploid systems in which progeny are reproductively isolated from their parents. If tetraploidy may appear once, then it may reappear; obviously, the parent species is then paraphyletic, and the daughter species is polyphyletic. Further, as suggested by Crowson (1970), the tetraploid progeny might in turn spontaneously produce diploid progeny, so that both the diploid and the tetraploid forms are at once paraphyletic and polyphyletic. It is not my intention here to discuss plant speciation, but Crowson does suggest that diploid-tetraploid shifts may have also played some part in animal evolution. If so, and if such diploid-tetraploid pairs are accepted as biological species, then it follows that strictly monophyletic species are not always definable; Hennig's techniques provide no practical way to distinguish stem species from daughter species in such systems.

That the stem species concept, a theoretical element of the cladist's phylogenetic system, should not be confused with the biological species concept is clear. Indeed, the very point of the stem species concept is to make a monophyletic definition of extant biological species possible. But, as in diploid-tetraploid sister species, the concept fails in practice. And an even more radical departure from the pattern of a stem species resolved into two monophyletic daughter species results when two parent species hybridize successfully to produce an unquestionably polyphyletic hybrid species (Hull, 1964).

What really is wrong with the stem species as a rigid concept, and of the concept of rigidly monophyletic taxa, however, is to be found where species differentiation is gradual, as it must ordinarily be. If geographic isolation develops such that each isolate initially includes two or more populations, those populations of each isolate that once shared the most gene flow are genetically most closely related to one another. If species differentiation follows, daughter species are paraphyletic; and evidence of paraphyletic relationships may remain for some time after completion of reproductive isolation. If geographic isolation results from establishment of a founder population, the parental isolate is paraphyletic because initially some individuals or populations are genetically more closely related to the founder than are other individuals or populations. And if limited gene flow continues in one or both directions even while species differentiation takes place, one or both isolates are polyphyletic in the early stages of species differentiation. Thus, rigid monophyly cannot be required of species level taxa, since paraphyly and even polyphyly may be inherent in their evolutionary histories. And if this is so, then by extension I think the requirement of rigid monophyly in taxa of higher categories is voided.

I do not accept as species taxa geographic isolates which are evidently paraphyletic, as judged from character clines, and probably would not do so even if these geographic isolates were known to be reproductively isolated, for reasons discussed in section 4.13. For instance, in *Schizogenius tibialis*, I suspect that the Indian Creek Cave form is reproductively isolated from its geographically nearest neighbors; but it is more similar and doubtless more closely related genetically to them than to any geographically more distant populations of that species. I look for evidence of propinquity of ancestry at the population level, and, if I find such evidence, I regard the forms in question as conspecific. At some indeterminate time after reproductive isolation is achieved, such evidence of propinquity of ancestry should disappear, and I would then treat the forms in question as distinct species, or, where genetic relationships are in doubt, as subspecies. This propinquity of ancestry criterion depends on whether paraphyly remains evident, or whether such evidence is lost. Thus, at species level, I in fact approach the rigidly monophyletic taxa required by Hennig. But having decided that there is no theoretical basis for rigidly monophyletic taxa, I do not insist that higher taxa always be monophyletic, though I think such a criterion is normally desirable.

The important point here is not whether or not taxa should be rigidly monophyletic. The real question is how to devise classifications and reconstructed phylogenies that best show relationships and best suggest hypotheses to be tested by other workers. If they are intended to have maximum heuristic value, their construction cannot be rigidly bound by any concepts other than evolutionary theory. The simplest possible models should be used initially, but should freely be modified for particular situations as complexities in these situations become evident. I accept cladistic concepts as working models, but do not insist that all situations fit a model in all ways. My views on this subject are analogous to my use of the biological species concept as a model, as discussed in section 4.13.

Secondary cladistic concepts. - Three of Darlington's (1970) criticisms of Hennig's (1966) and Brundin's (1966) methodologies are: that there is no fundamental reason why species should invariably split in a simple, dichotomous fashion; that phylogenies need not be strictly dichotomous; and that rates of evolution and divergence need be neither constant nor the same for different groups. If the range of a species is divided into three or more approximately equal parts by the same or related phenomena, and if rates of evolution and divergence are constant, then reproductive isolation must develop at nearly equal rates in all geographic isolates. If speciation results from a gradual process, there should be no clearly definable branching points. And if these isolates form a pattern in which the intermediate isolate has undergone the least amount of evident evolutionary change, then it might be difficult or even impossible to determine sister species relationships even if their phylogeny truly was dichotomous. Nevertheless, it may still be possible to realistically simplify most such situations, and, as I prefer a dichotomous system I attempt to do so; an example, concerning the species taxa *S. planulatus*, *S. ozarkensis*, and *S. planuloides*, is given in section 4.14.

That rates of evolutionary change and divergence are neither always constant nor the same in all groups is well known. But, at least for balanced continental faunas, I think it worthwhile to assume an average rate of speciation in the group studied, because on that basis its phylogeny can be tested against known paleogeological events. This assumption, in other words, makes available an analytical method for testing a reconstructed phylogeny for compatibility with historical zoogeography. Some correlated assumptions are the following. Changes in evolutionary rates imposed by gradual environmental change are negligible. In a major taxon whose phylogeny has been worked out, at least one major lineage is sufficiently diverse and complete that extinction patterns may be disregarded. And apparent large gaps between related genus-group taxa are associated with rapid rates of evolutionary change and divergence resulting from exploitation of new habitats and resulting major new adaptations. Analytical methods required to test a reconstructed phylogeny for compatibility with historical zoogeography are the following. The average time required for speciation is determined from what is known about living species taxa of the group in question, and from probable historical factors involved in their evolution. In the phylogeny to be tested, this average time is treated as equal to the time between successive dichotomies in the lineage with the maximum number of known dichotomies. The age of any desired common ancestry is thus the maximum number of dichotomies between that ancestry and the present, multiplied by the average time span required for speciation. These assumptions and methods are generalizations, and perhaps even gross oversimplifications, but the interesting point is that where

I have tested them they seem to work. Examples are given in section 4.14 for the carabid division Brachinida and the carabid genus *Evarthrus*. I used these techniques to help place such species taxa as *S. arimao* in both classification and reconstructed phylogeny, whenever morphological data suggested two or more nearly equally plausible evolutionary pathways.

4.13 Phylogeny, classification, and the biological species

Various relationships among phylogeny, classification, and biological species were discussed by Hull (1970). I here summarize my views about relationships and compatibilities among these, with particular emphasis on the biological species concept as a unifying model of great evolutionary importance. I also discuss how I apply the biological species concept in certain situations in which reproductive relationships are discordant with suspected phylogenetic relationships, and explain my rationale for interpreting these situations. In this discussion, I accept Hull's (1970) restricted definition of "classification," Hennig's (1966) definition of "phylogenetic relationships," and Mayr's (1969) definition of "species."

A concise statement of my interpretation of relationships among phylogeny, classification, and biological species is the following. Organisms are classified into taxa, each of which is based on the hypothesis that included organisms are more closely related to one another than to excluded organisms. A reconstructed phylogeny is based on hypotheses about how taxa are related to one another. In this system, the species is not a necessarily fundamental evolutionary unit; but the classification and reconstructed phylogeny are unified by the biological species concept, which consequently is a fundamental evolutionary model.

Compatibility of evolutionary classification and reconstructed phylogeny. - I prefer evolutionary classifications over phylogenetic classifications, because the cladistic relationships implied in the latter may be adequately expressed in a reconstructed phylogeny. Inherent in an evolutionary classification is the hypothesis that extant elements of a taxon share closer patristic relationships with one another than with extant elements of excluded taxa. A reconstructed phylogeny, on the other hand, must reflect evolutionary history, and is based on hypotheses about cladistic relationships between taxa. The evolutionary classification and the reconstructed phylogeny are therefore statements based on different sets of hypotheses. For heuristic purposes, however, they are interdependent, and must therefore be compatible with one another.

Compatibility between an evolutionary classification and a reconstructed phylogeny is achieved if units of at least one level are common to both. Taxa of species rank are such units. Higher taxa in an evolutionary classification may not be compatible with the reconstructed phylogeny, and units below species rank do not normally appear in the reconstructed phylogeny. Taxa of species rank are the units best suited to insure compatibility between the evolutionary classification and the reconstructed phylogeny for the following additional reasons.

Hennig (1966) discussed differences between ontogenetic, tokogenetic, and phylogenetic relationships, which apply respectively to semophoronts, individuals, and reproductively isolated groups of individuals or populations. An evolutionary classification is possible because semophoronts, individuals, and populations cluster to form more or less discrete groups which are linked by phylogenetic relationships. Semophoronts, individuals, and populations that share ontogenetic and tokogenetic relationships are conspecific, but these relationships are not sufficient to define a species. Ontogenetic and tokogenetic relationships between geographic isolates are replaced by phylogenetic relationships, but are renewed if gene exchange occurs before reproductive isolation is achieved. This potential instability of phylogenetic relationships is sufficient reason for units of compatibility between an evolutionary classification and a reconstructed phylogeny to be taxa of at least species rank.

A species is a unit of classification based on known or hypothetical relationships among included semophoronts, individuals, and populations; these relationships are interpreted in terms of a model, the biological species concept. Since only for taxa of species rank is there such a model, species level taxa are better suited as units of compatibility between an evolutionary classification and a reconstructed phylogeny than are taxa of higher rank. Thus, species have the important function of unifying facts, hypotheses, and theories, and this is why I consider the biological species concept as a fundamental evolutionary model.

Some problems in applying the biological species concept. - Semophoronts and individuals may be classified (Blackwelder, 1962; Hennig, 1966), but since they are characterized by having ontogenetic or tokogenetic relationships they do not evolve independently from one another and therefore are not fundamental evolutionary units. Some authors believe that species are the real units of evolution (Mayr, 1969). Others (see Hull, 1970) suggest that species are not fundamental evolutionary units, and that populations may be such units(Ehrlich and Raven, 1969; Sokal and Crovello, 1970). Their basic arguments are that selection is the prime factor in evolution and that gene flow normally is negligible. But how can one explain patterns of continuous or nearly continuous geographic variation if gene flow is negligible? One might argue that similarities between geographically proximate populations result exclusively from similar selective regimes. But such an argument is superficial; it does not explain, for example, the circular pattern of variation in relative eye size in *S. tibialis* (Fig. 188). I think that all character clines in *Schizogenius* species studied by me indicate genetic relationships between at least some geographically proximate population samples, and that these genetic relationships result from relatively recent gene flow. However, though populations must interact with some frequency if there are non-random patterns of geographic variation, they must be sufficiently independent of one another for selection to act to produce this variation. Except in such species that include only one population, species normally are not really fully integrated evolutionary units since included populations are independent of one another to varied degrees.

A problem raised by the notion that species are not necessarily fundamental evolutionary units is that reproductive relationships may not be concordant with suspected phylogenetic relationships. This problem arises as a consequence of loss of tokogenetic relationships between populations or groups of populations (i.e., geographic isolation) before reproductive isolation is attained. These populations or groups of populations have phylogenetic relationships, but according to the biological species concept they are conspecific. If the evolutionary classification and reconstructed phylogeny are to have maximum heuristic value, interpretations of discordant reproductive and phylogenetic relationships must be flexible and must be made at the population level. That some species taxa may not perfectly fit the biological species concept does not diminish the importance or validity of that model. Data compared with a model either fit it or fail to fit it, and models in biology are not exceptionless; why whould they be, when life itself has no rigorous, universally accepted definition? Indeed, from evolutionary theory the existence of exceptions is to be predicted. The biological species concept is a good model because most data do fit it, and its importance is that it provides a reasonably consistent basis for species recognition.

In section 2.24 I describe my criteria for recognition of species of *Schizogenius*. Reproductive isolation is a criterion for defining species in terms of discrete evolutionary potential. However, before reproductive isolation is attained, isolates may have a marked evolutionary potential even if that potential is not discrete. An example, concerning the taxa *S. pygmaeus* and *S. scopaeus*, is discussed in section 4.14. Alternatively, if possible reproductive isolates retain evidence of paraphyletic relationships, their evolutionary potential, though discrete, may be of relatively recent origin, and may be limited. An example of this alternative, the taxon *S. tibialis* is also discussed in section 4.14. I base species taxa on hypotheses about past or present genetic relationships between populations in addition to known or suspected relationships among semophoronts and individuals. Recognition of these taxa depends on evidence about how or perhaps whether populations most probably interact or have interacted with one another. Thus, some species taxa in *Schizogenius* such as *S. tibialis*, *S. pygmaeus*, and *S. scopaeus* do not, or may not, exactly fit the biological species concept. But even if they are not fundamental evolutionary units, these taxa seem more consistent with the differing hypotheses on which I define species, base classifications, and reconstruct phylogenies than they would if redefined in terms of discrete evolutionary potential. I think they should be reclassified if, and only if, underlying hypotheses fail, regardless of additional data on reproductive isolation.

4.14 Some examples of phylogenetic analyses

In this section I illustrate with examples, some from the literature and some from my study of *Schizogenius*, certain points raised in preceeding sections. These examples are keyed to the pertinent section of discussion. A further reason for including these examples is to give the reader insight into details of my phylogenetic methods. Not all of the *Schizogenius* phylogeny is discussed in detail, but these examples are representative of my methods throughout.

Compatibility of phylogeny and zoogeography. - See sections 4.11 and 4.12. The examples given here, both from the literature, are chosen to show how compatibility tests between phylogeny and zoogeography can be made. To test techniques outlined in section 4.12, I examined the phylogeny and historical zoogeography proposed for *Brachinus* (Erwin, 1970) and *Evarthrus* (Ball and Freitag, *in* Freitag, 1969). For reasons developed in section 5.232, the average time required for speciation in the genus *Schizogenius* is considered to be approximately 3,000,000 years. The *Brachinus* and *Evarthrus* examples were selected to find if this time span might be common among North American carabid beetles.

Erwin's proposed phylogeny suggests a maximum of 23 dichotomies to reach the common ancestor of American *Neobrachinus* species. The true number, as determined from known species taxa, may be somewhat less, since Erwin's data suggest that the following taxa form monophyletic groups: *B. oaxacensis, B. patruelis*, and *B. conformis; B. ovipennis* and *B. medius*; and *B. tenuicollis* and *B. cyanipennis*. This would reduce the required minimum number of dichotomies to 19. If the 3,000,000 year time span is correct, ancestral *Neobrachinus* entered North America some 57,000,000 to 69,000,000 years ago. This fits Erwin's hypothesis that entry into North America occurred at some time before Eocene while land connections to South America still existed, probably during Paleocene some 58,000,000 to 63,000,000 years ago. Erwin further suggested that the primitive ancestor of the bombardier beetles of the Division Brachinida evolved in Middle to Late Cretaceous. His phylogeny indicates a minimum of seven and a maximum of ten additional dichotomies to reach back to this brachinine ancestor. At 3,000,000 years per dichotomy, this ancestor evolved between 78,000,000 and 99,000,000 years ago, a period well within Erwin's suggested limits. The only fault I found with Erwin's work is that his phylogeny is incompletely reconstructed. It is sufficiently complete, however, that it can be tested for compatibility and correlation with the zoogeography, and I find that there is indeed a strong, positive correlation. I therefore suggest that Erwin's work may be used with confidence, for heuristic purposes.

There are limits to the applicability of these procedures. Ball and Freitag suggest that the ancestor of the pterostichine genus *Evarthrus* entered North America via the Behring land bridge in Early Tertiary. No dating of this early event by my techniques is possible from the *Evarthrus* phylogeny, because all western lineages, if there were any, have become extinct. Whether this dating can be done from examination of the phylogeny of the Old World sister group cannot be judged until such a phylogeny is reconstructed. However, suggestions about subsequent events can be tested and dated according to the suggested *Evarthrus* phylogeny. Members of the genus spread across temperate Arcto-Tertiary forests in the north, but in Middle Tertiary receded eastward as did those forests. The common ancestor of living *Evarthrus* species evolved after this eastward recession. Depending on how the peculiar taxa *E. gravesi* and *E. hypherpiformis* fit the phylogeny, there may be as few as nine to as many as eleven dichotomies needed to reach that common ancestor. Its age thus falls between 27,000,000 and 33,000,000 years, which corresponds to Oligocene, or Middle Tertiary, in support of Ball and Freitag's ideas. Moreover, members of only the *substriatus* and *torvus* groups extend much westward of southeastern forested regions. Just four dichotomies are required to reach their common ancestor, which may still have been a component of the eastern forest fauna; the timing is about 12,000,000 years ago, in Early Pliocene. This supports Ball and Freitag's idea that Gulf Coast grassland habitats were not entered by *Evarthrus* species before post-Miocene time, because if they were the genus should today be represented in northeastern Mexico. My conclusions are that Ball and Freitag's phylogenetic and zoogeographic analyses are compatible, and so probably correct, and that therefore their work may confidently be used for heuristic purposes.

The data required for these compatibility tests are the authors' suggested phylogenies and suggested timings for zoogeographic events. For both Brachinida and *Evarthrus*, compatibilities were found at two different points in time. General conclusions from these analyses are that for each the phylogeny and zoogeography are compatible, and that both of these taxonomic works are therefore probably highly reliable. The taxonomy must have been carefully done and well thought out for these compatibilities to be evident. An additional conclusion is that the 3,000,000 year time span between dichotomies may be a useful generalization for North American Carabidae, although in *Evarthrus* this time span may be somewhat shorter as my datings are at upper limits of acceptability.

Incompatibility of taxonomy, phylogeny, and zoogeography. - See section 4.11. Hoffman (1967), in his review of the milliped genus *Cleptoria*, proposed aesthetically pleasing phylogenetic and zoogeographic patterns but gave no indication about timing. Thus, my test for compatibility between phylogeny and zoogeography, illustrated above for

Evarthrus and *Brachinus*, is inapplicable. A user interested in studying relationships between species must assess the reliability of the taxonomy, phylogeny, and zoogeography by other means, if given no firm basis to believe the phylogeny and zoogeography have good heuristic value. Without personal experience with the organisms, the only way he can judge the soundess of their taxonomy is to carefully read and compare all descriptive material, including information about geographic variation. Based on his conclusions about taxonomy, he must then decide for himself about phylogeny and zoogeography.

Hoffman's data indicate that all five species taxa included in *Cleptoria*, except perhaps *C. rileyi* and *C. bipraesidens*, have long been reproductively isolated. These data also support his ideas that the taxon *C. divergens* is the most primitive in the genus, and that the origin of the genus was in the southern Appalachians. But, though I think the taxonomy is sound, I think Hoffman's explanation of the phylogeny and zoogeography (Fig. 259) in *Cleptoria* is improbable. He suggests that the five allopatric species taxa evolved in a "hop-scotch" pattern, from the southern Appalachians southward into the piedmont region. Such a pattern would probably be comparatively recent in development, and some evidence of gene flow patterns should remain; I would expect to find evidence of paraphyletic relationships, as discussed for *Schizogenius tibialis* later in this section. However, no gene flow patterns are evident between species taxa in *Cleptoria*. I think an orderly "hop-scotch" pattern is unlikely, if species taxa really are reproductive isolates, since if isolates are so readily founded they should also be susceptible to replacement or displacement by subsequent founders. The pattern suggests much greater vagility than is reflected in known facts of distribution and morphology. An essentially linear sequence among reproductive isolates would more probably result from a "taxon cycle" system of displacement (Wilson, 1961); but then the taxon *C. divergens* should be the most apomorphic of the genus, not the most plesiomorphic.

A review of Hoffman's data suggests that a more plausible system of evolutionary pathways in the milliped genus *Cleptoria* (Fig. 260) is the following. The first dichotomy in the phylogeny of *Cleptoria* was a split of a piedmont form, with telopodite shortened and thickened and gonopods not interlocked, from the more conservative montane *C. divergens*. The piedmont form developed isolates north and south of the Savannah River, with the peculiarly specialized *C. abbotti* representing the latter. A subsequent extension by the northern isolate southward across the Savannah River resulted in the separation of the northern *C. macra* from the southern ancestor of *C. rileyi* and *C. bipraesidens*, which lost the prefemoral process. These forms diverged somewhere near their present ranges, and displaced *C. abbotti* from the western part of its range. I thus do not think that *C. abbotti* is closest to *C. rileyi*, and in fact suspect that *C. macra* is closer to *C. rileyi* and *C. bipraesidens* than is *C. abbotti*. Support for these suggestions is evident in Hoffman's diagrams of the process of sternum three, which show *C. rileyi* and *C. macra* as intermediate between *C. divergens* and *C. abbotti*; I doubt that this similarity is a coincidence. Thus, though I have not personally studied specimens of *Cleptoria*, my reinterpretations from Hoffman's data seem to explain evolutionary pathways at least as well as do Hoffman's interpretations.

When phylogenetic and zoogeographic analyses are published, they should allow a user to verify for himself the probable correctness of suggested relationships. If an author's own interpretations are compatible with morphological and chorological data, no reinterpretations should be needed. But the heuristic value of an author's interpretations are suspect if his published data suggest more plausible interpretations.

Phylogeny: dichotomous or trichotomous? - See section 4.12, secondary cladistic concepts. The taxa *Schizogenius planulatus, S. ozarkensis*, and *S. planuloides* have ranges now separated by the Mississippi and Red Rivers (Fig. 189). Perhaps these rivers were at one time not effective barriers, but became so because of some major change in climate which increased water loads and thus eliminated suitable habitats by deposition of silt or mud. The three isolates evolved independently, and male genitalia became more specialized in *S. planulatus* (Fig. 175) and *S. planuloides* (Fig. 177) than in the geographically intermediate *S. ozarkensis* (Fig. 176). This sequence of events suggests a trichotomous phylogeny. But other zoogeographic factors suggest that a dichotomous phylogeny is more probable.

The Mississippi River, near its confluence with the Ohio River, should pose no major barrier to these organisms, since limestone uplands in southern Illinois nearly link those of western Kentucky and eastern Missouri. Drainage systems from uplands of this entire region should provide suitable habitats for members of this complex. Indeed, there may be extant populations of one or both of *S. planulatus* and *S. ozarkensis* in southern Illinois. Further, these species range primarily in regions of deciduous forests and may therefore be adapted to cooler conditions than is *S. planuloides*, a species of warmer, more arid regions. I think the ancestor of these taxa evolved in subtropical Texas or northeastern Mexico, since that is the region of greatest diversity among their relatives. The first dichotomy in their phylogeny followed establishment of a northern isolate, which became cool adapted and spread across temperate forested areas in the Ozark and Appalachian regions. Meanwhile, the male genitalia of the southern isolate evolved its specialized characteristics. The second dichotomy developed when Early Pleistocene climatic deterioration caused the northern isolate to subdivide into isolates restricted to the southern Ozark and southern Appalachian regions. Then the Appalachian isolate diverged in characteristics of the male genitalia from the more conservative Ozark isolate. Following retreating Pleistocene glaciations, the ranges of Ozark and Appalachian isolates expanded northward, and may now approach or even overlap one another in the region near the confluence of the Mississippi and Ohio Rivers.

Problem species. - See sections 4.12 and 4.13. Some species of *Schizogenius* may not fit precisely the biological species concept. Examples are the taxa *S. tibialis*, *S. pygmaeus*, and *S. scopaeus*. Where evidence from geographic variation indicates relatively recent gene flow between geographically proximate populations, I regard them as conspecific. If no evidence of such gene flow between these populations exists, either directly or through some alternative geographic sequence, and if morphological and chorological evidence suggests reproductive isolation, then I recognize them as distinct species.

Lindsay and Vickery (1967) found from studies of *Mimulus* "a picture of the frequent emergence, change, and disappearance of distinctive populations with only the rare formation of one sufficiently distinct to be on its own evolutionary path." I suspect the same is true in *Schizogenius*.

In the taxon *S. tibialis* (Fig. 188), the Indian Cave Creek form may or may not be a reproductive isolate, but regardless shows evidence of past genetic continuity with geographically proximate populations to the south. It is restricted and peripheral in known distribution, is undoubtedly of comparatively recent origin, and probably has a low potential for survival. Suspected reproductive and phylogenetic relationships are discordant; if this form is recognized as a separate species because of reproductive isolation, the southern form is reduced to an evidently paraphyletic taxon. I regard the Indian Cave Creek isolate as conspecific with other populations of *S. tibialis* because it is patristically more closely related to geographically proximate populations than to more distant ones. I do not here regard possible reproductive isolation as a useful criterion for species recognition, because though evolutionary potential may be discrete I do not think it is great. I would not recognize the Indian Cave Creek form as a distinct species even if known to be reproductively isolated, unless hypotheses about patristic relationships were found to fail. One such failure would be to find the two forms sympatric; the hypothesis of paraphyletic relationships would then be falsified.

In contrast, certain geographically distant populations of the taxa *S. pygmaeus* (Fig. 239) and *S. scopaeus* (Fig. 238) may well not be reproductively isolated from one another, but geographically proximate populations evidently are. These taxa, both of which are abundant and widespread, are sympatric in northeastern Mexico where they are doubtless reproductively isolated. No certain evidence of paraphyly remains between geographically proximate populations of these taxa, and the possible lack of reproductive isolation between certain distant populations is not a useful criterion for species recognition. These taxa, if marked by a lack of discrete evolutionary potential, seem nevertheless to have such evolutionary potential well developed, and probably have had it so developed much longer than have had the isolates of *S. tibialis*. Along the Rio Conchos and Rio Grande in Chihuahua, clinal continuity between *S. pygmaeus* and *S. scopaeus* is suggested in several statistical characteristics (Fig. 243-246) but not in structures of the male genitalia (Fig. 234). I would treat these taxa as conspecific only if unexpected evidence from a geographically intermediate sample showed my interpretation of differences in the male genitalia to be wrong.

4.2 Subgenera and species groups of *Schizogenius*

In this section I attempt to reconstruct the phylogeny of major lineages of the genus *Schizogenius*, using contrasting phyletic and phenetic methods. For purposes of this discussion, the *truquii*, *lineolatus*, *longipennis*, *depressus*, *brevisetosus*, *pluripunctatus*, *sallei*, and *tristriatus* groups are treated as a monophyletic group, the *truquii* lineage. The *capitalis*, *lindrothi*, *quadripunctatus*, *darlingtoni*, and *ocellatus* groups form another monophyletic group, the *capitalis* lineage. All other species groups are considered as separate lineages.

Relationships of the genus *Schizogenius* to other genera were discussed in section 3.11, and in a separate paper (1966b). From those intergeneric comparisons, I judge that ancestral character states in the common ancestor of living *Schizogenius* species included the following: mandibles more or less arcuate laterally; lacinia setose along outer margin; mentum deeply emarginate at middle, median tooth distinct; gula less than 0.3 maximum width of mentum; antennal article two not plurisetose; eyes not bordered by dorsal carinae; frontal carinae not perfectly regular, parallel, equidistant, or equally raised; occiput punctate dorsally, extended laterad along posterior margin of eyes; hind leg with tarsus more than 0.6 length of tibia; paramedian carinae of sternum three strongly developed; and pygidium with well developed median longitudinal rows of files. Additional probable plesiomorphic character states, determined from intergeneric and infrageneric comparisons, are listed in Table 65. Character states so listed are designated or coded as apomorphic or plesiomorphic, based on what I think is primitive in a group or lineage (see Ball and Erwin, 1969). The apomorphic state of several characters arose in more than one lineage, but in this phylogeny none of the characters studied reverted to the plesiomorphic state except the elongate paronychia of the *arechavaletae-truquii-capitalis* and *strigicollis-elongatus-carinatus* lineages.

The genus is most diverse in South America, which I therefore think is the primary center of radiation. Penetration of North and Middle America over the water gap that separated this area from South America during Middle Tertiary is considered an apomorphic zoogeographic characteristic. Ancestors of only the *crenulatus*, *ferrugineus*, and *truquii* lineages made these crossings. These zoogeographic data were not considered in reconstructing the phylogeny, but are not in conflict with it; see section 5.233.

Phylogeny reconstructed by phyletic techniques. - See section 4.12, phylogenetic methods. The reconstructed phylogeny of major lineages of *Schizogenius* is shown in Fig. 255, and the principal data used are listed in Table 65; the time scale suggested is discussed in section 5.232. I here summarize principal features of this phylogeny, indicate its weaknesses and strengths, and note apomorphic character states thought to have arisen in more than one lineage. I am confident that all branching points are correctly positioned, and have indicated apomorphic character states for nearly all dichotomies. I think that each lineage is monophyletic, and that this phylogeny is most probably a correct representation of evolutionary relationships; this reconstructed phylogeny should therefore have strong heuristic value for predicting patristic relationships.

Ancestral *Schizogenius* differentiated into two stocks, the subgenera *Genioschizus* and *Schizogenius*. Apomorphic character states in ancestral *Genioschizus* included flared and pitted lateral channel of elytron, and reduced numbers of discal setae on elytron; the latter character state evolved independently in several lineages of *Schizogenius*. In ancestral *Schizogenius*, apomorphic conditions included shortened paronychia, and loss of paralateral pronotal sulci; the latter condition evolved independently in the *tenuis* group of *Genioschizus*.

Genioschizus differentiated into three known groups. This differentiation took place comparatively recently, as *Genioschizus* is far

Table 65. Characters and character states used in phyletic analysis of phylogeny of major lineages of *Schizogenius*.

	Character	Character state	
		Plesiomorphic	Apomorphic
	Head		
(1)	Paramedian clypeal carinae:	tuberculate	not tuberculate
(2)	Clypeal suture:	shallow	deep
(3)	Occiput punctation:	uniform	reduced medially
(4)	Antennae:	moniliform	filiform
(5)	Arrangement of bristles on terminal palpal articles:	transverse	longitudinal
(6)	Mentum epilobes:	produced	truncate
	Pronotum		
(7)	Paralateral sulci:	present	absent
(8)	Paramedian sulci:	present	obsolete
(9)	Paralateral carinae:	absent	present
(10)	Hind angles:	rounded	prominent
	Elytra		
(11)	Apex of lateral channel:	not foveate	foveate
(12)	Apices of intervals:	not carinate	carinate
(13)	Setae of interval five:	normal	basal
(14)	Setae of intervals three, five, and seven:	present	absent from interval seven (') interval five ('') interval three (''')

Table 65. (Continued.)

	Character	Character state	
		Plesiomorphic	Apomorphic
	Legs		
(15)	Male front tarsi:	narrow	dilated
(16)	Hind tarsi:	short	long
(17)	Paronychia:	long	(') short ('') long
	Abdomen		
(18)	Sternal carinae:	straight	rounded at apices
(19)	Patch of microsculpture in coxal area of sternum three:	present	absent
(20)	Female anal ambulatory setae:	present	absent
(21)	Female pygidium apex:	entire	crenulate
(22)	Basal collar spines of internal sac of male median lobe:	indistinct	distinct

less diverse than is *Schizogenius*. Among known forms, the *crenulatus* group is the most distinctive. Its ancestor entered North America across a water gap between North and South America, and developed the apomorphic condition of truncated mentum epilobes. The ancestor of its sister group remained in South America, developed the apomorphic condition of elytral intervals carinate at apices, and differentiated into the *quinquesulcatus* and *tenuis* groups. An apomorphic condition of ancestral *tenuis* group was loss of paralateral pronotal sulci, an apomorphic condition also of ancestral subgenus *Schizogenius*. A weakness in my reconstructed phylogeny of *Genioschizus* is that I found no useful synapomorphic condition to characterize the *quinquesulcatus* group.

The first major dichotomy in the phylogeny of the subgenus *Schizogenius* reflects the differentiation of the *jacarensis-optimus* lineage from the remainder of the subgenus. The ancestor of its sister group had the apomorphic sharply engraved clypeal suture; this condition reappeared in some members of the *optimus* group. Numerous apomorphic features distinguished the ancestor of the *jacarensis-optimus* lineage, but among those indicated in Fig. 255 only the condition of elongate tarsi was not repeated elsewhere in the phylogeny of the genus. The *jacarensis-optimus* lineage subsequently differentiated into the *optimus* and monotypic *jacarensis* groups. Apomorphic features of the ancestor of the *optimus* group included apex of male median lobe abruptly bent, and bristles on terminal palpal articles longitudinally arranged.

The ancestor of the *ferrugineus* group entered Middle and North America where it lost the female paramedian ambulatory setae from sternum seven, but this loss was repeated later in the phylogeny of its sister group. Apomorphic conditions of the ancestor of that sister group were antennae filiform and female pygidial margin crenulate.

The ancestor of the South American *basalis* group differentiated from the ancestor of its sister group when the latter lost the female paramedian ambulatory setae from sternum seven. This apomorphic condition also characterized ancestors of the *jacarensis-optimus* and *ferrugineus* lineages. A weakness in this dichotomy is that I found no synapomorphic characteristic for the *basalis* group. In most members of the sister group the paronychia are elongate as in subgenus *Genioschizus*.

The *strigicollis-elongatus-carinatus* lineage developed the apomorphic condition of strongly developed paralateral pronotal carinae, while the *arechavaletae-truquii-capitalis* lineage had as apomorphic the curved apices of paramedian carinae of sternum three. Some members of the *truquii* lineage have weakly developed paralateral pronotal carinae, obviously an independent apomorphy. Members of the *strigicollis* lineage have accessory setae on submentum, while members of the *elongatus-carinatus* lineage lack discal setae on elytron. Members of *elongatus* lineage have shortened paramedian pronotal sulci, while members of *carinatus* lineage have carinate elytral intervals. Loss of discal setae and reduced pronotal sulci are also characteristic in some members of the *optimus* lineage, and in the *quinquesulcatus-tenuis* lineage of subgenus *Genioschizus* the apices of elytral intervals are carinate.

The ancestor of the *arechavaletae* lineage lost discal setae from the apical half of interval seven, and in the ancestor of the *truquii*-

capitalis lineage the paramedian clypeal carinae extended to median clypeal tooth. The ancestor of the *capitalis* lineage lost discal setae from interval seven. A weakness of this dichotomy is that I found no synapomorphic morphological characteristic in the *truquii* lineage. But zoogeographic evidence supports this dichotomy; the ancestor of the *truquii* lineage entered Middle and North America, while the ancestor of the *capitalis* lineage remained in South America. Loss of discal setae from interval seven occurred in ancestors of five lineages: *Genioschizus*, *jacarensis-optimus*, *elongatus-carinatus*, *arechavaletae*, and *capitalis*. Discal setae were lost completely in ancestors of the *jacarensis-optimus* and *elongatus-carinatus* lineages, and in some derived members of *Genioschizus* and the *capitalis* lineage. In the ancestor of *Genioschizus*, setae of interval five were restricted to the base, while in the ancestor of the *arechavaletae* group they were distributed in the basal half. Some members of the *strigicollis-elongatus-carinatus* lineage have the paramedian clypeal carinae weakly extended to median tooth, but this condition is apparently unstable; in the *truquii-capitalis* lineage the condition is synapomorphic, stable, and well developed.

Evident weaknesses in this reconstructed phylogeny concern the relative positions of the *Genioschizus* and *jacarensis-optimus* lineages, and the *ferrugineus* and *basalis* lineages. Justifications for my interpretations are given below. Otherwise, the reconstructed phylogeny appears sound, and requires no further discussion.

On first examination, it is difficult to decide whether the *crenulatus-quinquesulcatus-tenuis (Genioschizus)* lineage or the *jacarensis-optimus* lineage was the first to differentiate from the rest of the genus. Members of the former are plesiomorphic in most characteristics, and thus appear to be the most primitive element of *Schizogenius*. Members of the *jacarensis-optimus* lineage have in combination numerous apomorphic characteristics, and thus appear more strongly differentiated than do members of the *Genioschizus* lineage. My interpretation is based on the following observations. In the *Genioschizus* lineage the apomorphic characteristics of the lateral channel form a complex not found in other carabid beetles. The one apomorphic characteristic of members of the *jacarensis-optimus* lineage that distinguishes them from other members of the genus, the elongate tibiae, seems a much less complex characteristic. These observations alone suggest that the *Genioschizus-Schizogenius* dichotomy is the most likely. An even more compelling reason, if the simplest system of evolutionary pathways is the most probable one, is that at least two extra evolutionary steps are needed if the *jacarensis-optimus* lineage is the first dichotomy. These are: paronychia shortened twice, not once; and paralateral pronotal sulci lost thrice, not twice. No evolutionary steps are saved if the *jacarensis-optimus* lineage is regarded as the sister group of the rest of the genus.

An extra evolutionary step is required if the apomorphic condition of lost female paramedian ambulatory setae evolved independently in the *ferrugineus* and *strigicollis-truquii* lineages, as well as in the *jacarensis-optimus* lineage. But the evolutionary significance of this character condition is uncertain, for the following reasons. Males of some species of the *optimus* group lack anal ambulatory setae. Occasional females of various species of the *truquii* and *capitalis* lineages have been found with one or even both of these setae. And females of *S. pluripunctatus* of the *truquii* lineage have regained both setae as a clearly apomorphic condition. Future genetic studies may show that some mechanism such as a suppressor gene controls the presence or absence of female ambulatory setae. If so, their loss was apomorphic in the ancestor of the subgenus, and they were regained in both the *basalis* group and in *S. pluripunctatus*. Otherwise, the relative positions of the *ferrugineus* and *basalis* lineages in this reconstructed phylogeny are the most parsimonious. The following apomorphies arose once rather than twice: antennae filiform; female pygidium crenulate; basal collar spines strongly developed; and male front tarsi markedly dilated. Of these apomorphic character states, the most stable is that of the antennae; all members of the *basalis-truquii* lineage have filiform antennae, though of variable length. The other three characters do not appear in the apomorphic condition in all members of the *basalis-truquii* lineage, but most probably were apomorphic in the ancestor of that lineage.

Whatever the phylogeny of the major groups of *Schizogenius* really was, many characteristics of external morphology are convergent. The reconstructed phylogeny proposed here is the most parsimonious, but even so at least the following conditions evolved more than once: apices of elytral intervals carinate, twice; paralateral pronotal sulci lost, twice; paramedian ambulatory setae lost from female sternum seven, three times; setae lost from elytral interval seven, five times; setae lost from apical half of interval five, twice; and setae entirely lost from interval five, twice. The apomorphic zoogeographic characteristic, penetration of Middle and North America, happened three times. The paronychia shortened in the ancestor of subgenus *Schizogenius*, but became secondarily elongated in some of the more derived lineages.

Phylogeny reconstructed by phenetic techniques. - Some methods of numerical cladistics were proposed by Camin and Sokal (1965) for deducing phylogeny, one of which was satisfactorily tested for a group of tiger beetles by Willis (1971). Necessary assumptions are that character states are discrete and may be arranged sequentially from primitive to derived, and that while derived character states may have arisen repeatedly, none reverted to the ancestral condition. In the phylogeny of major groups of *Schizogenius* these assumptions appear valid, except that the paronychia are secondarily elongate in some members of the *strigicollis-elongatus-carinatus-arechavaletae-truquii-capitalis* lineage. I used this method to test the logic of my reconstructed phylogeny of major lineages; as a technique for determining the most parsimonious system of evolutionary pathways, it should produce the same result as my phyletic analysis. In the phylogeny of species, as in the *truquii* lineage, character states of many characters have evidently reverted to the ancestral condition, so that numerical cladistics, at least in their simple form (Willis, 1971), cannot be used.

Coded character states are given in Table 66, and fitted to a data matrix in Table 67 and a compatibility matrix in Table 68. The character state of any given character is the one regarded as ancestral in the operational taxonomic unit (OTU) concerned, irrespective of

Table 66. Characters and coded character states used in phenetic analysis of phylogeny of major lineages of *Schizogenius*.

Character	Character state
(1) Elytral lateral channel:	0, not foveate; 1, foveate
(2) Apices of intervals:	0, not carinate; 1, carinate
(3) Elytral intervals with discal setae:	0, three, five, and seven; 1, three and five; 2, three; 3, none
(4) Setae of interval five:	0, normal or absent; 1, basal
(5) Antennae:	0, moniliform; 1, filiform; 2, long
(6) Male front tarsi + female pygidium apex + basal collar spines:	0, narrow + not crenulate + not developed; 3, dilated + crenulate + developed
(7) Paralateral pronotal sulci:	0, present; 1, absent
(8) Anal ambulatory setae:	0, males and females; 1, males only
(9) Clypeal suture:	0, shallow; 1, deep
(10) Hind tarsi + microsculpture patch in coxal area of sternum three:	0, short + present; 2, elongate + absent
(11) Paralateral pronotal carinae:	0, absent; 1, present
(12) Paramedian clypeal carinae + pronotal hind angles:	0, tuberculate + rounded; 2, not tuberculate + produced
(13) Paronychia:	0, long; 1, short
(14) Paramedian sternal carinae:	0, straight; 1, curved at apices

Table 67. Data matrix for phenetic analysis of phylogeny of major lineages of *Schizogenius*.

		OTU: major group or lineage														
		crenulatus group	*quinquesulcatus* group	*tenuis* group	*jacarensis* group	*optimus* group	*ferrugineus* group	*basalis* group	*strigicollis* group	*carinatus* group	*elongatus* group	*arechavaletae* group	*truquii* lineage	*capitalis* lineage	Character states (c)	Minimum steps (c-1)
Characters	(1)	1	1	1	0	0	0	0	0	0	0	0	0	0	2	1
	(2)	0	1	1	0	0	0	0	0	1	0	0	0	0	2	1
	(3)	1	1	1	2	2	0	0	0	3	3	1	0	1	4	3
	(4)	1	1	1	0	0	0	0	0	0	0	1	0	0	2	1
	(5)	0	0	0	0	0	0	1	2	2	1	1	2	2	3	2
	(6)	0	0	0	0	0	0	3	3	3	3	3	3	3	4	3
	(7)	0	0	1	1	1	1	1	1	1	1	1	1	1	2	1
	(8)	0	0	0	1	1	1	0	1	1	1	1	1	1	2	1
	(9)	0	0	0	0	0	1	1	1	1	1	1	1	1	2	1
	(10)	0	0	0	2	2	0	0	0	0	0	0	0	0	3	2
	(11)	0	0	0	0	0	0	0	1	1	1	0	0	0	2	1
	(12)	0	0	0	0	0	0	0	0	0	0	0	2	2	3	2
	(13)	0	0	0	1	1	1	1	1	1	1	1	1	1	2	1
	(14)	0	0	0	0	0	0	0	0	0	0	1	1	1	2	1
																21

Table 68. Compatibility matrix for phenetic analysis of phylogeny of major lineages of *Schizogenius*.

	Patterns															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Compatibilities	Extra steps
(1)	X	1	0	0	0	0	1	0	0	0	0	0	0	0	11	2
(2)	1	X	1	1	1	1	1	1	1	0	1	0	1	0	3	10
(3)	1	3	X	1	5	2	1	1	2	2	2	1	1	1	0	23
(4)	1	1	0	X	1	1	1	1	1	0	0	0	1	1	4	9
(5)	0	2	4	1	X	1	0	1	0	0	2	2	0	2	6	14
(6)	0	3	6	3	3	X	0	3	0	0	3	3	0	3	5	27
(7)	1	1	3	1	1	1	X	1	1	1	1	1	1	1	0	15
(8)	0	1	3	1	1	1	0	X	1	1	1	1	0	1	3	12
(9)	0	1	2	1	2	1	0	0	X	0	1	1	0	1	5	10
(10)	0	0	0	0	0	0	0	0	0	X	0	0	0	0	13	0
(11)	0	1	1	0	1	0	0	0	0	0	X	0	0	0	10	3
(12)	0	0	2	0	0	0	0	0	0	0	0	X	0	0	12	2
(13)	0	1	3	1	2	1	0	1	1	1	1	1	X	1	2	14
(14)	0	0	1	1	1	0	0	0	0	0	0	1	0	X	9	4
Compatibilities	9	3	3	4	3	6	9	6	7	9	5	5	9	5	83	--
Extra steps	4	15	26	11	18	8	4	9	7	5	12	11	4	11	--	145

possible specializations in various derived members of that OTU. The secondarily elongate paronychia of some members of the *strigicollis-elongatus-carinatus-arechavaletae-truquii-capitalis* lineage are coded as short. Only those characteristics represented in the derived character state by two or more OTU's were used in this analysis, but additional, autapomorphous, characteristics were used to relate terminal elements in various lineages. If two or more characteristics produced the same cladogram pattern, they are combined and coded accordingly.

As seen in Table 68, cladogram patterns one, seven, and thirteen are the most parsimonious; each requires a minimum of four extra evolutionary steps. The first and third of these link all three species groups of *Genioschizus* as a clade, but the second excludes the *tenuis* group. Substudies revealed that pattern seven is less parsimonious than patterns one and thirteen, as in the completed phylogeny extra evolutionary steps are required to account for convergences in characteristics one, three, and four. In patterns one and thirteen, three OTU's cluster on one branch, and ten on the other. Substudies done for the major branch revealed that cladogram pattern ten is the most parsimonious, with two OTU's on one branch and eight on the other. In the final cladogram (Fig. 256), 33 evolutionary steps are needed, 12 more than the 21 minimum steps indicated in Table 67. This cladogram is the same as the reconstructed phylogeny suggested in Fig. 255, as expected, and I arbitrarily fitted it to the same time scale for ready comparison.

4.3 The *truquii* lineage

Relationships among species and species groups of the *truquii* lineage are obscured by the lack of evident and strongly developed synapomorphous characteristics. My reconstructed phylogeny (Fig. 257) is provisional, and needs to be tested in future studies by analysis of non-morphological characteristics, but it is supported by zoogeographic evidence considered in section 5.233. Morphological characteristics, including statistical characteristics obtained from Tables 8-64, are listed in Table 69.

The *truquii* lineage includes eight species groups. Four of them, the *truquii*, *brevisetosus*, *sallei*, and *lineolatus* groups, are monobasic. The *pluripunctatus*, *tristriatus*, *longipennis*, and *depressus* groups all include several known species taxa. In the following discussion, I treat first the suspected relationships between groups, and then the suspected relationships within the larger groups.

Relationships of species groups. - The *truquii* group, the only group of the lineage not represented north of the Tropic of Cancer, includes one living species from central Mexico. I suspect the ancestor of the *truquii* group entered Pacific areas of southern Mexico, while the ancestor of its sister group penetrated Atlantic areas in northeastern Mexico. Specialized features of the *truquii* group include male front tarsus narrowed, female pygidial crenulations lost, and paramedian pronotal sulci extended nearly to anterior transverse impression. Loss of female pygidial crenulations was probably also ancestral in the *brevisetosus* and *pluripunctatus* groups, and in some species of

Table 69. Characters and character states in *truquii* lineage.

	Character	Character state	
		Plesiomorphic	Apomorphic
	General		
(1)	Form (mean DP/LP):	0.80-0.84	(a) 0.75-0.79 (b) 0.85-0.89
(2)	Size (mean, LE, mm):	2.50-2.95	(a') 2.21-2.49 (a'') under 2.21 (b) over 2.95
(3)	Color:	piceous	(') paler ('') piceous
	Head		
(4)	Eye size (mean WF/WH):	0.60-0.63	(') 0.64-0.67 ('') 0.68-0.71
(5)	Clypeal field:	narrow	broad
(6)	Bases of frontal carinae:	free	confused
(7)	Microsculpture of paramedian frontal sulci:	strong	weak
(8)	Antennae:	long	short
	Prothorax		
(9)	Form (mean LP/WP):	0.89-0.96	(a) wider (b) narrower
(10)	Relative size (mean LP/WE):	0.75-0.80	(') smaller ('') reverted

Table 69. (Continued.)

Character	Character state Plesiomorphic	 Apomorphic
(11) Length of paramedian sulci (mean PS/LP):	0.67-0.74	(a) shorter (b') 0.75-0.82 (b'') longer
(12) Pronotal hind angles:	prominent	rounded
(13) Paralateral pronotal carinae:	absent	evident
(14) Accessory marginal setae:	absent	present
(15) Pleura:	impunctate	punctate
(16) Pleural microsculpture:	absent or weak	strong
Elytral setae		
(17) Mean number per elytron:	23 or fewer	(') 24-34 ('') more
(18) Length:	short	long
Legs		
(19) Tarsal length (mean Ta/Ti):	over 0.60	under 0.60
(20) Male front tarsi:	dilated	narrow
(21) Front tibia near base:	narrow	broad
Abdomen		
(22) Microsculpture of coxal depressions of sternum three:	present	absent
(23) Median microsculpture:	absent	present
(24) Lateral microsculpture:	absent	present
(25) Female pygidium apex:	crenulate	not crenulate

the *depressus* group. This characteristic, and the narrowed male front tarsi, are secondary specializations convergent with ancestral conditions in the genus. A weakness of this dichotomy is the lack of an evident synapomorphous characteristic in the sister group. But the dichotomy is supported by distributional data, and by the amount of phenetic difference between members of the *truquii* group and members of its sister group.

Relationships among the remaining seven species groups are unclear from morphological evidence, and my arrangement is suggested partly by geographic evidence and partly by the rule of parsimony. Probable sister groups are: *brevisetosus* and *pluripunctatus*, increased discal setae; *sallei* and *tristriatus*, abdominal microsculpture; and *longipennis* and *depressus*, reduced hind angles. Members of the *brevisetosus*, *sallei*, and *tristriatus* groups are largely confined to limestone regions, and their pale color may be an adaptation to that habitat. Their ancestor was a Texan vicariant of the Tamaulipan ancestor of the *lineolatus*, *longipennis*, and *depressus* groups. Ancestors of the *brevisetosus* and *pluripunctatus* groups were Texan-Sonoran vicariants, and ancestors of the *sallei* and *tristriatus* groups were Texan-Tamaulipan vicariants. If the ancestor of the *lineolatus* group was Texan, the ancestor of the *longipennis* and *depressus* groups was Tamaulipan, and in turn the ancestors of those two groups were tropical-Tamaulipan vicariants. These geographic relationships are expressed in Fig. 265-269, and further discussed in section 5.233. This is the most parsimonious arrangement I can develop, is consistent with the premise that geographic isolation precedes speciation, and requires the shortest sequence of branching points. Unfortunately, I found no synapomorphous characteristics to justify either main branch, aside from the pale coloration of members of the *brevisetosus*, *sallei*, and *tristriatus* groups.

Among ancestors of species groups of the *truquii* lineage, my reconstructed phylogeny requires at least the following character convergences: color pale, twice, one reversion; pronotum small, twice, one reversion; paramedian pronotal sulci long, twice; pronotal hind angles rounded, twice; and female pygidium not crenulate, twice.

Relationships within larger species groups. - Relationships among species and subspecies taxa of the *pluripunctatus* group are quite straightforward, and vicariant relationships are shown in Fig. 266. If the ancestor of the group was Sonoran, the ancestor of *S. seticollis* and the ancestor of its sister group were Californian-Sonoran vicariants characterized respectively by accessory pronotal setae and relatively short antennae. The taxa *S. seticollis seticollis* and *S. seticollis vandykei* diverged from one another as north-south vicariants. A taxon cycle system of displacement (Wilson, 1961) would account for the general distribution of members of the *pluripunctatus* subgroup and for the presence of accessory pronotal setae in the taxa *S. seticollis* and *S. plurisetosus*. It would not account for various similarities between geographically proximate populations of *S. plurisetosus* and *S. multisetosus*. I suggest that the ancestor of the taxa *S. plurisetosus* and *S. multisetosus* and the ancestor of the taxa *S. pluripunctatus* and *S. kulti* were Sonoran-tropical vicariants, distinguished sharply by differences in form of male median lobe (Fig. 131-136). Subsequently, *S. plurisetosus* and *S. multisetosus* diverged as Tamaulipan-tropical vicariants, and *S. pluripunctatus* and *S. kulti* diverged as Sonoran-tropical vicariants. The apomorphic condition of accessory pronotal setae is convergent in the taxa *S. seticollis* and *S. plurisetosus*.

The *tristriatus* group is divisible into four clearly distinguished subgroups: *S. tristriatus*, *tristriatus* subgroup; *S. amphibius*, *amphibius* subgroup; *S. dilatus* and *S. tibialis*, *dilatus* subgroup; and *S. planulatus*, *S. ozarkensis*, and *S. planuloides*, *planulatus* subgroup. Detailed relationships among species taxa of the *planulatus* subgroup were discussed in section 4.14. The *amphibius*, *dilatus*, and *planulatus* subgroups share the synapomorphic characteristic of flattened body form; their ancestor and the ancestor of the *tristriatus* subgroup were Tamaulipan-tropical vicariants. Dark coloration is a secondarily acquired characteristic in members of the *tristriatus* subgroup, and relatively enlarged pronota is secondary in the other three subgroups. Members of the *amphibius* and *planulatus* subgroups differ strikingly in size, but agree in increased numbers of elytral setae and reduced eye size. Their ancestor and the ancestor of the *dilatus* subgroup were Texan-Tamaulipan vicariants. And, as judged from the distribution of living species, the ancestors of the *amphibius* and *planulatus* subgroups were temperate-Texan vicariants. Ancestors of the taxa *S. dilatus* and *S. tibialis* were clearly Tamaulipan-tropical vicariants, but some forms of *S. tibialis* reentered the Tamaulipan area from the west, and even entered the Texan area (Fig. 188). These vicariant relationships are shown in Fig. 267.

Among taxa included in the *longipennis* group, *S. longipennis* and *S. neovalidus* are clearly sister species linked by the synapomorphous condition of enlarged virga in the male endophallus, and *S. pacificus* with elongate tarsi and convex body is the most divergent form. My views on vicariant relationships are expressed in Fig. 268. Three of the four included species are represented in Arizona, two apparently as relicts. One might therefore suspect that ancestors of the *depressus* and *longipennis* groups were Tamaulipan-Sonoran vicariants, rather than Tamaulipan-tropical. But no members of the group are known either from Texas or the Mexican Central Plateau, and, further, if the ancestor of the group was Sonoran one could not convincingly explain the presence of the Arizona relicts. I think a taxon cycle system of displacement (Wilson, 1961) was responsible for present distributions. The ancestor of the group spread across tropical regions of southern Mexico; the ancestor of *S. pacificus* and the ancestor of its sister group were Pacific-Atlantic vicariants. When the ancestor of that sister group again spread to the Pacific slopes, *S. pacificus* was well differentiated, and not subject to displacement. The ancestor of *S. chiricahuanus* and the ancestor of its sister group were Sonoran-tropical vicariants, but the range of *S. chiricahuanus* recessed when its sister group entered the Sonoran region. The ancestors of *S. neovalidus* and *S. longipennis* were again Sonoran-tropical vicariants, and the range of *S. neovalidus* recessed when *S. longipennis* entered the Sonoran region.

The aggregate range of members of the *depressus* group is nearly as great as that of the entire genus. Thus evolutionary relationships are difficult to interpret, and my analysis of vicariant relationships (Fig. 269) is difficult to justify. For purposes of this discussion, I recognize three subgroups: *S. arimao, S. emdeni*, and *S. "apicalis"*, *arimao* subgroup; *S. sulcifrons* and *S. litigiosus*, *sulcifrons* subgroup; and *S. pygmaeus*, *S. scopaeus*, *S. falli*, *S. ochtocephalus*, and *S. depressus*, *depressus* subgroup. Members of the *arimao* subgroup agree in the synapomorphous characteristic of shortened pronotal sulci, also characteristic of members of the *pluripunctatus* and *longipennis* groups. I found no clear synapomorphous characteristic of its sister group, but suspect the ancestor of that group had slightly increased numbers of elytral setae. Ancestors of the *arimao* subgroup and its sister group were probably tropical-Tamaulipan-Texan vicariants. I suspect an ancestral condition in the *arimao* subgroup was the presence of weakly developed paralateral pronotal carinae, subsequently lost in *S. emdeni*. The ancestor of *S. arimao* may have entered Cuba via a Middle American land bridge, and its ancestor and the ancestor of its sister group thus may have been Cuban-Middle American vicariants. Whether the ancestors of *S. emdeni* and *S. "apicalis"* were early Middle American-South American vicariants, or whether they diverged in Middle America, is uncertain.

Chorological data suggest that the ancestor of the *sulcifrons* and *depressus* subgroups was Texan, and that their respective ancestors were temperate-Texan vicariants. The ancestor of the latter subgroup was characterized by small size and pale color. The ancestor of the *sulcifrons* subgroup diverged into cool-adapted western and eastern vicariants during Pleistocene time. The common ancestor of *S. falli*, *S. ochthocephalus*, and *S. depressus* and the common ancestor of *S. pygmaeus* and *S. scopaeus* were Sonoran-Texan vicariants, as suggested particularly by the pattern of geographic variation in *S. falli* (see section 3.528). The ancestor of *S. falli, S. ochthocephalus*, and *S. depressus* was characterized by reduced eye size and flattened body, while the ancestor of *S. scopaeus* and *pygmaeus* was characterized by reduced body size. The ancestor of *S. depressus* and the ancestor of *S. falli* and *S. ochthocephalus* diverged as temperate-Sonoran vicariants, and the respective ancestors of *S. falli* and *S. ochthocephalus* diverged as Sonoran-Californian vicariants. Simple vicariance does not, however, explain the evolutionary history of the taxa *S. scopaeus* and *S. pygmaeus*. Their distribution patterns are best explained by an early split into Texan-Tamaulipan+tropical vicariants, a later split of the Texan form into Texan-Sonoran vicariants, and a still later reestablishment of reproductive continuity between the tropical and Sonoran vicariants.

The weakest parts of this reconstructed phylogeny (Fig. 257) are in the relationships of the *lineolatus, longipennis*, and *depressus* groups, and in relationships within the *depressus* group. In particular, present distributions of all members of both the *arimao* and *sulcifrons* subgroups are far removed from both the Texan and Tamaulipan regions, so that my suggested vicariant relationships are not well justified. In general, however, the suggested vicariant relationships lend support to the reconstructed phylogeny, or at least do not contradict it, and they seem to satisfactorily explain known distributions of modern species and subspecies taxa. I think they suggest the most probable of an astronomical number of possible evolutionary pathways.

4.4 Other groups and lineages

Hypothetical relationships among species and subspecies taxa of the genus *Schizogenius*, excluding members of the *truquii* lineage, are shown in Fig. 258. Most of these taxa are South American, and as the South American fauna is poorly known this reconstructed phylogeny is incomplete, and my comments on it are brief.

Among the three included taxa of the *quinquesulcatus* group, *S. szekessyi* and *S. janae* share maculate coloration. They are at most sister species, and may not even be biologically distinct entities.

Within the *tenuis* group, *S. impressicollis* is divergent from other taxa in form of male genitalia, but plesiomorphic in having parallel rather than convergent paramedian frontal carinae. Relationships among other taxa in the *tenuis* group are unclear, and cannot be properly interpreted until the South American fauna is better known. I think *S. sculptilis* is least closely related, as judged by amount of phenetic difference; in particular, I doubt that it shares a direct common ancestry with *S. tenuis*. My phylogeny suggests a possible pre-Pleistocene entry into Middle America for the ancestor of *S. sculptilis*, but there may well be an as yet unknown sister species in South America. More probably, the ancestor of *S. sculptilis* entered Middle America in Early Pleistocene, and *S. tenuis* followed in Late Pleistocene.

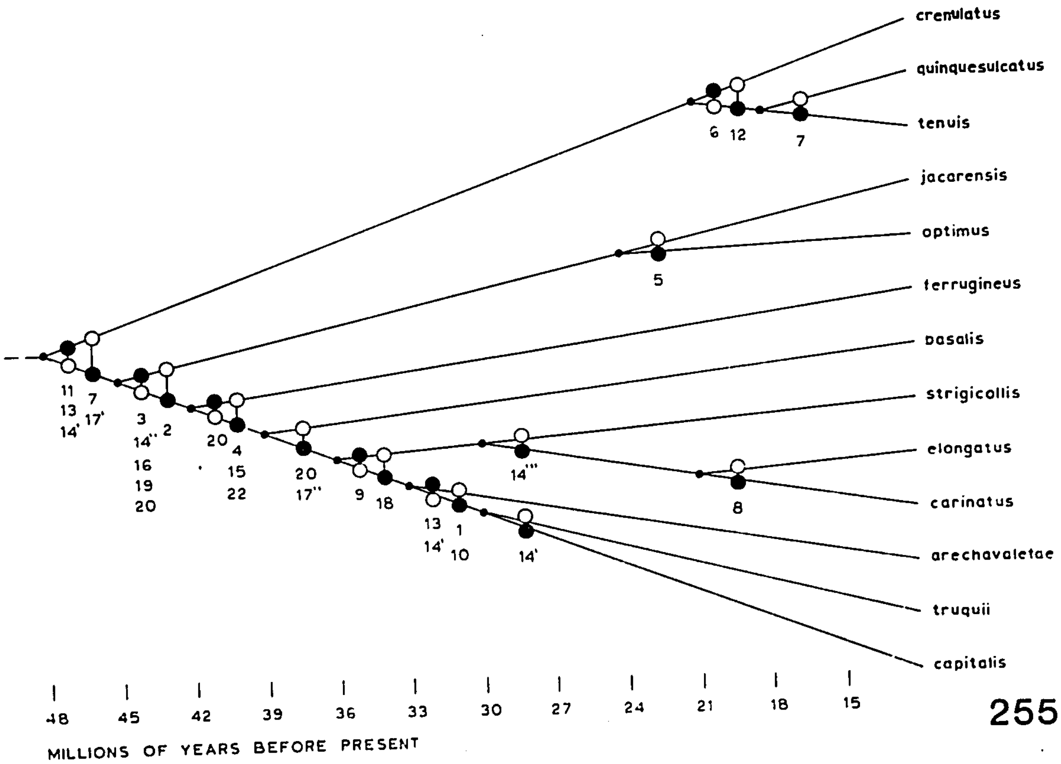
The ancestor of the *optimus* group gave rise to one line with shortened pronotal sulci, and another with discal setae lost: respectively, *S. optimus*, *S. dyschirioides*, and *S. clivinoides*; and *S. bicolor* and *S. grossus*. *S. optimus* and *S. dyschirioides* are evidently sister species, and the ancestor of *S. optimus* was most probably an Early Pleistocene entrant into Middle America.

Among the four included taxa of the *basalis* group, *S. basalis* and *S. cearaensis* seem most closely related to one another, and together with *S. negrei* agree in having reduced occiput punctation.

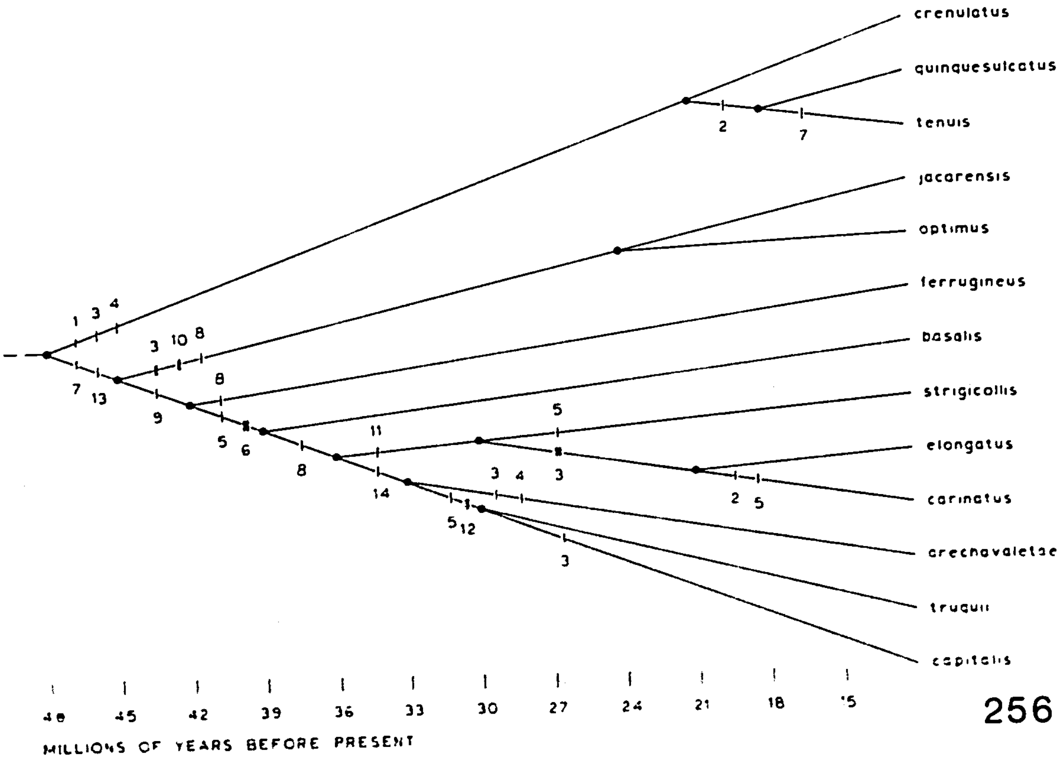
Aside from the *truquii* lineage, the most diverse lineage in *Schizogenius* is the *capitalis* lineage, with five included species groups. Similarities among some members of the *darlingtoni* and *ocellatus* group in size, color, and ventral microsculpture suggest possible relationships, but radical specializations of members of the *ocellatus* group imply considerable antiquity for the common ancestor of these two groups. Within the *darlingtoni* group, the taxa *S. darlingtoni* and *S. interstriatus* agree in having extensive abdominal microsculpture. Of the remaining three species groups, the *quadripunctatus* group is the most divergent and hence probably the oldest. Loss of discal setae from all but elytral interval three in this and the *ocellatus* group is probably convergent. The ancestor of the *lindrothi* group had reduced pronotal hind angles and shortened antennae, as in some groups of the *truquii* lineage. Ancestors of *S. lindrothi* and *S. banningeri* were probably Early Pleistocene Middle American-South American vicariants.

This reconstructed phylogeny suggests the following Middle and South American faunal exchanges. Ancestors of the *crenulatus* group, the *ferrugineus* group, and the *truquii* lineage entered Middle America well before Pleistocene time. Early Pleistocene Middle American immigrants included ancestors of *S. sculptilis*, *S. optimus*, and *S. lindrothi*; the ancestor of *S. "apicalis"* was a probable Early Pleistocene immigrant. During Late Pleistocene, *S. tenuis* spread into Middle America, and *S. pygmaeus* spread into South America. Thus, three south-north migrations occurred over water, three south-north migrations and one north-south migration occurred soon after establishment of land connections, and one north-south migration and one south-north migration occurred comparatively recently.

Fig. 255-256. Phylogeny of major groups and lineages of genus *Schizogenius; crenulatus, quinquesulcatus,* and *tenuis* groups are in subgenus *Genioschizus*. 255. Phylogeny reconstructed by phyletic techniques. 256. Phylogeny reconstructed by phenetic techniques.


crenulatus
quinquesulcatus
tenuis
jacarensis
optimus
ferrugineus
basalis
strigicollis
elongatus
carinatus
arechavaletae
truquii
capitalis
48
45
42
39
36
33
30
27
24
21
18
15
MILLIONS OF YEARS BEFORE PRESENT

255


crenulatus
quinquesulcatus
tenuis
jacarensis
optimus
ferrugineus
basalis
strigicollis
elongatus
carinatus
arechavaletae
truquii
capitalis
48
45
42
39
36
33
30
27
24
21
18
15
MILLIONS OF YEARS BEFORE PRESENT

256

Fig. 257. Reconstructed phylogeny of *truquii* lineage of genus *Schizogenius*.

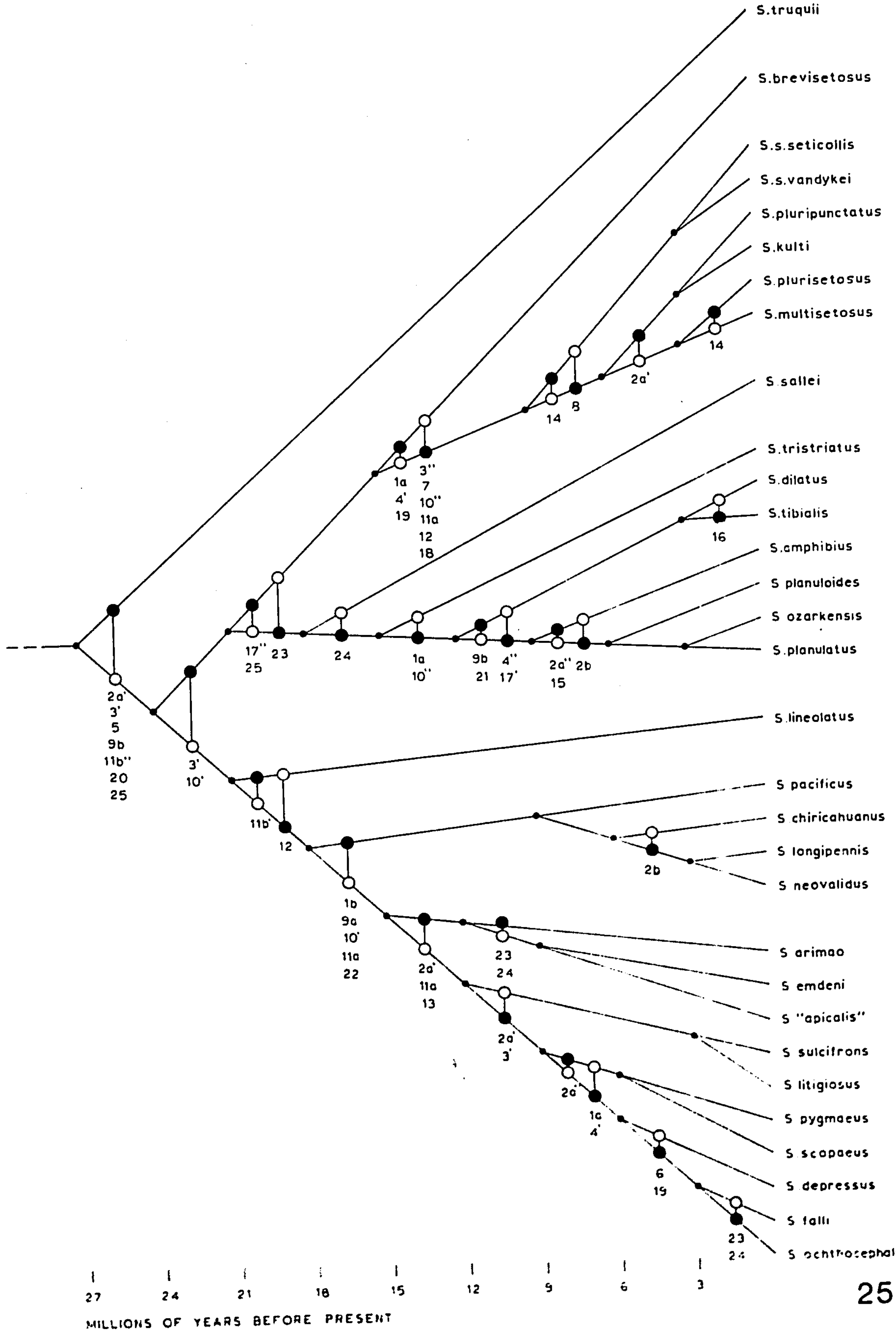

S.truquii
S.brevisetosus
S.s.seticollis
S.s.vandykei
S.pluripunctatus
S.kulti
S.plurisetosus
S.multisetosus
S sallei
S.tristriatus
S.dilatus
S.tibialis
S.amphibius
S planuloides
S ozarkensis
S.planulatus
S lineolatus
S pacificus
S chiricahuanus
S longipennis
S neovalidus
S arimao
S emdeni
S "apicalis"
S sulcifrons
S litigiosus
S pygmaeus
S scopaeus
S depressus
S falli
S ochthocephalus
2a' 3' 5 9b 11b'' 20 25
3' 10'
17'' 25
23
24
1a 4' 19
3'' 7 10'' 11a 12 18
14
8
2a'
14
1a 10''
9b 21
4'' 17'
2a'' 15
2b
16
11b'
12
1b 9a 10' 11a 22
2b
2a' 11a 13
23 24
2a' 3'
2a'
1a 4'
6 19
23 24
27
24
21
18
15
12
9
6
3
MILLIONS OF YEARS BEFORE PRESENT

Fig. 258. Reconstructed phylogeny of subspecies and species taxa of genus *Schizogenius*, excluding components of *truquii* lineage.


S.c.crenulatus
S.c.chiapatecus
S.quinquesulcatus
S.szekessyi
S.janae
S.impressicollis
S.sculptilis
S.suturalis
S.maculatus
S.impuncticollis
S.tenuis
S.jacarensis
S.optimus
S.dyschirioides
S.clivinoides
S.bicolor
S.grossus
S.ferrugineus
S.auripennis
S.multipunctatus
S.negrei
S.basalis
S.cearaensis
S.strigicollis
S.elongatus
S.costiceps
S.carinatus
S.costipennis
S.arechavaletae
S.reichardti
S.capitalis
S.putzeysi
S.lindrothi
S.banningeri
S.quadripunctatus
S.darlingtoni
S.interstriatus
S.riparius
S.ocellatus
S.truquii
48
45
42
39
36
33
30
27
24
21
18
15
12
9
6
3
MILLIONS OF YEARS BEFORE PRESENT

5.0 ZOOGEOGRAPHY

5.1 Introduction and general patterns of distribution

I discussed the importance of zoogeographic analyses, and the relationship of zoogeography and phylogeny, in section 4.1. Various classes of clues available to help assess the movements of animals include number clues, extent of area, continuity of area, degree of differentiation, and vicariance (Darlington, 1957; Erwin, 1970). In my study of *Schizogenius*, I found number clues and vicariance clues especially useful. In this section, I comment briefly on the zoogeography of the genus as a whole, with particular emphasis on faunal exchanges between North and South America, and in section 5.2 I give a detailed treatment of the zoogeography of North and Middle American species.

The genus *Schizogenius* is a sister group of New World *Halocoryza*; the ancestor of these organisms diverged from an African ancestor, and all other related genera are of Old World origin. The genus *Schizogenius* is best developed and most diverse in South America, and only three old lineages are restricted to or diversified in North and Middle America. The ancestor of the genus was therefore clearly South American, and it must have differentiated from *Halocoryza* stock no earlier than Eocene, after North and South America became separated by Middle American water gaps. One major water gap was across the Isthmus of Tehuantepec, and another across Panama, closing respectively in Late Miocene and Late Pliocene (Maldonado-Koerdell, 1964). These gaps approximately defined the area I recognize as Middle America, in the south bounded approximately by the Panama-Costa Rica border, and in the north including Pacific drainages of southeastern Chiapas but excluding the Usumacinta and Grijalva Rivers in Guatemala.

Of 23 species groups in *Schizogenius*, ten evolved in North America and 13 in South America. North American species groups arose from three early migrations from South America. One early immigrant gave rise to the *crenulatus* group, with one subspecies ranging to the southern limits of North America. A second early immigrant was the ancestor of the *ferrugineus* group, one species of which extends from North America to the southern limit of Middle America. The third immigrant gave rise to eight species groups, all centered in North America. One species of the *pluripunctatus* group enters the northern part of Middle America. One species of the *tristriatus* group extends to the southern limit of North America. One species of the *longipennis* group extends to the southern limit of North America, and another to the southern limit of Middle America. And in the *depressus* group, three endemic Middle American, Cuban, and South American species form a monophyletic subgroup of old Middle American ancestry, while another extends to northern South American from North America. I judge that the endemic South American form arrived there soon after the Panamanian water gap closed, and that it may have an as yet unknown vicariant sister species in Middle America.

Six of the 13 South American groups are not known from Panama, Colombia, or Venezuela. Some members of the *capitalis, darlingtoni, quinquesulcatus*, and *strigicollis* groups, are known from this region but not from Middle America. The *lindrothi* and *optimus* groups include vicariant Middle and South American sister species, but except for Floridian populations of *S. lindrothi* are otherwise unrepresented in North and Middle America. Only the *tenuis* group, with one species endemic in southern North America and another extending through Middle America to northern Mexico, is represented north of the Isthmus of Tehuantepec. The endemic species, *S. sculptilis*, probably also occurs in Middle America; its ancestor probably arrived there soon after re-establishment of land connections, and it may have an as yet unknown vicariant sister species in South America.

Middle America serves as a funnel (Simpson, 1950) between North and South America for *Schizogenius* species, and also shows a notable filter effect at both ends. Tropical insect faunas of Mexico and Middle America derive primarily from South American ancestors (Halffter, 1964), but for *Schizogenius* Halffter's notions about timing of immigrations are inadmissible. If the genus originated in South America after Eocene, the first wave of migrations northward was not earlier than mid-Tertiary. After closure of the Panamanian portal, early migrants evolved as endemic Middle American species. Later migrants, *S. tenuis* and *S. pygmaeus*, were more probably Late Pleistocene than Late Pliocene. Despite evidence for two-way mammalian interchanges between Middle and South America since Late Miocene (Hershkovitz, 1966), no evidence of free interchange before Late Pliocene exists for *Schizogenius* species.

The Middle American *Schizogenius* fauna is poorly known, but probably not so poorly as suggested by the limited numbers of known species. Among Mexican species not yet recorded from Middle America, only *S. sculptilis* is really likely to be found there. Also expected is a sister species of the South American *S. "apicalis"*, and perhaps other South American species enter southern parts of the area. Of nine species known from the region, four enter from North America, one from South America, and four are endemic; two endemics have South American sister species, while the others differentiated there from an earlier penetration from North America. Through much of Middle Tertiary, Middle America was an isolated, often partitioned land mass, and despite probable continuity with Cuba during much of this period was relatively small in area (Maldonado-Koerdell, 1964). Although the Tehuantepec portal closed in Late Miocene, the Isthmus was not elevated until Late Pliocene; the Isthmus may have been a continuously significant barrier since Early Oligocene. And, since Early Miocene and particularly since Late Pliocene, Middle America suffered much volcanic activity. These observations suggest that the *Schizogenius* fauna of Middle America may never have been really large. Support for this conclusion is evident from known distributions of species in the area. Aside from one species endemic to Cuba, all species except *S. kulti* are widely distributed from north to south, suggesting lack of barriers and consequent reduced geographic isolation and species diversification. Thus, while mid-Tertiary fracturing of Middle America may have contributed greatly to speciation in Trichoptera (Ross, 1967), it had no apparent effect on speciation in *Schizogenius*. After closure of the Tehuantepec portal in Late Miocene, some North American elements penetrated the area, and may have replaced some endemic forms. Further elimination of endemic forms may have resulted from arrival of South American immigrants after closure of the Panamanian portal in Late Pliocene.

5.2 Distribution patterns in North and Middle America

5.21 Introduction

The genus *Schizogenius* is represented throughout North and Middle America, south of 52°N in the west and 48°N in the east, except in the West Indies where known only from Cuba. Since this fauna originated in South America, most included species and subspecies are tropical or subtropical, and relatively few have acquired truly temperate adaptations. Their distribution patterns were regulated by the development of Middle and Late Tertiary climatic and physiographic features, and were modified particularly in the north by Pleistocene events. In section 5.22 I use number clues to evaluate distribution patterns, generally according to techniques developed by Ball and Freitag (*in* Freitag, 1969) and Erwin (1970), and compare my observations with some of their observations on *Evarthrus* and *Brachinus*, respectively. In section 5.23 I consider vicariance clues, particularly in relation to the *truquii* lineage, and attempt to reconstruct the historical zoogeography of the genus in North and Middle America.

5.22 Methods and general patterns

Following Erwin's (1970) methods, I show on a 5° longitudinal and latitudinal grid map the number of species or subspecies known to occur in each interval (Fig. 261), and list "total interval values" (TIV) and "average landmass interval values" (ALIV) in Table 70. The number of

Table 70. Total number of species and subspecies, "average landmass interval values" (ALIV), and "total interval values" (TIV) derived from Fig. 261.

Interval	#spp.	ALIV	TIV	Interval	#spp.	ALIV	TIV
A	-	-	-	a	1	1.0	1
B	5	4.8	12	b	4	1.7	10
C	5	3.1	14	c	10	3.1	33
D	11	4.9	22	d	14	4.7	45
E	16	5.9	31	e	20	7.7	48
F	20	6.6	43	f	18	8.8	31
G	22	9.2	46	g	20	16.9	38
H	17	6.9	26	h	17	14.4	36
I	11	5.2	21	i	6	12.0	12
J	13	5.7	23	j	7	10.6	8
K	7	4.4	13	k	1	1.3	1
L	6	4.4	10	l	-	--	-

species is maximum in southern and central Mexico, and slightly less in Arizona. Numbers decrease rapidly in all directions from these centers. To the north, numbers decrease least rapidly in the humid forested regions of the Appalachians and the Pacific coast. To the south, numbers decrease sharply near the Panama-Costa Rica border. And the *Schizogenius* fauna of Florida and the West Indies is notably depauperate. The general pattern is similar to that for *Brachinus*, except for absence of an evident east-west lateral asymmetry and reduced numbers in extreme southeastern United States.

These general patterns are readily explained. Few species are cool-adapted, and none are cold-adapted; hence, reduction to the north, particularly in central North America and in the Rocky Mountain region. Most species inhabit riparian gravel bars; hence reduction in extreme southeastern United States, and lack of east-west asymmetry in the United States. The reduction of numbers in Middle America was considered in section 5.1.

Maximum linear ranges (Erwin, 1970) are given in Table 71, and compared with data on linear ranges for *Brachinus* species (Erwin, 1970) and *Evarthrus* species (Ball and Freitag, *in* Freitag, 1969). Maximum ranges of *Schizogenius* species are almost exactly intermediate between those of *Brachinus* and *Evarthrus*; average maximum distances between localities were determined as about 700 miles for *Evarthrus*, 1000 miles for *Schizogenius*, and 1300 miles for *Brachinus*. One of the *Schizogenius* species, *S. pygmaeus*, has a linear distribution of more than 1000 miles greater than any species of *Evarthrus* or *Brachinus*.

If barriers limit distributions of *Evarthrus* species, and broad

Table 71. Frequency distribution of maximum linear range in miles of species of *Brachinus**, species of *Evarthrus***, and species and subspecies of *Schizogenius* in North and Middle America.

	Brachinus		*Evarthrus*		*Schizogenius*	
Class	#	%	#	%	#	%
3501-3750	0		0		1	
3251-3500	0	0	0	0	0	3
3001-3250	0		0		0	
....						
2751-3000	0		0		1	
2501-2750	5	19	0	2	2	13
2251-2500	5		0		2	
2001-2250	2		2		0	
....						
1751-2000	9		1		1	
1501-1750	2	39	3	16	1	21
1251-1500	8		1		1	
1001-1250	5		2		5	
....						
751-1000	11		8		6	
501-750	4	42	5	79	5	63
251-500	3		10		6	
0-250	8		12		7	
....						

* From Erwin (1970)

** From Ball and Freitag (*in* Freitag, 1969) climatic zones limit distributions of *Brachinus* species, a mixture of barriers and climatic zones may account for distributions of *Schizogenius* species. Barriers, for inhabitants of riparian gravel bars, include the following: high altitudes; rivers or sections of rivers without gravel bars; and land or water gaps between rivers. Limiting climatic zones correspond roughly to tropical, subtropical, warm temperate, and cool temperate. Another limiting factor in distributions of some *Schizogenius* species and subspecies is almost certainly one of ecological displacement. In North and Middle America, at least, no more than seven species may be taken in gravel bars at a single locality, and normally no more than five. Ecological displacement is particularly obvious in some allopatric sister species, which inhabit adjacent river systems or even separate segments of the same river system.

An example of a mountain barrier is the Sierra Madre Occidental. Species found on both sides of this range, such as *S. pluripunctatus* and *S. pygmaeus*, evidently lack gene flow across the mountains. Others, such as *S. depressus* to the east and *S. longipennis* to the west, have ranges limited by the mountains. Lack of suitable habitat along portions of the Red and Mississippi River probably accounts for limits of ranges in *S. planuloides*, *S. ozarkensis*, and *S. planulatus*. And the apparent isolation of *S. s. seticollis* and *S. s. vandykei* is probably due to a large gap between suitable habitats in northern Baja California.

Climatic zones are not sharply limited, but nonetheless seem at least partly responsible for range limitations. Of 13 species groups represented in North and Middle America, including representatives of three South American groups, all are represented in tropical or subtropical regions, seven in warm temperate regions, and six in cool temperate regions. Numerous species or subspecies have ranges limited near the Tropic of Cancer; twelve species or subspecies have southern or northern limits within 3 1/2°S, and eight within 3 1/2°N.

Some examples of allopatric sister taxa found in adjacent drainage systems are: *S. kulti* and *S. pluripunctatus*, Rio Grande de Santiago and Rio Acaponeta; *S. multisetosus* and *S. plurisetosus*, Rio Panuco and Rio Tamesi; and *S. c. crenulatus* and *S. c. chiapatecus*, Rio Grande de Santiago and Rio Ameca. Adjacent river systems may also limit sharply differentiated forms within a taxon, as in *S. tibialis*: large eyed forms occur from the Rio Panuco southward, moderate eyed forms from the Rio Panuco to the Rio Grande, and small eyed forms in the Nueces River basin. An example of displacement on a single river system is the occurrence of *S. pygmaeus* on the Rio Conchos, rather than *S. scopaeus* which occurs elsewhere along the Rio Grande. Somewhat less closely related taxa may also be subject to displacement, and an example may be the displacement of *S. dilatus* south of the Rio Tamesi by *S. tristriatus* or large-eyed *S. tibialis* and north of the Rio Sabinas Hidalgo by *S. sallei* or *S. planuloides*. Faunal compositions along river systems may vary from downstream to upstream. The taxa *S. multisetosus* and *S. kulti* are known from the same river systems but not from the same localities; when both occur on a drainage system, *S. multisetosus* is found upstream from *S. kulti*. Along the Rio Grande, seven species are known from the Del Rio region, three of them from the Big Bend region, and one of them plus another from northern New Mexico. Part of these faunal changes are probably due to lack of suitable habitat, as in the

Las Cruces-El Paso segment of the Rio Grande.

Techniques described by Erwin (1970) for finding centers of concentration are not useful for Central America and southern Mexico, because the 5° grid crosses the entire continent and obscures possible Atlantic and Pacific centers. Instead, I plotted centers of geographic distribution of all species and subspecies taxa with ranges less than 1250 miles, and circled these centers to enclose all geographic distributions up to a 300 mile radius (Fig. 262). Not surprisingly, resulting centers of concentration correspond to presence of endemic species. Based on these centers of concentration, areas of concentration (Fig. 263) were determined by comparisons of geographic distributions and by notions about barriers. Area 5 is judged to include peninsular Florida, because of the presence there of only the Middle American *S. lindrothi*. Area 6 is of doubtful reality, as it includes only one known species which, though endemic, is related to a species in area 5. Area 7 is also of doubtful reality, because the endemic species there, *S. sculptilis*, most probably ranges into Middle America. Distributions of species and subspecies are compared with these centers and areas in Table 72, dissimilarity values (Erwin, 1970; Ball and Freitag, 1969) are listed in Table 73, and an index of dissimilarity is given in Table 74.

Peripheral areas 1, 6, 11, and 12 are most distinct, as were Erwin's centers 1, 5, and 8. Areas 5 and 7, with a dissimilarity value of 64, are least distinct, and perhaps not distinct at all. In general, more central areas are least distinct, as was found by Erwin for *Brachinus*. All contiguous areas share one or more taxa, but subtraction patterns are

Table 72. Distribution of North and Middle American species and subspecies of *Schizogenius* in relation to centers of concentration.

Taxon	Centers 1	2	3	4	5	6	7	8	9	10	11	12
amphibius												xx
arimao						xx						
auripennis		xx	xx	xx	xx		xx					
brevisetosus									x	xx		
chiapatecus				xx								
chiricahuanus		xx										
crenulatus		xx		x								
depressus	xx	xx		x				x	x	x		
dilatus									xx			
emdeni					xx							
falli	x	xx	xx	x					xx	xx	xx	x
ferrugineus		xx								xx	xx	xx
kulti				xx	x		xx	xx				
lindrothi					xx							
lineolatus										xx	xx	xx
litigiosus	xx											
longipennis		xx		xx	xx		xx	xx	xx			
multisetosus				xx				xx				
neovalidus		xx										
ochthocephalus	xx											
optimus					xx							

Table 72. (Continued.)

Taxon	Centers 1	2	3	4	5	6	7	8	9	10	11	12
ozarkensis											xx	
pacificus		x		xx								
planulatus												xx
planuloides										xx		
pluripunctatus		xx										
plurisetosus									xx			
pygmaeus	xx	xx	xx	xx	xx		xx	xx	xx			
sallei										xx	xx	
scopaeus									xx	xx	xx	
sculptilis							xx					
seticollis	xx											
sulcifrons												xx
tenuis		x		xx	xx		xx	xx				
tibialis				xx				xx	xx	xx		
tristriatus								xx				
truquii		x		xx								
vandykei			xx									

x- in area, but not in center

xx-in center

Totals, x and xx	6	13	4	13	8	1	6	8	9	9	6	6

Table 73. Dissimilarity values among centers of concentration of the genus *Schizogenius* in North and Middle America.

		Center										
Center	Statistics*	2	3	4	5	6	7	8	9	10	11	12
1	t-c/t x 100	84	70	84	93	100	92	86	80	87	92	92
2	t-c/t x 100	--	82	65	81	100	79	81	86	86	90	90
3	t-c/t x 100	--	--	82	83	100	80	92	85	92	90	90
4	t-c/t x 100	--	--	--	76	100	74	76	77	86	95	95
5	t-c/t x 100	--	--	--	--	100	64	75	88	100	100	100
6	t-c/t x 100	--	--	--	--	--	100	100	100	100	100	100
7	t-c/t x 100	--	--	--	--	--	--	71	87	100	100	100
8	t-c/t x 100	--	--	--	--	--	--	--	76	88	100	100
9	t-c/t x 100	--	--	--	--	--	--	--	--	72	87	93
10	t-c/t x 100	--	--	--	--	--	--	--	--	--	67	80
11	t-c/t x 100	--	--	--	--	--	--	--	--	--	--	75

* + = total taxa

c = taxa in common

Table 74. Index of dissimilarity among areas of concentration of the genus *Schizogenius* in North and Middle America, determined from Table 73.

1*	Area 6	1100
2	Area 12	1015
3	Area 11	996
4	Area 1	980
5	Area 10	968
6	Area 5	960
7	Area 7	947
8	Area 3	946
9	Area 8	945
10	Area 9	931
11	Area 2	924
12	Area 4	910

*Ranked in order from most to least dissimilar.

evident. Curiously, area 2 is more similar in faunal composition to tropical area 4 than to subtropical or temperate areas 1, 9, 10, and 11. Physical barriers, such as the Sierra Nevada, Rocky Mountains, Mexican Plateau, and Colorado Desert, are probably responsible for this pattern.

In general, my areas of concentration for *Schizogenius* correspond fairly well with Erwin's centers of concentration for *Brachinus*, except for lack of a special area in southeastern United States and division of Mexico and Middle America into several separate areas. They are not, however, as well correlated with general climatic patterns, and a more detailed comparison follows.

My area 1 differs from Erwin's center 1 mainly by including arid regions south of the Tehachapi crest. In *Schizogenius*, the Tehachapi isolates *S. falli* from *S. ochthocephalus*, and also isolates distinctive populations of *S. pygmaeus*, but otherwise is not evidently an important barrier. Area 2 differs from Erwin's center 2 by exclusion of western Texas, southern California (area 1), and Baja California (area 3). Although the endemic form in area 3 is most closely related to one in area 1, another form is shared with area 2 but not area 1, and populations of both other species in area 3 are more similar to populations in area 2 than area 1. Areas 10 and 11 correspond closely with Erwin's centers 4 and 3, except that western Texas is included in area 10. Area 12 includes Erwin's center 6 plus part of center 7.

Erwin's center 5 includes approximately my areas 4, 5, 7, 8, and 9. Area 7, which may be an artifact, and area 5 comprise Middle America plus the rest of the area east of the Isthmus of Tehuantepec. This region is not sharply differentiated climatically from areas 4 and 8 in southern Mexico, but probably reflects the past existence of a water gap. Areas 4 and 8 form the rest of the continental tropical region, their northern limits corresponding closely to northern limits of rain-forest formations. When the distributions of the various taxa of area 2 are better known, that area may be found divisible into subunits corresponding at least to the subtropical area 9 and the warm temperate area 10.

In summary, *Schizogenius* species are generally less vagile than *Brachinus* species but more vagile than *Evarthrus* species, and their distribution patterns are accordingly influenced by a balance of factors influencing distributions in *Brachinus* and *Evarthrus*. The riparian gravel bar habitat of most of the species is a further restraining variable, but also one which may permit penetration of otherwise unfavorable climatic zones. The westward extension of area 10, for example, is one which simply follows the Rio Grande drainage system; its *Schizogenius* fauna is depauperate, and contains some elements from area 2, but is still most closely related to the fauna of the rest of area 10.

5.23 Historical zoogeography

5.231 Paleogeography

According to Maldonado-Koerdell (1964), many important events occurred in Mexico and Middle America during Tertiary and Quarternary time. For purposes of this discussion, I use the following time scale, in millions of years before present: Pleistocene and Recent, 0-3; Pliocene, 3-13; Miocene, 13-25; Oligocene, 25-36; Eocene, 36-58; and Paleocene, 58-63. North and South America were separated in Late Paleocene by formation of the Peruvian-Venezuelan geosyncline. During Paleocene and Eocene, the Balsas portal was eliminated, the Sierra Madre Oriental was lifted, the Mexican Plateau began to rise, and Middle America bulged northward to include Jamaica but not Cuba. Near Early Oligocene, Middle America became separated from North America by the Tehuantepec portal, and extended further northward to include Cuba. Early Miocene saw the rise of the Sierra Madre Occidental, continued emergence of the Mexican Plateau, beginnings of volcanic activity in Middle America and along the Neo-Volcanic Axis, and approximate delimitation of modern climatic zones. In Late Miocene, the Tehuantepec portal closed, and Cuba and Jamaica became isolated from Middle America. In Middle Pliocene volcanic activity was generally interrupted, but renewed in Late Pliocene. Also in Late Pliocene, South and Middle America were reconnected, and uplands in the Isthmus of Tehuantepec were formed.

Pleistocene events are more difficult to interpret and collate. Presumably, the first two million years of the period were marked by a general deterioration in climate, followed in the last million years by a series of four major glaciations; the last of these glaciations, the Wisconsin, commenced about 100,000 years ago. In Mexico and Middle America, intermittent but intense volcanic activity occurred throughout the Pleistocene. The climate was probably warm humid in Late Pliocene, cool humid in Early Pleistocene, and cool dry during the first glaciation.

Subsequently the climate vaired cyclically through warm dry to warm humid during interglacials, returning through cool humid to cool dry during glaciations. Montane glaciers in central Mexico descended to as low as 2450 m, or about half the lower limits of present remnants of these glaciers. These observations suggest that climatic conditions at low elevations even in the south fluctuated, and in particular tropical conditions probably did not extend north of the Neo-Volcanic axis during glacial maxima.

5.232 Evolutionary and phylogenetic rates

As discussed in section 4.11, evolutionary and zoogeographic pathways developed interdependently, and phylogenetic and zoogeographic analyses should therefore be compatible with one another. One method for testing for compatibility is to correlate the reconstructed phylogeny with known or suspected paleogeographical events. To do this, I determined an average time between branching points in the reconstructed phylogeny, based on assumptions discussed in section 4.12; this method was tested and found useful for comparing phylogeny and zoogeography in *Brachinus* (Erwin, 1970) and *Evarthrus* (Ball and Freitag, *in* Freitag, 1969) in section 4.14. The average time between branching points was determined to be about 3,000,000 years, from the following lines of evidence and reasoning.

For Hawaiian birds, Bock (1970) suggests that time required for speciation may range between 100,000 and 1,000,000 years. For recent European mammals, Kurten (1968) suggested a time range of between 30,000 and 3,000,000 years; his upper limit corresponds to Early Pleistocene, while the lower limit may at least in part reflect inadequate knowledge. According to Halffter (1964), La Brea (Pleistocene) insects are no more than subspecifically distinct from extant species, though their distributions may have changed greatly. Several lines of evidence suggest that, for speciation in *Schizogenius* and other continental North American carabid beetle genera except those with highly insular distributions such as *Scaphinotus* (see Ball, 1966), Kurten's upper limit may be close to an average figure.

The ancestor of *Schizogenius* entered South America after formation of the Panamanian portal in Late Paleocene, no more and probably less than 60,000,000 years ago. According to my reconstructed phylogeny (Fig. 257-258), a minimum of 16 branching points are required to reach back to the common ancestor of American *Halocoryza* and *Schizogenius*. Thus the maximum possible time between branching points is 4,000,000 years. According to Halffter (1964), fossils in Upper Oligocene-Lower Miocene amber from Semojovel, Chiapas, about 25,000,000 years in age, include nine species of beetles, all extinct, as so far studied. These are arrayed in seven genera, five of which are extant. In the same amber deposit is a species of the carabid bembidiine genus *Tachys*, said to be related to living species (T. L. Erwin, *in litt.*). The extinct genera may represent sideline extinctions, or ancestral forms, and relationships of the extinct species of extant genera are unclear. But the *Tachys* specimen, at least, implies that existing species groups may already have evolved at that time. Therefore, the genus *Schizogenius* had probably evolved by at least Late Oligocene, and had probably even differentiated into at least the major lineages, such as the *truquii* lineage, by then. If the ancestor of *Schizogenius* had diverged from *Halocoryza* by Late Oligocene, but not yet differentiated into subgenera, the average time between dichotomies would be about 1,500,000 years. If the *truquii* lineage had differentiated by this time from its sister group, but not yet undergone radiation, the time required between dichotomies would be close to 3,000,000 years. In short, evidence from Semijovel amber suggests that at least the ancestor of *Schizogenius* had evolved by Late Oligocene, and that probably some differentiation had taken place.

Matthews (*in* Hopkins, et al., 1971) discussed a Late Pliocene insect fauna from the Bering Strait region, dated at approximately 5.7 million years. Among carabid beetles reported in this paper, some apparently represent extant species, while others probably represent extinct species closely related to extant forms. These data are significant in their implications of old age for living species of carabid beetles.

Faunal exchanges between Middle and South America offer a further clue to the age of the most recent dichotomies. Only three lineages are likely to have crossed over the Panamanian portal. I think that shortly after this water gap closed, one invasion of South America and three of Middle America occurred, and resulted in differentiation of distinctive species. I judge that these events took place between three and five million years ago, more probably three million years because there is no reason to believe immigration proceeded immediately. The Panamanian area is still evidently a significant barrier to the dispersal of *Schizogenius* species, as only two modern species are known from both Middle and South America.

Another general line of evidence concerns Pleistocene events in North America. In *S. falli*, there is statistical evidence of rapid change in a single characteristic over a short period of time in one area: 50 years, in the Dragoon Mountains of southern Arizona. In *S. depressus*, there is statistical evidence that differentiation of eastern and western groups of populations in the southwestern United States has taken place within the last 10,000 years. Perhaps in the north further differentiation has developed much more recently, as a result of character displacement. Also in the north, however, is evidence that genetic differentiation but not speciation is associated with much earlier Pleistocene events; at least Wisconsin (100,000 years), and more probably Nebraskan (1,000,000 years). My reasoning here presumes that the northern forms became isolated in early Pleistocene because of deteriorating climatic conditions, were subsequently alternately completely and partially isolated, and that by the first interglacial were partly genetically isolated. The common ancestor of the closely related but grossly disjunct *S. sulcifrons* and *S. litigiosus* was probably transcontinental in Early Pleistocene, but with the deterioration of climate formed eastern and western isolates before the Nebraskan glaciation. Similarly, I suspect that geographic isolates of the common ancestor of *S. planulatus* and *S. ozarkensis* formed in Early Pleistocene, before the onset of glaciation. Alternatively, one might date the initial isolations of *S. sulcifrons* from *S. litigiosus* and *S. planulatus* from *S. ozarkensis* as no earlier than the beginning of Wisconsin glaciation. But this would suggest that the entire evolution of the genus may have taken place within the last 2,000,000 years. If these isolations occurred in Early Pleistocene, however, they may be dated as about 3,000,000 years and thus agree with datings from other evidence.

A particularly difficult problem is posed by those species complexes in which included species are allopatric but proximate. If their ranges have long been proximate, and fixed, a period of 3,000,000 years seems difficult to explain. But boundaries unquestionably were not always contiguous, they most likely are not fixed, and there are doubtless interactions along these boundaries. Competitive exclusion (Mayr, 1963) is the probable reason for maintenance of proximate but allopatric distributions in *Schizogenius* species. For instance, *S. pluripunctatus* and *S. kulti* probably were isolated by Late Pliocene or Early Pleistocene vulcanism along the Neo-Volcanic Axis, in agreement with my suggested 3,000,000 year time limit. Subsequently, geographic isolation was maintained by competitive exclusion, but boundaries shifted northward with the northward extension of tropical climates after the end of the Pleistocene. If two species which are closely related or which are particularly similar in ecological requirements inhabit adjacent river systems, or separate segments of a single river, their distributions are unlikely to overlap. Undoubtedly, there is contact on an individual basis, as individuals migrate away from parental habitat. Evidence that this does happen is found in allopatric components of a species complex such as in *S. falli* and *S. ochthocephalus* or in *S. kulti* and *S. pluripunctatus*, or even in eastern and western forms of *S. depressus* in northwestern United States. Where ranges approach one another, proximate populations tend to be the most strongly differentiated, which, I think, is evidence of character displacement (Brown and Wilsen, 1956). I have used this observation, of interrupted gene flow, as one criterion for species recognition. But I think such patterns are best explained as the result of interspecific interaction. In northeastern Mexico, where *S. scopaeus* and *S. pygmaeus* are parapatric or sympatric in distribution they are also strongly differentiated morphologically and, probably, ecologically; elsewhere, where less strongly differentiated, they are allopatric. Near their boundary in the Big Bend Region of the Rio Grande, they probably are not strongly differentiated ecologically, and in that region they show evidence of character displacement in form of male median lobe.

In summary, the separation of North and South America in Late Paleocene suggests an upper limit for the age of ancestral *Schizogenius* of 60,000,000 years, and paleontological evidence from the Semijovel fossils suggests a lower limit of 25,000,000 years. In turn these datings suggest that intervals between dichotomies in the most complete lineage of the reconstructed phylogeny of the genus are at most 4,000,000 years and at least 1,500,000 years. The timing of overland faunal exchanges between South and Middle America, and Pleistocene events in North America, suggest that this interval is approximately 3,000,000 years. This is a crude approximation, and is an average, not a constant. For purposes of correlation with other paleogeographic events, an error of 20% is probably admissible; also, subtraction or addition of a dichotomy will not invalidate this interval as a working proposition.

With a 3,000,000 year interval between dichotomies, I judge that the common ancestor of *Schizogenius* evolved some 50,000,000 years ago, about Middle Eocene. Ancestors of the *ferrugineus* group, the *truquii* lineage, and the *crenulatus* group entered North America in Late Eocene, Middle Oligocene, and Middle Miocene, respectively. These suggested historical events are compared with paleogeological events in the following section. This 3,000,000 year interval is the basis of the time scale shown in my reconstructed phylogeny (Fig. 255-258).

5.233 Vicariance and historical zoogeography

In this section, I deal briefly with matters of vicariance and historical zoogeography pertaining to minor groups and lineages of the genus *Schizogenius* that have penetrated North and Middle America, and at some length as they apply to the *truquii* lineage.

The origin of the subgenus *Genioschizus* took place in South America about 48,000,000 years ago. This group is now poorly represented, with three closely related species groups, and extinctions undoubtedly account for its present lack of diversity. The ancestor of the *crenulatus* group entered Middle America in Early to Middle Miocene. No existing species are now known from Middle America, though the possibility that one may exist cannot be ruled out. The ancestor of living taxa entered southwestern North America after closure of the Tehuantepec portal, probably in Middle to Late Pliocene, and extended northward into the Sonoran region. Southern and northern isolates formed in Early Pleistocene because of orogenic activity in the Neo-Volcanic Axis, but, with northward extension of tropical climates in more recent times, their boundary shifted northward to its present location near the Tropic of

Cancer. The two living subspecies of *S. crenulatus* are north-south vicariants. Two other members of the subgenus *Genioschizus* represented in North and Middle America are distantly related members of the *tenuis* group. Ancestral *S. sculptilis* entered Middle America in Early Pleistocene, and extended westward as far as the Usumacinta-Grijalva area; this species probably remains a component of the Middle American fauna. More recently, *S. tenuis* has extended northward from Colombia through Middle America, as far as the northern limits of the tropics in eastern Mexico and the northern limits of the subtropics in western Mexico.

As do members of the subgenus *Genioschizus*, and at least *S. lindrothi* of the *lindrothi* group, members of the *ferrugineus* group are found mainly in sandy habitats. I suggest a particularly early entry into Middle America for this group, perhaps Early Eocene, before the Tehuantepec portal opened. The group is characterized by lack of diversity, no close relationship among existing species, and by widespread distributions of living species. The two existing species are largely allopatric, but are not true sister species and therefore vicariant relationships are doubtful. The group is not represented in far western United States, Florida, or eastern Mexico. These gaps in distribution are difficult to explain. *S. ferrugineus*, or a related form, may until comparatively recently have been represented in subtropical Florida, but displaced by the immigrant *S. lindrothi*. The distribution of *S. lindrothi*, Middle America and Florida, suggests that early distributions of the *ferrugineus* group may have followed a similar pattern. But if my conclusions about timing are correct, Florida did not then exist as such, and, further, there was no barrier to dispersal at the

Isthmus of Tehuantepec. The present continuity of range of the two species suggests that Middle America and southern Mexico were depopulated of the group for a long time, with extinction of tropic-subtropic elements initiated in Late Oligocene or Early Miocene. This may have been caused in part by orogenic activity and in part from displacement by newer immigrants of the *truquii* lineage. Surviving forms became adapted to temperate conditions in northeastern North America. A later isolate subsequently became established in the Sonoran area, from which it successfully penetrated southward along the Pacific coast of Mexico, and beyond to the southern limit of Middle America.

Other minor lineages represented in North and Middle America are the *lindrothi* and *optimus* groups, each with distinctive vicariant sister species in Middle and South America. Ancestors of Middle American species arrived there in Early Pleistocene. *S. lindrothi* subsequently became distributed across the Gulf of Mexico to peninsular Florida, where it may have displaced *S. ferrugineus* from sandy habitats in subtropical regions. Although Middle American and Floridian forms of *S. lindrothi* are quite distinctive, I suspect the species may also be represented in the West Indies, particularly in areas of Caribbean pines as discussed by Mirov (1967).

The ancestor of the *truquii* lineage passed through Middle America into southern Mexico in Middle Oligocene, over the Tehuantepec and Panamanian portals. After reaching tropical Mexico, it gave rise to two lineages, one centered in southwestern Mexico and the other in northeastern Mexico. One lineage is today represented by a single species and species group, *S. truquii*. The other lineage diversified into seven species groups, comprising the main part of the genus represented at present in North and Middle America.

The major part of the evolutionary history of the *truquii* lineage unfolded in Mexico and the southern part of the United States. To analyze the zoogeography of this lineage, I made detailed comparisons between species for geographic distributions, geographic variation, and vicariance, and refined limits for the areas of concentration in Fig. 263 accordingly. Resulting major areas of vicariance are shown in Fig. 264. Vicariance areas 1 and 6 are peripheral, corresponding approximately to concentration areas 1, 5, 6, 7, 11, and 12. High altitude regions of northern and central Mexico form a potent barrier to the dispersal of *Schizogenius* species, as suggested by greater dissimilarity between eastern and western areas of concentration than between northern and southern areas. Area 2 excludes all portions of the Colorado River except the Gila system, in recognition of northern limits of numerous species. Area 5 was recognized as separate from area 2 to account for northern limits of several southern species, to conform with distributional limits of *S. depressus*, and to exclude certain species endemic to area 2. And the northwestern limit of area 3 was refined to exclude *S. depressus*.

Vicariance areas 2 and 3, Sonoran and Texan regions, have similar latitudinal limits, and climates that may be described as warm temperate. Vicariance areas 4, 5, and 6 may be described as subtropical regions, respectively the Baja Californian, Sinaloan, and Tamaulipan regions. All these areas represent broad climatic zones; their boundaries are inexact, and surely have not been constant in the past. Probably, for example, northern boundaries of tropical areas 7 and 8 shifted southward to the Neo-Volcanic Axis during Pleistocene glacial maxima. These suggested boundaries are intended only to describe general, climatically limited, centers of speciation, not specific areas of distribution. Thus, exact locations of some boundaries such as those between areas 5 and 7 in the west and between areas 3 and 6 in the east are quite arbitrary, but this defect is more apparent than real. Other boundaries, as between areas 6 and 8, do represent abrupt faunal limits, but as noted above have not been constant over long periods of time.

Fig. 265-269 are vicariance maps showing evolutionary and zoogeographic pathways for species groups of the *truquii* lineage, and for taxa included in the *pluripunctatus*, *tristriatus*, *longipennis*, and *depressus* groups. These vicariance relationships were described in section 4.3 on the phylogeny of the *truquii* lineage, and following is a correlation of evolutionary and zoogeographic pathways with paleogeological events.

When the ancestor of the *truquii* lineage arrived in North America in Middle Oligocene, orogenic activity in Mexico was minimal. After divergence into eastern and western lineages in Late Oligocene distributions of the ancestors of these lineages were maintained initially through competitive exclusion. In Early Miocene, orogenic and volcanic activity commenced along the Neo-Volcanic Axis and Sierra Madre Occidental, rendering vicariance areas 2, 5, and 7 relatively inhospitable for colonization. In areas 3 and 6, however, no mountain building took place then or subsequently, and these areas were thus particularly suitable for speciation of *Schizogenius* species.

Nothing certain can be said of the zoogeographic history of the *truquii* group. Doubtless some species diversification did take place, and doubtless vicariance was a factor, but all species except *S. truquii* subsequently disappeared. Limitations of habitat caused by orogenic disturbances hindered evolution of the group, and when elements of the more progressive sister group entered regions formerly occupied by members of the *truquii* group, the latter were simply eliminated.

Most early diversification in the rest of the *truquii* lineage, before Middle Pliocene volcanic quiescence, took place in Atlantic areas 3, 6, and 8, and resulted from isolations caused by shifts in climatic tolerance. The ancestor of the *arimao* subgroup of the *depressus* group entered Middle America over the Tehuantepec portal in Late Miocene, and spread to Cuba before the West Indies separated from Middle America. Also in Late Miocene or Early Pliocene, the ancestor of the *pluripunctatus* group entered the northern part of area 2, north of the intense tectonic activity in the Sierra Madre Occidental region. In Fig. 265 I show the split of the ancestor of the *truquii* group from its sister group in southern Mexico, latitudinal vicariance shifts in the ancestry of other groups in the lineage, and the immigration to the Sonoran region of the ancestor of the *pluripunctatus* group.

During the long geological quiescence of Middle Pliocene, ancestral elements of the *pluripunctatus* group became firmly entrenched in the Sonoran region, and spread westward and southward from there. One form, the ancestor of *S. seticollis*, became isolated in California, and spread into southern Baja California; in Early Pleistocene, in turn, this southern form became isolated as the ancestor of the living subspecies *S. s. vandykei*. Another form, the ancestor of *S. plurisetosus* and *S. multisetosus*, became isolated in southern Mexico in Late Pliocene, perhaps by renewed volcanic activity in the Neo-Volcanic Axis. Vicariance patterns in the *plurpiunctatus* group were completed in Early Pleistocene when ancestral forms of *S. pluripunctatus* and *S. kulti*, and of *S. plurisetosus* and *S. multisetosus* were divided into tropical and subtropical isolates, perhaps also by vulcanism in the Neo-Volcanic Axis. Subsequently, northern limits of the tropical forms shifted northward to their present locations, and the more progressive *S. kulti* displaced the more conservative *S. multisetosus* from most lowland parts of its range. These events are summarized in Fig. 266.

No elements of the *tristriatus* group evolved in Pacific drainage systems (Fig. 267), although one species, *S. tibialis* (Fig. 188), has successfully penetrated the area. The ancestor of one species, *S. tristriatus*, reacquired tropical adaptations in Late Miocene or Early Pliocene, but probably never did penetrate south of the then active Neo-Volcanic Axis. The ancestor of its sister group, which had retained subtropical adaptations, subsequently differentiated into warm temperate and subtropical lineages. Of the subtropical lineage, differentiation into subtropical and tropical forms led to the speciation of *S. dilatus* and *S. tibialis*. Ancestral *S. tibialis* spread southward to the Isthmus of Tehuantepec, from there into the Rio Balsas and Rio Grande de Santiago drainages, and returned northward across the highlands of central Mexico into subtropical area 6 and even into southermost warm temperate area 3. Zoogeographic history of the warm temperate ancestor of the *amphibius* and *planulatus* subgroups was one of a tendency to acquire cool temperate adaptations. In Middle Pliocene, ancestral *S. amphibius* became isolated in cool temperate area 1 and subsequently spread into the Appalachian region, to which it was restricted in Pleistocene time. In Late Pliocene, the ancestor of *S. planulatus* and *S. ozarkensis* was isolated in the cool temperate area, and differentiated into those species in Pleistocene.

The ancestor of the *longipennis* group (Fig. 268) was the first element of the subtropical and warm temperate adapted branch of the *truquii* lineage to return to tropical areas and extend south of the Neo-Volcanic Axis. In Middle Pliocene, a western vicariant, ancestor to *S. pacificus*, spread through western areas 5 and 7. The eastern vicariant followed later, and in Late Pliocene the ancestor of *S. chiricahuanus* was isolated in area 2 by renewed volcanic activity in the Neo-Volcanic Axis. In Early Pleistocene, the ancestor of *S. neovalidus* and *S. longipennis* spread into area 2, and ancestral *S. neovalidus* became isolated there by Pleistocene events. More recently, the progressive *S. longipennis* also extended northward into area 2, and displaced the more conservative *S. chiricahuanus* and *S. neovalidus* from most parts of their ranges except relict higher elevation strongholds.

The ancestor of the *arimao* subgroup (Fig. 269) acquired tropical adaptations in Late Miocene, and was the only member of the *truquii* lineage to enter Middle America over the Tehuantepec portal. Indeed, it was the only North American member of the genus to enter Middle America before Late Pliocene elevation of the Isthmus of Tehuantepec. This ancestral form spread into Cuba before severance of Cuba from the mainland, but since Early Pliocene *S. arimao* evolved in isolation. The ancestor of remaining Middle American forms differentiated into the ancestors of *S. emdeni* and *S. "apicalis"*. In Early Pleistocene, after closure of the Panamanian portal, South America was penetrated and widely colonized by the ancestor of *S. "apicalis"*.

The ancestor of the rest of the *depressus* group entered warm temperate Texas, and differentiated into one line that continued to evolve there and another that became isolated in cool temperate areas. The cool temperate form spread across northern parts of the continent, and differentiated into modern *S. litigiosus* and *S. sulcifrons* in Early Pleistocene. In Middle Pliocene, the long period of volcanic quiescence in the west, one line of the *depressus* subgroup became isolated in the Sonoran Region. The ancestor of *S. depressus* penetrated northward, acquired cool temperate adaptations, and subsequently extended southward through the Sonoran region into high elevation areas of central Mexico. In Early Pleistocene, another cool temperate form, ancestor of *S. ochthocephalus*, was isolated in northern California. Its sister species spread southward through area 5 into northern parts of area 7, northward into the Colorado River area of western part of area one, and eastward into area 3 from which it spread north into central parts of area 1 and south into area 6. Zoogeographic origins of *S. pygmaeus* and *S. scopaeus* are less well shown in Fig. 269. Their ancestor was widespread in eastern areas 3, 6, and 8 in Middle Pleistocene, but Late Pliocene vulcanism resulted in northern and southern isolates. In Late Pliocene or Early Pleistocene, the ancestor of the northern form spread westward into the Sonoran region, and formed an isolate there. This western form spread northward into California, and southward into southern Mexico where it reestablished genetic contact with the southern isolate. By Late Pleistocene, however, reproductive isolation had developed between the form in Texas, ancestral to *S. scopaeus*, and the southern form which, reconnected with the Sonoran form, constitutes modern *S. pygmaeus*. Also in Late Pleistocene, Californian *S. pygmaeus* evolved into statistically differentiated northern and southern isolates.

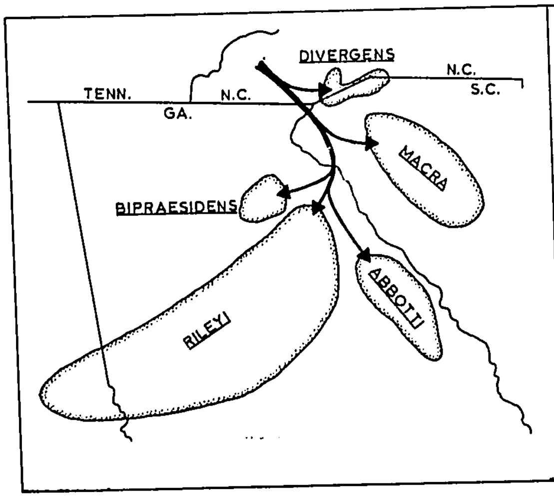
With this background, more can be said about distribution of the *ferrugineus* group. Probably before entry of the *truquii* lineage into the area, ancestral forms of the *ferrugineus* group were represented throughout Mexico and southern United States. Paleogeological events in southern and western Mexico from early Miocene contributed to elimination of the group from that area. Concurrently, spread of progressive and actively evolving members of the *truquii* lineage into eastern areas 3. 6, and 8 resulted in displacement of members of the *ferrugineus* lineage from that entire region. One line did reach cool temperate areas of central and eastern United States, and there perfected adaptations to life in sandy habitats, and, consequently, was not eliminated when gravel bar adapted forms of the *truquii* lineage penetrated cool temperate regions. Western United States meanwhile may have been generally untenable for colonization by members of the *ferrugineus* lineage because of tectonic and orogenic activity. Alternatively, members of the group living there lacked special adaptations and were displaced by more progressive elements of the *truquii* lineage from Middle Pliocene onward. In Middle Pliocene, however, the ancestor of *S. auripennis* succeeded in penetrating the Sonoran region, and subsequently extended southward into tropical regions as far as southern Middle America, and special adaptations prevented competitive displacement by members of the *truquii* lineage.

Before Early Pliocene, members of relatives of the *truquii* group may well have occupied the Sonoran region and perhaps even California, but since then and particularly since Middle Pliocene were in competition with members of more advanced lineages, and gradually eliminated. A study of ecological specializations of *S. truquii* might reveal reasons for its apparent success in continued survival.

Little can be said about the evolutionary and zoogeographic histories of the monotypic *brevisetosus*, *sallei*, and *lineolatus* groups, all with probable Texan origins (Fig. 265). *S. brevisetosus* seems a relict species, and other elements of the *brevisetosus* group may have been eliminated through competitive displacement by other forms with better developed limestone adaptations (see section 4.3). Curiously, the known distribution of *S. brevisetosus* is allopatric in relation to distributions of members of the *pluripunctatus* group, despite loss of limestone adaptations of the latter. In contrast, distributions of *S. sallei* and *S. lineolatus* are not evidently relict, and within their respective ranges both tend to be numerically dominant over all others in the genus. Perhaps the relatively great vagility of these species is a partial explanation of the absence of close relatives; if new areas are colonized, gene flow tends to continue, and no geographic isolation results. The only clear exception to this pattern is in the Rio Grand isolate of *S. lineolatus*. I suspect this form is a relict from cooler Pleistocene times, when the distribution of the northern form of the species extended further south than it presently does.

In summary, my reconstructed phylogeny seems completely compatible with what is known about paleogeological events, and I think I have described evolutionary and zoogeographic pathways that have a high probability of correctness. It is my hope that future workers will test these hypotheses in comparative studies on ecology, physiology, biochemistry, and larval taxonomy.

Fig. 259-260. Evolutionary zoogeography of the milliped genus *Cleptoria*. 259. As suggested by R. L. Hoffman (after Hoffman, 1967). 260. As reinterpreted. Fig. 261. Numbers of species of *Schizogenius* in 5° intervals, as used in Table 70.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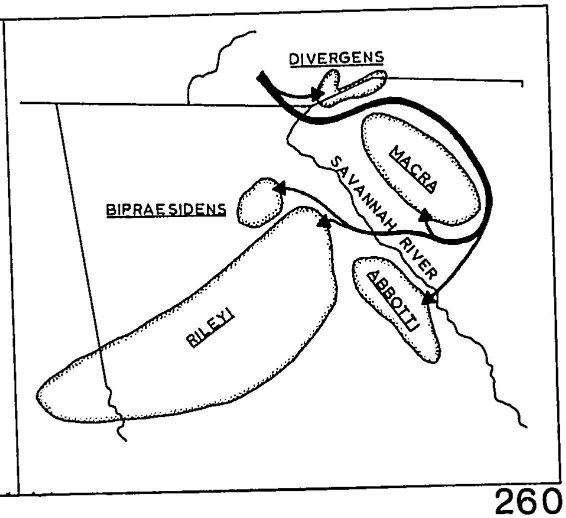
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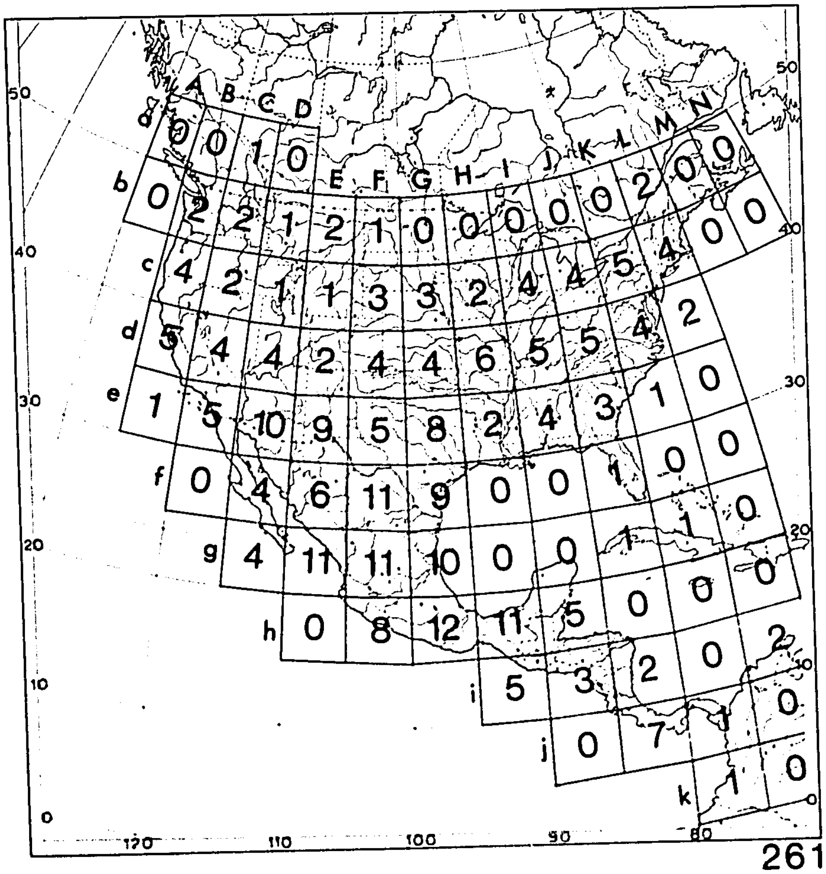
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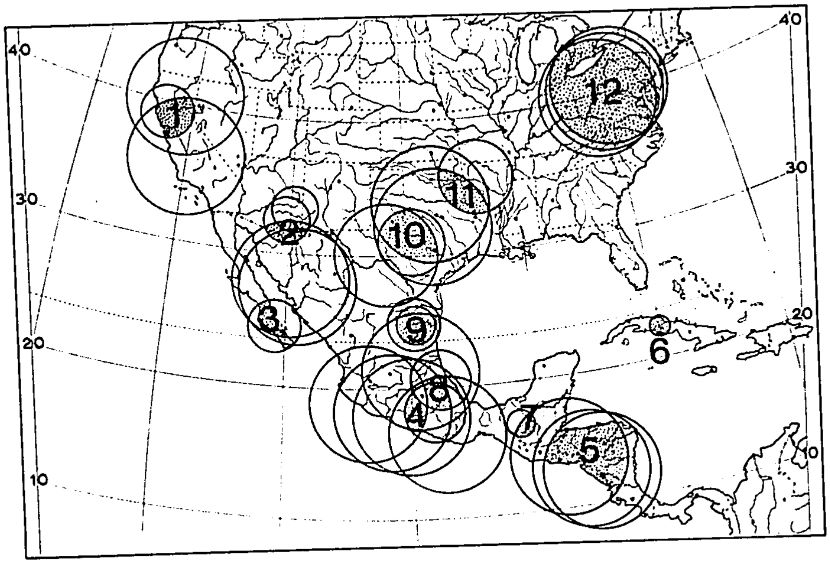
Fig. 262. Centers of concentration of species of the genus *Schizogenius* in North and Middle America. Fig. 263. Areas of concentration of species of the genus *Schizogenius* in North and Middle America. Fig. 264. Areas of vicariance for species of the genus *Schizogenius* in North and Middle America.



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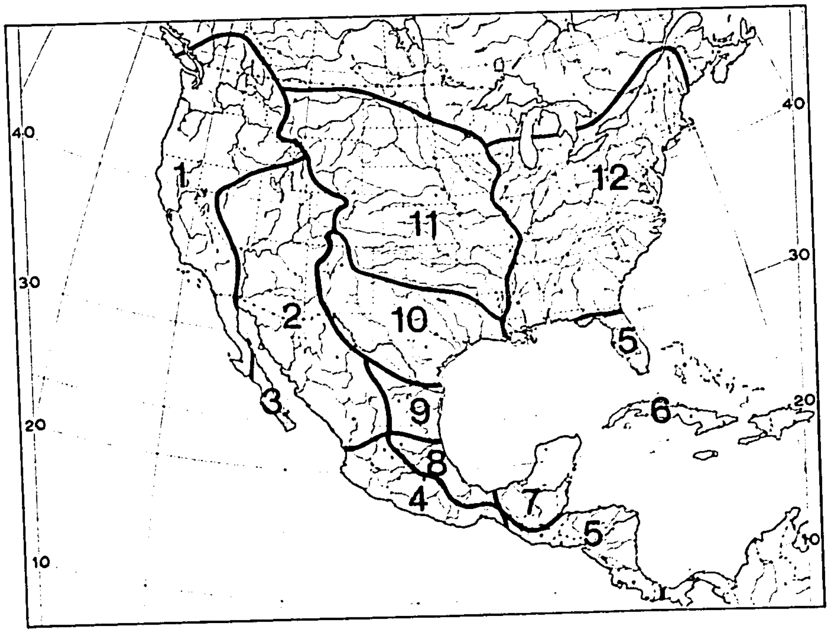

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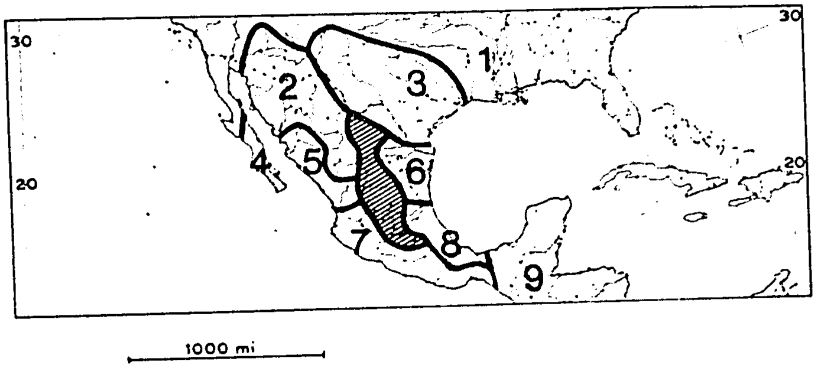

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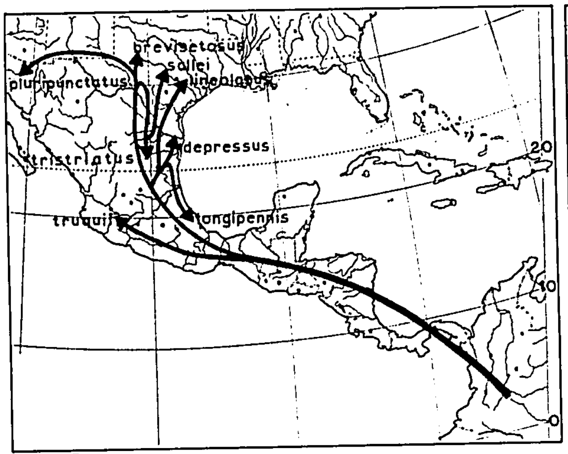
Fig. 265-269. Evolutionary zoogeography. 265. Species groups of *truquii* lineage. 266. Species and subspecies of *pluripunctatus* group. 267. Species of *tristriatus* group. 268. Species of *longipennis* group. 269. Species of *depressus* group.



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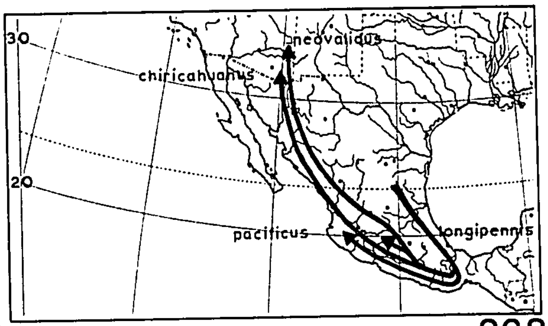

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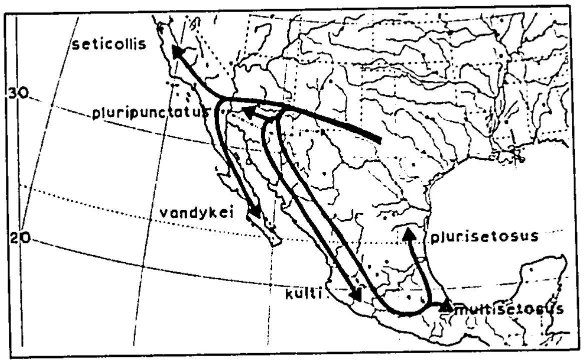

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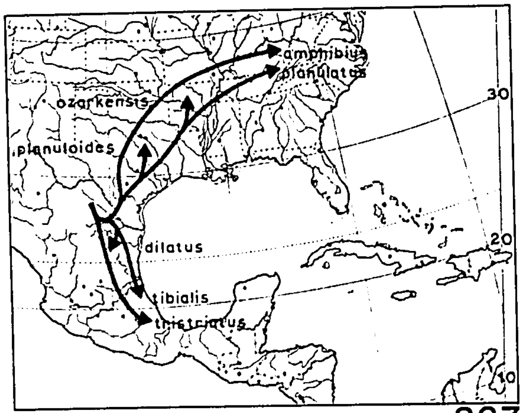

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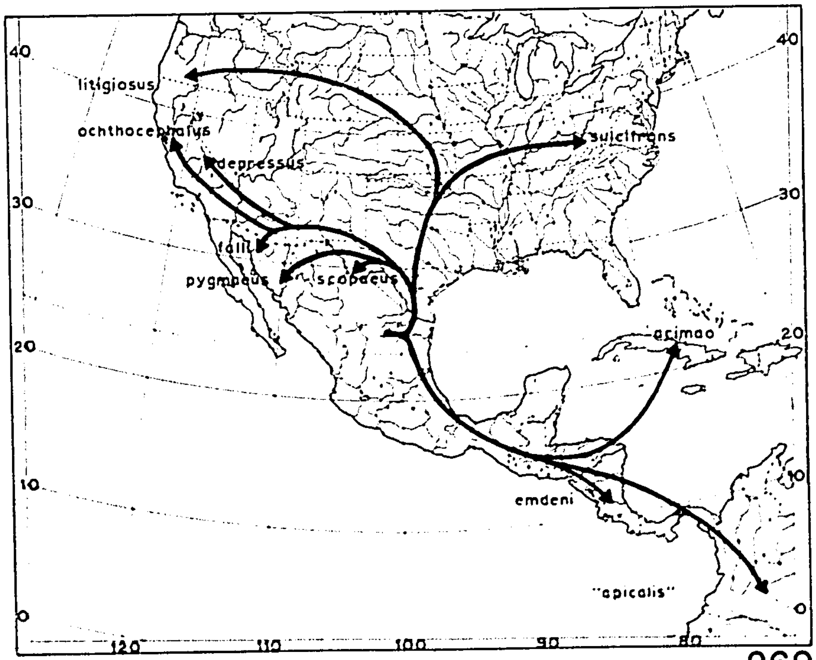

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