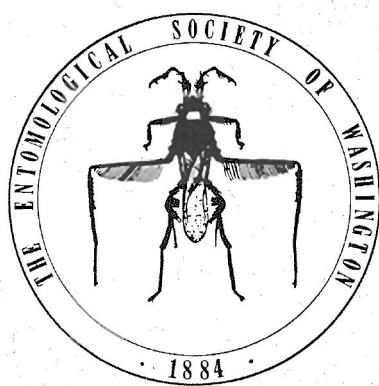


THE GENERA OF
ELAPHIDIINI THOMSON 1864
(COLEOPTERA: CERAMBYCIDAE)



BY

STEVEN W. LINGAFELTER

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This work is dedicated to

Dr. Byron Alexander

with appreciation for his inspiring talent and dedication
to teaching, research, and scientific illustration.

TABLE OF CONTENTS

Abstract	6
Introduction	7
Taxonomic History	7
Distribution and Diversity	8
Special Problems Associated with Monotypic Taxa	8
Biology and Natural History	8
Materials and Methods	9
Cladistic methods	9
Choice of taxa	9
Unavailable and fossil taxa	9
Specimen preparation	10
Character descriptions and states	10
Characters not used in analyses or key	12
Characters used in key only	12
Characters used in analyses	12
Implied Weighting Method of Parsimony	30
Phylogenetic analyses	32
Results of Phylogenetic Analyses	33
Discussion of Implied Weighting Consensus Tree	33
Discussion of Subset of Obtained Trees: The Five Shortest, Fittest Trees of the Implied Weighting Analysis	38
Problematic Taxa and Discussion of Outgroup	38
Summary of Classification Changes	39
Generic Treatment	40
Tribe Elaphidiini	41
<i>Adiposphaerion</i>	47
<i>Ambonus</i>	49
<i>Amethysphaerion</i>	49
<i>Aneflomorpha</i>	50
<i>Aneflus</i>	51
<i>Anelaphus</i>	52
<i>Anopliomorpha</i>	52
<i>Anoplocurius</i>	53
<i>Apoclausirion</i>	55
<i>Aposphaerion</i>	55
<i>Appula</i>	55
<i>Astromula</i>	56
<i>Atharsus</i>	56
<i>Atylostagma</i>	57
<i>Castiale</i>	57
<i>Centrocerum</i>	57
<i>Clausirion</i>	58
<i>Conosphaerion</i>	58
<i>Curtomerus</i>	60
<i>Elaphidion</i>	60
<i>Elaphidionopsis</i>	61
<i>Enaphalodes</i>	62
<i>Etymosphaerion</i>	63
<i>Eurysthea</i>	63
<i>Eustromula</i>	63
<i>Gymnospyra</i>	64
<i>Hemilissopsis</i>	64
<i>Ironeus</i>	65
<i>Linsleyonides</i>	65
<i>Mallocera</i>	67
<i>Meganeflus</i>	67
<i>Megapsyrassa</i>	68
<i>Mephritus</i>	68
<i>Metironeus</i>	69

<i>Micraneflus</i>	70
<i>Micranoplium</i>	70
<i>Micropsyrassa</i>	70
<i>Miltesthus</i>	72
<i>Minipsyrassa</i>	73
<i>Miopteryx</i>	73
<i>Morphaneflus</i>	74
<i>Neaneflus</i>	74
<i>Neomallocera</i>	74
<i>Neoperiboenum</i>	75
<i>Nephaliodes</i>	75
<i>Nesanoplium</i>	76
<i>Nesiosphaerion</i>	76
<i>Nesodes</i>	77
<i>Nyssicostylus</i>	77
<i>Nyssicus</i>	79
<i>Orwellion</i>	79
<i>Pantonyssus</i>	80
<i>Paramallocera</i>	80
<i>Parasphaerion</i>	81
<i>Parastizocera</i>	81
<i>Parelaphidion</i>	82
<i>Periboenum</i>	82
<i>Piezophidion</i>	84
<i>Pilisphaerion</i>	84
<i>Poecilomallus</i>	85
<i>Protomallocera</i>	85
<i>Protosphaerion</i>	86
<i>Pseudomallocera</i>	86
<i>Pseudoperiboenum</i>	87
<i>Psyrassa</i>	87
<i>Psyrassaforma</i>	88
<i>Rhomboidederes</i>	89
<i>Romulus</i>	89
<i>Sphaerioeme</i>	89
<i>Sphaerion</i>	91
<i>Sphaerionillum</i>	92
<i>Stenelaphus</i>	92
<i>Stenosphenus</i>	93
<i>Stizocera</i>	93
<i>Terpnissa</i>	94
<i>Trichophoroides</i>	96
<i>Tropimerus</i>	97
Key to Genera of Elaphidiini	98
Conclusion	106
Acknowledgments	106
Literature Cited	107
Appendix 1: Taxa Used in Phylogenetic Analyses	114
Appendix 2: Provisional Ingroup Genera Not Represented in Phylogenetic Analyses	115
Index	116

Abstract.—A generic-level phylogenetic analysis of the tribe Elaphidiini Thomson 1864 (Coleoptera: Cerambycidae) is presented. Cladistic methods using morphological features and implied weighting parsimony were employed. The monophyly of the tribe is weakly supported by presence of antennal carinae, tibial carinae, and an abruptly rounded anterior margin of the mesonotum. Based on the results of the implied weights phylogenetic analysis and classificatory decisions, the following taxonomic changes are made: Four genera are transferred into other tribes and six genera are synonymized leaving 77 genera in Elaphidiini. Phoracanthini Lacordaire 1869 is removed from Elaphidiini and resurrected as a tribe with *Phoracantha* Newman 1840b as the type genus. *Cordylomera* Serville 1834 and *Allotraeus* Bates 1887 are not elaphidiines and are tentatively returned to Phoracanthini. *Championa* Bates 1880, and *Orion* Guérin-Méneville 1844 are removed from Elaphidiini and placed as *incertae sedis* in Cerambycinae. The following six new generic synonymies are proposed: *Eutrichophoroides* Linsley 1961b and *Neotrichophoroides* Linsley 1961b both = *Trichophoroides* Linsley 1935a. *Nesostizocera* Linsley 1961b = *Stizocera* Audinet-Serville 1834. *Hemistizocera* Linsley 1961b = *Psyrassa* Pascoe 1866. *Peranoplium* Linsley 1957b = *Anelaphus* Linsley 1936. *Axestinus* LeConte (1873) = *Aneflus* LeConte (1873). The following 29 new combinations are proposed: *Aneflus obscurus* (LeConte 1873), *Anelaphus eximium* (Bates 1885), *Anelaphus hoferi* (Knull 1934b), *Anelaphus inornatum* (Chemsak and Linsley 1979), *Anelaphus maculatum* (Chemsak and Noguera 1993), *Anelaphus piceum* (Chemsak 1962), *Anelaphus simile* (Schaeffer 1908), *Anelaphus subdepressum* (Schaeffer 1904), *Anelaphus tuckeri* (Casey 1924), *Anelaphus undulatum* (Bates 1880), *Psyrassa cribricollis* (Bates 1885), *Stizocera atiaia* (Martins and Napp 1983), *Stizocera caymanensis* (Fisher 1941), *Stizocera dozieri* (Fisher 1947), *Stizocera floridana* (Linsley 1949), *Stizocera insulana* (Gahan 1895), *Stizocera jassuara* (Martins and Napp 1983), *Stizocera phtisica* (Gounelle 1909), *Stizocera poeyi* (Guérin-Méneville 1838), *Stizocera punctiventris* (Cazier and Lacey 1952), *Stizocera submetallicus* (Chemsak and Linsley 1968), *Stizocera suturalis* (Martins and Napp 1992), *Stizocera vanzwaluwenburgi* (Fisher 1932), *Stizocera wagneri* (Gounelle 1913), *Trichophoroides albisparsus* (Bates 1872), *Trichophoroides jansoni* (Bates 1885), *Trichophoroides aurivillii* (Linsley 1961), *Trichophoroides decipiens* (Bates 1880), *Trichophoroides pilicornis* (Fuchs 1961). Diagnoses of all genera are presented with notes on distribution, diversity, and relationships. A key to genera of Elaphidiini is presented.

INTRODUCTION

The Elaphidiini is among the most generically diverse tribes in Cerambycidae. Seventy-seven genera and over 520 species are currently known for this group of wood-boring beetles. Most species are nocturnal, and in some regions of México at certain times of the year, elaphidiines are the most abundant cerambycids attracted to lights. As currently defined, elaphidiines occur from Canada to South America, with the greatest species diversity in the warmer latitudes. Characters to define and diagnose genera have rarely been found or applied in this group, and the morphological similarity among genera has precipitated its confused taxonomic history. With this study, I present an overview of what is known on the taxonomy, diversity, and biology of Elaphidiini. I developed a list of explicitly defined characters and states for all elaphidiine genera and potentially closely related taxa and coded these characters in an extensive matrix. I provided the first cladistic analyses of genera in this tribe in an attempt to discover the evolutionary history and decipher their relationships. For each genus, I provide a diagnosis, description (in the matrix), comments on distribution and diversity, and a discussion of relationships and similarities to other taxa. A key to all the genera of Elaphidiini (and similar taxa with mesally spined antennae) is provided for their identification.

TAXONOMIC HISTORY

Thomson (1864) proposed the "Division" Elaphidionitae to include ten genera. This family group name was based on the genus *Elaphidion* Audinet-Serville. Elaphidionini has been used since 1930, but Ivie (1985) indicated Elaphidiini should be the appropriate name of the tribe. The basis of Ivie's suggestion rests on the actual stem of *Elaphidion*. The ICZN (Article 29a) states that the appropriate family group suffix is added to the stem of the name of the type genus. *Elaphidion* was based on the Greek

elaphos, meaning deer, and latinized with the nominative singular termination, *-on*. Thus the stem is *Elaphidi* and the tribal suffix, *-ini* must be added, forming Elaphidiini (following *Ilion* = Iliidae example from ICZN, page 211). Until this study only two of these original genera (*Orion* Guérin-Méneville and *Elaphidion* Audinet-Serville) were still in the tribe. The others are currently distributed among other tribes including Hesperophanini, Callidiopini, and Methiini. Thomson further characterized the tribe Eburitae, originally proposed by Blanchard (1845), as including many other currently recognized elaphidiine taxa including *Atylostagma* White, *Centrocerum* Chevrolat, *Ambonus* Gistel, *Sphaerion* Audinet-Serville, *Periboeum* Thomson, *Appula* Thomson, *Stizocera* Audinet-Serville, *Mallocera* Audinet-Serville, and *Eurysthea* Thomson. Thomson (1864) defined the Elaphidiini as having body convex, eyes coarsely faceted, femora slightly clavate, and elytral apices spinose. These characters separated Elaphidionitae from his Eburitae which had body subdepressed, elytra without apical spines, and femora clavate. Lacordaire (1869) proposed the groups Hesperophanides (including taxa which are currently in Elaphidiini and Hesperophanini, characterized by the non-globose anterior coxae, externally open intermediate coxal cavities, and generally unspined antennae), *Éburiides* (mainly consisting of taxa with ebumeous elytral calli but identified primarily on the basis of externally-closed intermediate coxal cavities, globose anterior coxae, and unspined antennae), Phoracanthides (including taxa currently in Elaphidiini and Phoracanthini, characterized by spined but non-carinate antennae, intermediate coxal cavities open externally, procoxal cavities not angulate externally), and *Sphérionides* (including nearly all of Thomson's Eburitae, characterized by spines and carinae on antennae, anterior coxal cavities angulate externally, and intermediate coxal cavities open externally).

The variability of the characters above

(antennal carinae, open/closed intermediate coxal cavities, procoxal cavities angulate/not angulate, and antennal spines) was acknowledged by Linsley (1936). He noted that the distinction of Sphaerionini from Phoracanthini (including Elaphidiini) was not satisfactory. In typical Phoracanthini (including Elaphidiini), he indicated that the anterior coxal cavities may be either closed or open in closely related species of the same genus, and therefore was not a useful character. He felt that the most reliable characters were the non-carinate antennae and tibiae in Phoracanthini, but recognized that even those characters were not consistent in species of *Elaphidion*. Linsley (1963) included the sphaerionine and phoracanthine genera in his new concept of Elaphidiini, rendering Phoracanthini and Sphaerionini as junior synonyms.

DISTRIBUTION AND DIVERSITY

The Elaphidiini as recognized herein, have a widespread distribution, but with distinct concentrations of diversity. The "elaphidiine" group is most concentrated in México and the West Indies, extending into South America and Canada. The "sphaerionine" group is most concentrated in South America, extending into Central America and México. The number of described Elaphidiini in the Western Hemisphere exceeds 500 species (Monné 1993). In México alone the number is over 200 species (Chemsak 1991, Monné 1993, Monné and Giesbert 1993). This tribe has a very unusual ratio of species to genera. There are 86 genera of which 32 are monotypic (37%), 15 are bitypic (17%), and only 39 (46%) have more than two species (many have only three species).

SPECIAL PROBLEMS ASSOCIATED WITH MONOTYPIC TAXA

The existence of small and monotypic genera is an important problem in this study. Generic taxa should be erected to convey information on characteristics that bind sets of species together, not unique

characters or combinations of characters which endlessly split natural groups of species. These are the same attributes expected of a phylogeny. The carefully defined genus taxon (or clade) should allow one to make predictions or generalizations about other species included (Clayton 1972, Gauld and Mound 1982). No group of taxa should be removed from a clade if it will render either paraphyletic. If this happens, one loses the potential predictive attributes (for host plant associations, biological compound prospecting, adaptive characters, rates of speciation, etc.) of the phylogeny and the classification becomes meaningless. However, there will always be subjectivity in determining the amount of difference necessary to erect a new taxon in cases where this will not render one paraphyletic with respect to the other.

The Elaphidiini have a history of generic concepts based on presumed unique combinations of widespread character states and such genera do not convey the information or allow the predictions or generalizations that would be preferred. It is my intention to lessen this problem by redefining genera on the basis of detailed morphological examination and results of the phylogenetic analyses.

BIOLOGY AND NATURAL HISTORY

Very little is known of the biology of Elaphidiini. As nearly all of them are nocturnal as adults, over 95% of the specimens are taken at lights and thus are collected without any host or association records. Their abundance at lights can be remarkable. In western México, 13 nights of collecting at one illuminated roadside sign produced 1700 specimens of longhorn beetles. Elaphidiines represented 63% of all specimens and 35% of all species (Chemsak, et al. 1988)!

The following is a generalized life cycle of elaphidiines (for temperate species, summarized and generalized from Solomon 1995). Adults emerge in spring or summer, mate, and females lay the eggs in notches

in bark of dead branches. The larvae either feed for some time under the bark, or immediately enter the wood, feeding and developing within the heartwood. Larval development most often takes one to three years, correlated with the size of the beetle. A pupal cell is created in the region between the bark and sapwood at the end of larval development. Pupation occurs in either late summer to early fall, or early spring. Adults do not emerge until spring or summer, regardless of when pupation occurs.

It is assumed that adults of most elaphidiines (like many longhorned beetles) feed very little or not at all, but few references to feeding behavior exist. Specimens in some genera (*Anelaphus*, *Elaphidion*, *Par-elaphidion* Skiles, *Enaphalodes* Haldeman) are attracted in great numbers to brown sugar bait solutions (Lingafelter and Homer 1993), indicating their natural attraction to sap flows or other natural high-sugar sources of nutrition. Adults of at least two diurnal genera including *Tropimerus* Giesbert (Giesbert 1987), and *Stenosphenus* Haldeman (Giesbert and Chemsak 1989) are commonly encountered on flowering trees. *Aneflomorpha tenuis* (LeConte) adults have been reported feeding in large numbers on *Karwinskia* blossoms (Tumbow and Wappes 1981). Adults of *Anelaphus albofasciatus* Linell have been reported feeding on new growth of *Opuntia* (Raske 1972).

Twig-girdling—cutting off the flow of nutrients or chemicals to a portion of the plant, thereby killing part of it—is a behavior most commonly associated with the distantly related Onciderini. In this group the girdling is performed by the adult female prior to oviposition. Girdling has also been noted to occur in at least three genera of Elaphidiini including *Psyrassa* Pascoe (Champlain, et al. 1925); *Aneflomorpha* Casey (Craighead 1923); and *Anelaphus* Linsley (Craighead 1950), although in these groups the girdling is internal and done by the larvae.

Larval hosts are not known for most spe-

cies. Many taxa in the southern United States and México are associated with leguminous plants of the genera *Prosopis* and *Acacia* (Linsley 1963, and references cited therein). Much additional information is being discovered by G. Tavakilian in French Guyana.

MATERIALS AND METHODS

Cladistic methods.—The goals of this study are to: recharacterize the tribe Elaphidiini and the included genera based on examination of morphological characters of the adults; perform a phylogenetic analysis in order to propose a hypothesis of generic relationships and reveal needed changes in classification; and develop a key to genera. I have used the principles and tenets of cladistics to guide the methods described here (Forey, et al. 1994, Hennig 1966, Wiley 1981, and Wiley, et al. 1991).

Choice of taxa.—I have used the type species for each provisional elaphidiine genus in the analyses when possible. If the type species was not available, I hypothesized that the chosen taxon was a comparable representative for the genus based on knowledge of the type species and at least superficial similarity to it by the chosen taxon. I also included additional representatives of large, diverse genera to better allow tests for their monophyly.

Because the Elaphidiini have had no phylogenetic investigations previously, it is important to avoid a restricted outgroup choice. In fact, all potentially closely related taxa should be included in the analyses to allow for the most rigorous test of monophyly for the ingroup (Nixon and Carpenter 1993). I have included a broad representation of additional, potentially closely related tribes within the subfamily Cerambycinae.

Unavailable and fossil taxa.—Due to the number of rare, monotypic genera in this tribe, some genera could not be represented in the analyses either because the specimens were not available for examination, or because the few rare specimens could not be

dissected for examination of the full range of phylogenetically important characters. Omission of taxa is probably very common in phylogenetic analyses since most extinct taxa have an undiscovered or absent fossil record, or insufficient information can be gleaned from their fossil record. The Elaphidiini have a poor fossil record with North American examples known only from Florissant, Colorado (Linsley 1942). I examined in the MCZC two of the three described fossil species of Elaphidiini, *Anelaphus extinctus* (Wickham) and *Stenosphenus pristinus* Wickham (Fig. 11). I have compared my observations with those of Wickham (1914) and have concluded that these fossils convey insufficient information for inclusion in the phylogenetic analyses. These taxa, along with *Elaphidion fracticorne* Wickham, should be designated *incertae sedis* at the level of genus.

Summary of terminal taxa.—I included 89 provisional ingroup species and 10 provisional outgroup species as terminal taxa (Appendix 1) in the phylogenetic analyses. Specimens used in the analyses were obtained from the collections listed in Table 1. Listed in Appendix 2 are provisional elaphidiine genera which were excluded from the analyses because no specimens were available for dissection.

Specimen preparation.—For the phylogenetic analyses and key, I used characters of the adult morphology. Since the larvae are unknown for most elaphidiine species, this potential data set could not be used. Specimens were prepared by relaxing them in hot water for 5–10 minutes, depending on size. Then, the head, prothorax, abdomen, elytra, hind wings, and genitalia were disarticulated. The wings, and in some cases, genitalia, were placed directly into vials of 50% glycerin/50% of 80% ethanol. The remainder of the beetle was transferred to a vial containing a 5–10% KOH solution, and was carefully heated for 10–30 minutes, depending on size. This procedure caused digestion of the muscle tissue which otherwise would obscure characters of the

sclerites. Male genitalia, labia, maxillae, and mesonota were then transferred to the glycerin vial. The remaining body parts were partially cleared in 10% hydrogen peroxide solution for 1–10 minutes depending on structure and amount of melanization. When cleared, remaining structures were transferred to the glycerin vials.

Types of characters used in phylogenetic analysis and key.—The majority of characters used were exoskeletal features or cuticular processes visible through dissection microscopy with fiber optic illumination and magnification less than 20 \times . Additional characters could only be revealed effectively through the use of Nomarski interference compound microscopy. Presumptive homologous characters were compared and discretely variable states were identified and coded in the data matrix. Wilkinson (1992) presents an argument for and against ordering of characters. I have treated all characters as unordered according to the principle of indifference (Keynes 1921) summarized in Wilkinson (1992). This assumption proposes that transposition between states is equiprobable, and there is no information available to suggest otherwise. Some characters were found to be continuously variable. Thiele (1993) presents justification and a procedure for using continuous morphometric data in phylogenetic analyses. However, due to the limitations of software to deal with all potential states and the artificial state construction formula of Thiele (1993: 284), I chose to exclude continuously variable characters from the phylogenetic analyses. These characters were used in the key and coded multiple ways for taxa with ambiguous states.

Character descriptions and states.—A total of 102 derived character states for 70 characters was used in the phylogenetic analyses. These were entered and maintained using MacClade software (Maddison and Maddison 1992). As these are presented in an extensive matrix (Table 2), and the character states are thoroughly discussed below, the matrix substitutes as a presen-

Table 1. Institutions and private collections that provided material for this study

Institution	Visited?	Loan/gift received?
Academy of Natural Sciences, Philadelphia, Pennsylvania (ANSP, Donald Azuma)	no	yes
American Museum of Natural History, New York, New York (AMNH, Lee Herman)	yes	yes
Australian National Insect Collection-CSIRO, Canberra, Australia (ANIC, Tom Weir)	no	yes
Bernice P. Bishop Museum, Honolulu, Hawaii (BPBM, Al Samuelson)	no	yes
California Academy of Sciences, San Francisco, California (CASC, David Kavanaugh, Roberta Brett)	yes	yes
Canadian Museum of Nature, Ottawa, Ontario, Canada (CMNC, Bob Anderson)	yes	yes
Canadian National Collection, Ottawa, Ontario, Canada (CNCI, Ed Becker, Jean McNamara)	yes	yes
Carnegie Museum, Pittsburgh, Pennsylvania (CMNH, John Rawlins)	no	yes
Daniel Heffern private collection, Houston, Texas (DHPC)	yes	yes
David Marqua private collection, Davis Mountains, Texas (DMPC)	yes	yes
Edward Riley private collection, College Station, Texas (ERPC)	yes	yes
Edmund Giesbert private collection, Beverly Hills, California (EGPC)	yes	yes
Essig Museum of Entomology, Berkeley, California (CISC, John Chemsak, Cheryl Barr)	yes	yes
Estación del Biología Chamela, Jalisco, Mexico (EBCC, Felipe Noguera)	no	yes
Field Museum, Chicago, Illinois (FMNH, Al Newton, Philip Parrillo)	no	yes
Frank Hovore private collection, Los Angeles, California (FHPC)	yes	yes
Henry Stockwell private collection, Panamá City, Panamá (HSPC)	yes	yes
Instituto Nacional de Biodiversidad, Santo Domingo, Heredia, Costa Rica (INBC, Angel Solís)	yes	yes
Jim Wappes private collection, Bulverde, Texas (JWPC)	no	yes
Marlin Rice private collection, Ames, Iowa (MRPC)	no	yes
Montana State University Entomology Collection, Bozeman, Montana (MTEC, Mike Ivie)	yes	yes
Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZSP, Ubirajara Martins)	yes	yes
Museu Nacional Quinta da Boa Vista, Rio de Janeiro, Brazil (QBUM, Miguel Monné)	yes	yes
Muséum National d'Histoire Naturelle, Paris, France (MNHN, Jean Menier)	no	yes
Museum of Comparative Zoology, Cambridge, Massachusetts (MCZC, David Furth, Cleone Graham)	yes	yes
National Institute Agro-Env. Sciences, Kannondai, Tsukuba, Ibaraki Pref., Japan (ITLJ, T. Matsumura, Akiko Saito)	no	yes
Natural History Museum, London, England (BMNH, S. Shute)	no	yes
Smithsonian Tropical Research Institute, Panamá City, Panamá (STRI, Annette Aiello and Donald Windsor)	yes	yes
Snow Entomological Museum, Lawrence, Kansas (SEMC, J. Steve Ashe)	yes	yes
Steven Lingafelter private collection, Washington, D. C. (SLPC)	—	—
Texas A&M University, College Station, Texas (TAMU, Horace Burke, Ed Riley)	yes	yes
National Museum of Natural History, Washington, D. C. (NMNH, Terry Erwin and Gloria House)	yes	yes
Universidade Federal do Viçosa, Minas Gerais, Brazil (UFVB, Dr. Fiuza)	yes	no
Universidade Federal do Paraná, Curitiba, Paraná, Brazil (DZUP, Solange Napp)	yes	yes
Universidad Nacional Autonomia de México, D. F. (UNAM, Silvia Santiago Fragoso)	no	yes
University of Nebraska State Museum, Lincoln, Nebraska (UNSM, Brett Ratcliffe)	yes	yes
University of Colorado Museum, Boulder, Colorado (UCMC, Virginia Scott)	no	yes

tation of detailed descriptions for each genus. Additionally, male genitalia were examined for all available taxa and (as explained below) not found to be useful for the analysis or key. Leg shape was also examined and these data were included in the key but could not be coded for the phylogenetic analyses. A discussion of all characters examined in this study follows.

Characters not used in analyses or key.—Genitalia of many genera of Elaphidiini and related taxa were examined. In males, variation was discovered in the length of the parameres, paramere setae, and shape of the eighth tergite (Fig. 3). In females, variation was observed in the position of the stylus of the coxite and the length and number of setae present on the stylus (terminology based on Saito 1989). Because males and females were not available for all terminal taxa and the noted variation was not discrete, genitalic characters were not included in the phylogenetic analyses. Since the key was intended to be practical and not require dissections, genitalic information was not included.

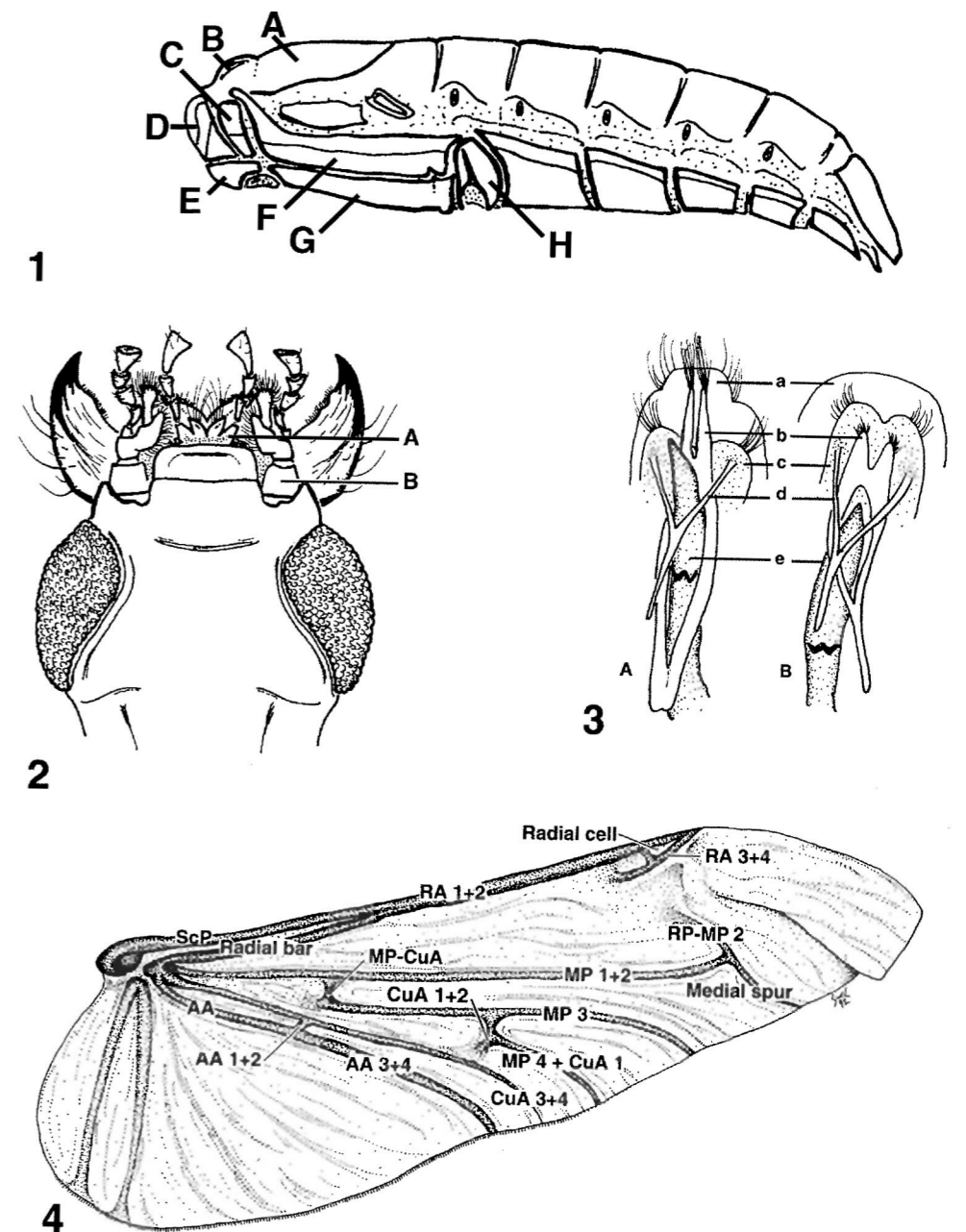
Characters used in key only.—Femoral shape (Fig. 37) was found to vary tremendously among genera. Historically, the terms "clavate," "pedunculate," and "linear" have been applied to qualitatively define this variation. I attempted to devise formulae based on six measurements of the femur that could give a quantitative and consistent basis for these terms. I present an example (Fig. 47) which shows and defines these measurements and how they are used. All measurements and variables are defined in that figure legend. Two ratios are used, "CR" and "PR." I developed the ratio "CR" to determine presence or absence of clavate femora. CR is x/y from Fig. 47. I developed the ratio PR to determine presence or absence of pedunculate femora. PR is A/B from Fig. 47. If PR and $CR > 3$, then I determined the femur to be pedunculate. If $CR > 2.5$, but $PR < 3$, then the femur is clavate. If $CR < 2.5$, then the femur is gradually enlarged or linear. I

found, however, that these ratios did not adequately account for the differences in femoral shape and they also varied continuously. Therefore, I excluded these characters from the phylogenetic analyses, but I did include leg-shape descriptions in the key, coding them multiple ways for borderline values.

CHARACTERS USED IN ANALYSES

The following is a description of all the characters used in the phylogenetic analyses. Some of these characters were also used in the key. Character and state numbers refer to the data matrix (Table 2). This matrix, combined with the detailed character and state discussion below, serves the function of generic descriptions. Many of the following characters and their states are illustrated (Figs. 1–49). Additional morphological information is presented in Figs. 1–5A, 6, 8–10, and 49 as a reference aid for the characters used in the analyses. The terminal taxa used in the analyses are meant to be representative of the genera and fine morphological details such as setae and punctuation are not always shown, since these attributes can vary among individuals. No comments are included here as to primitive and derived states since all terminals included in the analyses were treated as potential ingroup taxa. For most characters, comments are included here regarding the states possessed by terminal taxa (including the provisional outgroup taxa).

Character 1.—Ommatidial size (Fig. 39): (0) large (coarse), Fig. 39B; (1) small (fine), Fig. 39A. Taxa with coarse ommatidia usually have the lower eye lobe occupying $>50\%$ of the head when viewed laterally. Each coarse facet is relatively large and convex with light reflected only from the outermost point. The overall surface of the coarsely faceted eye appears uneven. Most taxa with fine ommatidia have smaller eyes, with the lower lobe occupying $<50\%$ of the head when viewed laterally. Each fine facet is relatively small and reflects light evenly from all points. The overall surface of the



Figs. 1–4. Morphology of Elaphidiini. 1, Lateral habitus of *Elaphidion mucronatum* (head pronotum, elytron, hindwing, and legs removed). (A) metanotum; (B) mesonotum; (C) mesepimeron; (D) mesepisternum; (E) mesosternum; (F) metepisternum; (G) metasternum; (H) metacoxa. 2, Venter of head of *Elaphidion mucronatum*. (A) labium; (B) maxilla. 3, Ventral view, variation in male genitalia of (A) *Phoracantha semipunctata* (Fabricius) and (B) *Eburia haldemani* LeConte. (a) eighth tergite; (b) parameres; (c) eighth sternite; (d) sternite-8 apodeme; (e) median lobe. Terminology from Fragoso (1985) and Fragoso, et al. (1987). 4, Hind wing of *Aneflus protensus* with terminology of Kukalová-Peck and Lawrence (1993).

Table 2. Character state matrix for taxa of Elaphidiini and other Cerambycinae used in phylogenetic analysis.

TAXON	1		2		3		4		5		6		7	
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
<i>Ambonus d.</i>	0010021011	0110002012	1200011101	200010201?	0000001011	2221000000	1000210000							
<i>Aneflomorpha r.</i>	0000021011	1112002012	1200010100	1000101011	0010010011	2220000000	1000100000							
<i>Aneflomorpha l.</i>	0000121011	1112002012	1200010101	1000101011	0010010011	2220000000	1000100000							
<i>Aneflomorpha p.</i>	0000021011	1112002012	1200010101	1000101011	0010010011	2220000000	1000100000							
<i>Aneflomorpha f.</i>	0000071021	1112002112	1200010101	1000101011	0010010011	2220000000	1000100000							
<i>Aneflus b.</i>	0000001010	2101012012	1100010100	1000101011	0010000011	2220000200	1000100000							
<i>Anelaphus m.</i>	0010121011	1011012012	1200010100	6000101001	0010212011	2220000100	1000210000							
<i>Anelaphus p.</i>	0010121011	1011012012	1200010100	6000102001	0010002011	2220000100	1000210000							
<i>Anelaphus s.</i>	0010121011	1011002012	1200010101	6000101001	0010012011	2220000100	1000210000							
<i>Anopliomorpha r.</i>	0010121011	1112012012	1300010100	?01010101?	0001010001	2220000100	1000210000							
<i>Anoplocurius a.</i>	0000131001	0012012012	1300000000	1000?0?0??	0000210011	2221010200	1000100001							
<i>Aposphaerion l.</i>	0020021011	1112001002	1200010100	2000101011	0000211000	1011000200	0000210000							
<i>Appula l.</i>	0010121001	1011012012	1200010100	1000001001	0000202011	2220001010	1000210000							
<i>Astromula n.</i>	0010001010	1111000012	1000010100	1000100011	0013000010	0101010200	1000101000							
<i>Atylostagma p.</i>	00001?1001	2001011012	1200010100	1000101011	0010200011	2220020100	1000210000							
<i>Axestinus o.</i>	0000021011	0110011002	1100011100	1000101011	0001000010	0001000000	1000210000							
<i>Castiale e.</i>	0000021011	0110011012	1200010101	1000100111	0010211011	2221010200	1000210000							
<i>Centrocerum e.</i>	0000111021	0011111012	1200010101	1000100111	0010211011	2221010200	1000210000							
<i>Championa e.</i>	1000141011	1012112012	0100011101	4100001011	0001000000	2221002000	1001210000							
<i>Clausirion c.</i>	0000121010	1112001112	1200010101	?000100001	0000100000	2221000000	1000010000							
<i>Conosphaerion s.</i>	0000001011	0112002011	1300010100	4000102011	0000010001	2221000200	1000210000							
<i>Curtomerus f.</i>	0000002001	1011001012	1000011100	1000101010	0010011011	2221010000	1000200000							
<i>Elaphidion m.</i>	0010121010	0012000012	1200010110	0000101001	0010002011	0101010100	1000210000							
<i>Elaphidion l.</i>	0010121010	0012001012	1200010110	0000101001	0010002011	0101010100	1000210000							
<i>Elaphidion e.</i>	0000121001	0112100012	1200011100	0000101011	0010001011	222?000000	1000210000							
<i>Elaphidion p.</i>	0110122011	1012100012	1100011100	0000101001	0010001011	0101020100	1000210000							
<i>Elaphidion s.</i>	0010121010	0012000012	1200010110	0000101001	0010002011	0101010100	10002?0000							
<i>Enaphalodes a.</i>	0010121010	0112100012	1200010101	2000100002	0000?02011	2220010200	1000210000							
<i>Eurysthea o.</i>	0000021001	0110100002	1200011100	1000100011	000011?001	2211000200	1000?00000							
<i>Eustrumula v.</i>	0010121011	1111100012	120001010?	0000101002	0000212011	2220000200	1000210000							
<i>Eutrichophoroidesa.</i>	0100021010	0110001012	1200011100	4000100011	0000001001	2221000000	1000210000							
<i>Eutrichophoroides j.</i>	0100021011	0110000012	1200011101	4000102011	0000?01001	2221000000	1000210000							
<i>Gymnospyra m.</i>	0010121010	1111012012	130001010?	4000101001	0000002011	2220000100	1000210000							
<i>Ironus s.</i>	00?0021011	0112012012	0000111101	10001020?1	0010000011	2220000200	1000110000							
<i>Ironus d.</i>	1000021011	0112001012	1000011100	1000102011	0010000011	2220000200	1000110000							
<i>Mallocera g.</i>	0020021011	0112100000	1000010100	1000102011	0000001001	1111000000	0000210010							
<i>Meganeflus f.</i>	0000131011	1112001012	1200010100	1000101013	00102?0011	2220000001	1000000000							
<i>Megapsyrassa x.</i>	0000001011	1111012112	1100010100	0000101011	0010000011	2210000200	1000000000							
<i>Mephritus d.</i>	0000021011	0110100000	1200011100	4000102011	0001?01001	2221000200	1010110000							
<i>Metironeus h.</i>	0000001011	0112002012	0000011100	0000101011	0010000011	2220000000	1000210000							
<i>Micraneflus i.</i>	0000?01001	2111112012	1200010100	1000101011	0010200011	2220010200	1000110000							
<i>Micropsyrassa b.</i>	0000021021	0112002012	1300011101	1000100011	0010010011	2221000200	1000210000							
<i>Miltesthus m.</i>	0020021011	0012102012	1000010100	0000102012	00002010?1	2221000100	1000210000							
<i>Miopteryx s.</i>	0000021111	0112000002	1100010100	4000100011	0103201001	2221000000	1010000000							
<i>Morphaneplus p.</i>	00000?1001	0112001012	1200010101	4000101011	0010201011	2220010210	1000010000							
<i>Neaneplus f.</i>	0000??1011	2011002012	1200010100	1000101011	0010210011	2220020200	1000000000							
<i>Neomallicera o.</i>	0000021011	1112100001	1200010100	0000101002	0000001001	2021000200	0000210000							
<i>Neoperiboeum j.</i>	0000021021	0112002012	1200011101	0000100011	10100?0011	2221000000	1000210000							
<i>Neotrichophoroides d.</i>	0100021011	0110000012	1200011100	4000100011	0000200001	2221000000	1000210000							

finely faceted eye appears smooth. This character has been used since Lacordaire (1869) for classification of Cerambycidae. Because ornatidial facet size is related to the diel activity of the beetle (finely faceted in diurnal adults, coarsely faceted in nocturnal adults), it cannot be used at higher

levels which contain many taxa of differing behaviors. My studies show ornatidial size to be consistent within genera, however. Virtually all traditional elaphidiine taxa have coarsely faceted eyes. Those with finely faceted eyes include: *Championa* Bates, *Ironus* Bates (in part), *Sphaerionil-*

Table 2. Continued.

TAXON	1		2		3		4		5		6		7	
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
<i>Neotrichophoroides p.</i>	0100021011	0110000012	1200011101	4000100011	0000200001	2221000000	1000210000							
<i>Nephaloides r.</i>	0000021011	0112001012	1100001100	0000102011	0010001011	2211000000	1000100000							
<i>Nesodes i.</i>	0010121011	1011102012	1200010100	6000101011	0000010011	2220010000	1000210000							
<i>Nesostizocera f.</i>	0000021011	0112000010	1000111101	1000100011	0010001011	1111000000	1000200000							
<i>Nesostizocera v.</i>	0000021011	0112002011	1000111101	1000100011	0010000011	1201000000	1000210000							
<i>Nyssicostylus a.</i>	0020021011	0110101001	1200010100	4000100011	0001201001	2221000200	1000210000							
<i>Nyssicus t.</i>	0000021010	1110010000	1201010100	4000100001	0001001001	0001000200	1000210000							
<i>Orion p.</i>	0000021011	0011102010	1000010101	6000101012	0000010011	2220010100	1000110100							
<i>Orwellion g.</i>	0110121010	0112100012	1200010100	6000101002	0000012011	2220000100	1000210000							
<i>Panfonyssa n.</i>	0000021011	0112001012	1100010100	0000101011	0010000011	1011000000	1000210000							
<i>Paramallicera c.</i>	0000021011	0010100010	1200010100	0000102001	0000000011	1111010000	1000210000							
<i>Parastizocera p.</i>	0000021011	0110000011	1000011100	0000101011	0010?10011	1011000000	1000210000							
<i>Parelapheidion i.</i>	0010121010	1012100012	1200010100	6000101011	0000202011	2220010100	1000210000							
<i>Peranoplium u.</i>	0011121011	1011012112	1300010100	6000102001	0010012011	2220000100	1000210000							
<i>Peranoplium s.</i>	0011121011	1011012112	1300010100	6000102001	0010012011	2220000100	1000210000							
<i>Peranoplium h.</i>	0011121011	1011012112	1300010100	6000102001	0010012011	2220000100	1000210000							
<i>Periboeum a.</i>	0000021010	1110000001	1200011100	100010001?	0000000011	2211000200	1000?10000							
<i>Phoracanthas.</i>	0000021010	0012000010	100001010?	0000102012	0000000001	0001010000	1000210000							
<i>Poecilomalilus p.</i>	00001?1010	1011002012	1000010101	2000101001	0010211011	2221000010	1000210000							
<i>Protornallicera h.</i>	0020021011	0112100001	1200010100	0000101011	0000201001	2221000000	0000210000							
<i>Protosphaerion v.</i>	0000021011	0010101012	1200010101	0000101011	00000000??	2221010100	1000210000							
<i>Pseudomallicera a.</i>	0000021011	1112100011	100001010?	2000101011	0002011001	1111000200	0000210010							
<i>Pseudoperiboeum s.</i>	0000021011	0112001010	1200011101	100010?011	0010001011	2220000000	1000110000							
<i>Psyrassa si.</i>	0000001011	0111002112	11000000100	1000101011	0010000011	2221000000	1000000000							
<i>Psyrassa b.</i>	0000011011	0111012112	11000000100	1000101011	0010010011	222								

are asymmetrical, with notches on one corresponding to **teeth** on the other (Fig. 29). To avoid inconsistency in designating these character states, I compared only right mandibles among taxa. State 0 is recognized by not having any indentation in the incisor region towards the apex of the mandible, when viewed from the ventral side. State 1 is recognized by having an apical and basal indentation, creating a raised plateau which also helps to define the prosthecal region. States 0 and 1 are widespread among terminal taxa. State 2 is recognized by having two apical indentations separated by a **small** tooth so that the apex appears bidentate. This state is much less widespread, occurring only in *Appula* Thomson, *Mallocera* Audinet-Serville, *Miltesthus* Bates, *Nyssicostylus* Melzer, *Protomallocera* Martins and Napp, and *Sphaerion* Audinet-Serville. Morphological terms for mandible are from Lawrence, et al. in Stehr (1991) and Napp (1994).

Character 4.—Subapical incisor region: (0) narrow; (1) wide. State 0 is the general condition among all Elaphidiini and related taxa examined and is characterized by a narrow width between the dorsal and ventral margins of the subapical incisor region (much less than one-third width of base of mandible viewed from mesal, biting surface). State 1, shared by *Peranoplum* and *Anelaphus*, is characterized by having widely separated dorsal and ventral planes of the subapical incisor region (distinctly greater than one-third width of base of mandible viewed from mesal, biting surface).

Character 5.—Digitiform sensillum patch on terminal labial palpomere: (0) present; (1) absent. See descriptive discussion of this feature in next character. Digitiform sensilla are absent from the labial palpi in the speciose, primarily North American genera including *Anelaphus*, *Peranoplum*, and *Elaphidion*. Most other taxa examined possess these sensilla on the labial palpi.

Character 6.—Digitiform sensillum patch on terminal maxillary palpomere (Fig. 5): (0) diffuse patch with sparse sensilla (Fig.

5B); (1) wide, apically positioned patch with indistinct edges (Fig. 5A); (2) narrow, apically positioned patch with defined edges (Fig. 5C, D); (3) digitiform patch absent; (4) narrow, distinct, basally positioned patch. The digitiform sensilla, which can occur on the terminal labial palpomeres (see Character 5) and maxillary palpomeres, are widespread and variable in beetles (Lawrence and Newton 1995) and particularly so in Chrysomeloidea (Mann and Crowson 1984). This character can only be seen effectively with Nomarski interference compound microscopy or scanning electron microscopy. In all Cerambycidae examined except *Championa*, the digitiform patches occurred towards the outer apex of the terminal palpomeres. This supports the observation of Mann and Crowson (1984) who noted this fundamental difference between Chrysomelidae and Cerambycidae, with most Chrysomelidae (except some *Sagra* and *Timarcha*) having basally positioned sensillum patches. The well-defined narrow, apical patch (State 2) is most widespread in the terminal taxa of this study.

Character 7.—Apex of terminal maxillary palpomere: (0) not expanded, width much less than half length; (1) moderately expanded (Figs. 5A, C, D); (2) very expanded, greater than three-fourths length (Fig. 5B). The moderate apical expansion of the terminal maxillary palpomere occurs in all traditional elaphidiine genera except *Curtomerus* Stephens, which has greatly expanded palpi. Most taxa in other Cerambycinae tribes (and other subfamilies) have unexpanded terminal maxillary palpomeres.

Character 8.—Maxillary palpomeres 3–5: (0) short and thick (each less than 1.5× longer than wide) (Fig. 5A–D); (1) elongate and narrow (each much greater than 1.5× longer than wide). The unique slender condition of this character in *Miopteryx spiniger* Blanchard was not seen in any other taxa. All other examined terminal taxa have shorter palpomere dimensions.

Character 9.—Mesal antennal spines: (0)

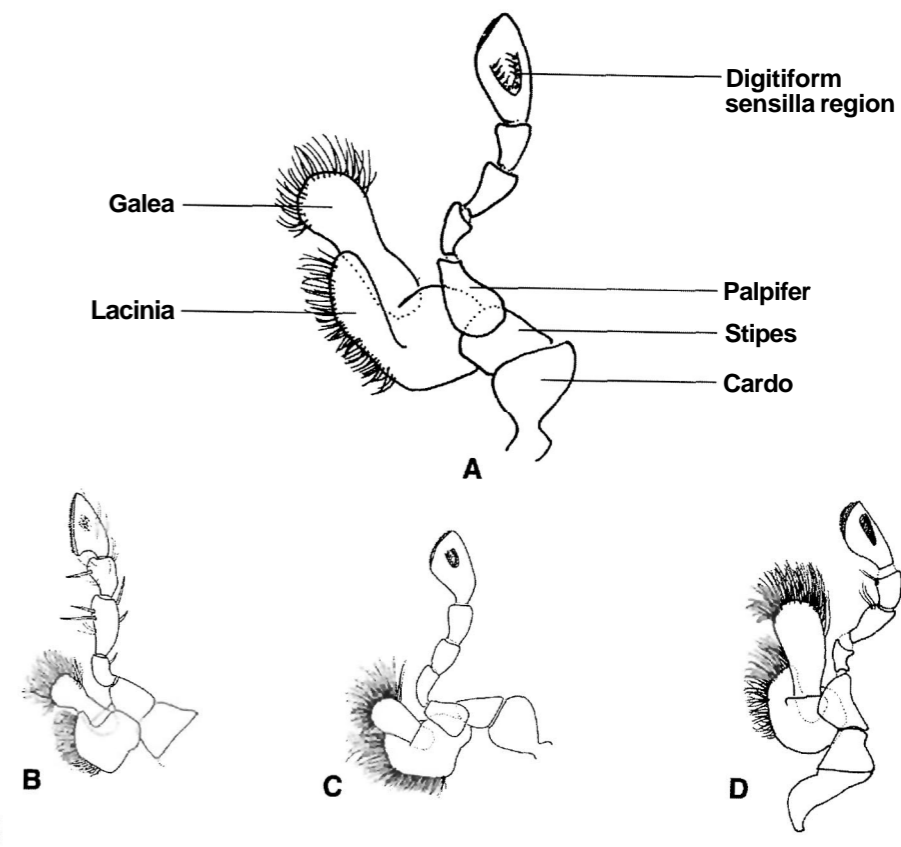


Fig. 5. Left maxillae of Elaphidiini (ventral view). (A) *Centrocerum exornatum*; (B) *Curtomerus flavus*; (C) *Elaphidion mucronatum*; (D) *Phoracantha semipunctata*.

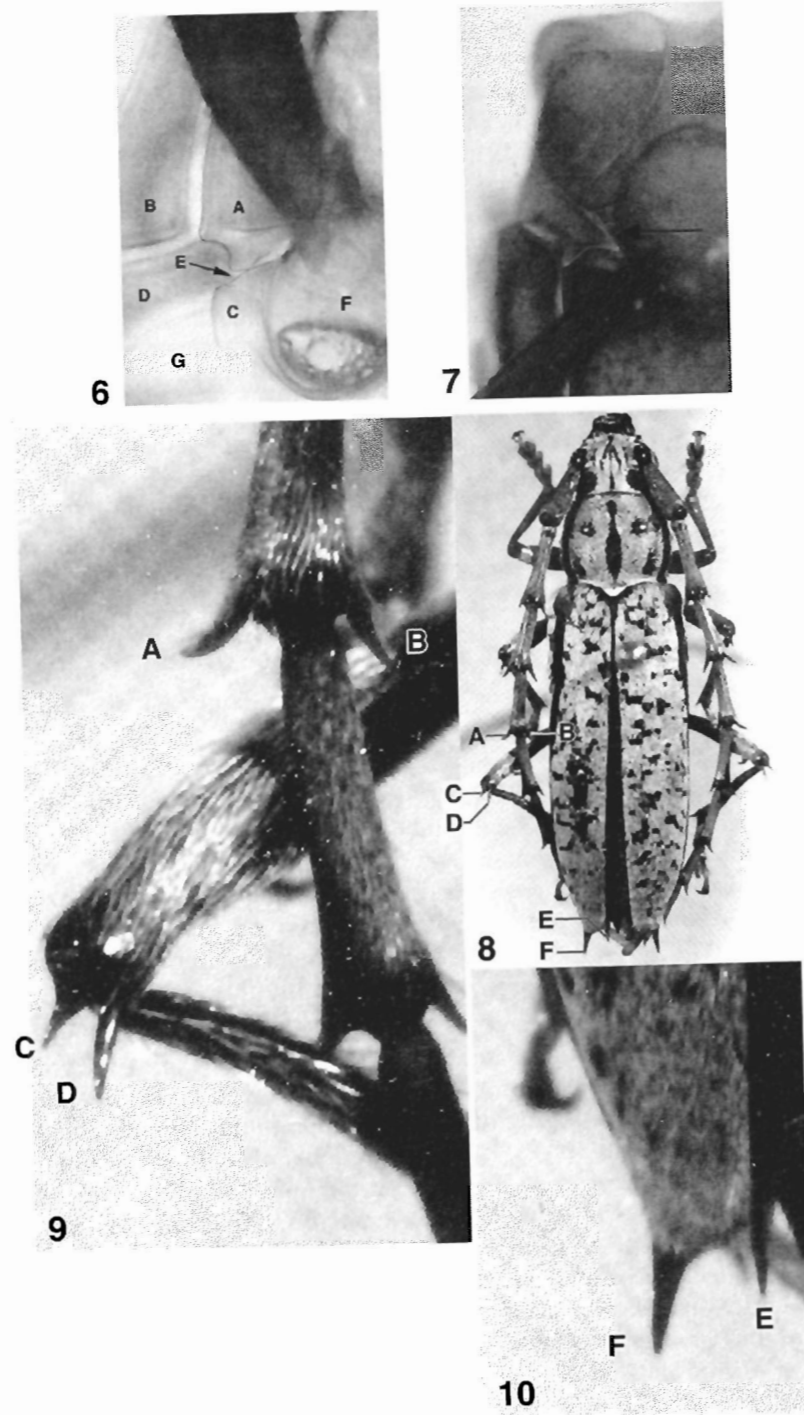
absent (Fig. 13); (1) present and acute (Figs. 8B, 9B, 45, 46); (2) present and blunt (Fig. 28). Nearly all traditional elaphidiine taxa possess mesal antennal spines on at least the third antennomere. All preliminary outgroup taxa lacked these spines except for *Allotraeus* and *Cordylomera*. *Anoplocurius* Fisher, *Axestinus* (Fig. 45), *Curtomerus*, *Elaphidion elegans*, *Eurysthea* Thomson, *Micraneflus* Linsley, and *Morphaneffus* Martins and Napp lack these spines. Some *Aneflomorpha* Casey species, *Centrocerum* Chevrolat, *Micropsyrassa* Linsley, *Neoperiboeum* Linsley, and most *Stenelaphus alienus* Linsley specimens have blunt spines on the third antennomere.

Character 10.—Lateral antennal spines: (0) present (Figs. 8A, 9A); (1) absent.

Character 11.—Lateral antennomere

shape: (0) linear (Fig. 22, 45A, B); (1) gradually widened at apices (Fig. 45C); (2) fully appendiculate (Fig. 13). The majority of taxa examined have antennomeres which are approximately parallel-sided for the entire length, i.e. linear or gradually widened at the apices. Only *Aneflus*, *Axestinus*, *Micraneflus*, *Neaneffus* Linsley, and *Coleoxestia* Aurivillius have the apices greatly expanded.

Character 12.—Antennal carinae: (0) absent; (1) single or double carinate (Fig. 45B, C). Antennal carinae are narrow ridges where the cuticle appears to be abruptly pinched in a long, straight line. Sometimes antennomeres are sulcate (Fig. 45A) and superficially appear carinate, however, this is a result of a broad depression and shadow which sometimes occurs along its edge.



Figs. 6-10. Lateral closure of mesocoxa and spination terminology in Elaphidiini. 6, Mesocoxa closed laterally in *Nesostizocera floridana*. (A) mesosternum; (B) mesepisternum; (C) metasternum; (D) mesepimeron; (E) closure separating mesocoxa from mesepimeron; (F) mesocoxa; (G) metepisternum. 7, Mesocoxa open laterally in *Megapsyrassa xestioder*. 8, Dorsal habitus of *Elaphidion spinicorne*. (A) lateral antennal spine; (B) mesal antennal spine; (C) lateral femoral spine; (D) mesal femoral spine; (E) sutural elytral spine; (F) apicolateral elytral spine. 9, Enlargement of Fig. 8, showing apex of left elytron. (A) lateral antennal spine; (B) mesal antennal spine; (C) lateral femoral spine; (D) mesal femoral spine. 10, (E) sutural elytral spine; (F) apicolateral elytral spine.

This character, like ornatidial structure, has been used historically to separate Sphaerionini (carinae present) from the rest of Elaphidiini (carinae absent) (Lacordaire 1869; Linsley 1936; Linsley 1961b). Linsley (1936) acknowledged, however, that this character was not absolute in that it occurred in some species of Elaphidion. I have found antennal carinae to be widespread in Elaphidiini, with no regional patterns. Carinae were absent from all provisional outgroup taxa examined, except *Neocompsa* Martins.

Character 13.—Antennal segmentation: (0) 12 antennomeres; (1) 11 antennomeres. Most species of *Aneflus* and all *Axestinus*, *Etymosphaerion* Martins and Monné, and *Psyrassaforma* Chemsak have antennae distinctly 12-segmented. Many additional taxa (including some *Aneflus* species) have the eleventh segment constricted, superficially appearing 12-segmented (Fig. 48), but this is not the case (see discussion of Character 15).

Character 14.—Length of third antennomere of male: (0) approximately length of pronotum or greater (Fig. 46C); (1) about half length of pronotum (this state also present in females) (Fig. 46A); (2) approximately two-thirds length of pronotum (Figs. 8, 46B). This character is sexually dimorphic. Generally, males have longer antennae than females in Elaphidiini. This is particularly evident in the length of the third antennomere. For this reason, comparing females of genus "a" with males of genus "b" would be inappropriate.

Character 15.—Pseudosegmental setae on terminal antennomere: (0) present (Fig. 48); (1) absent. The setae, if present, occur in a poorly defined post-medial ring around antennomere 11 and are often associated with a small constriction. I hypothesize that these setae are serially homologous to those at the apex of the other antennomeres and provide evidence of (1) fusion of two antennomeres, or (2) incomplete expression of a gene coding for a twelfth antennomere. This character has been discussed in Carter

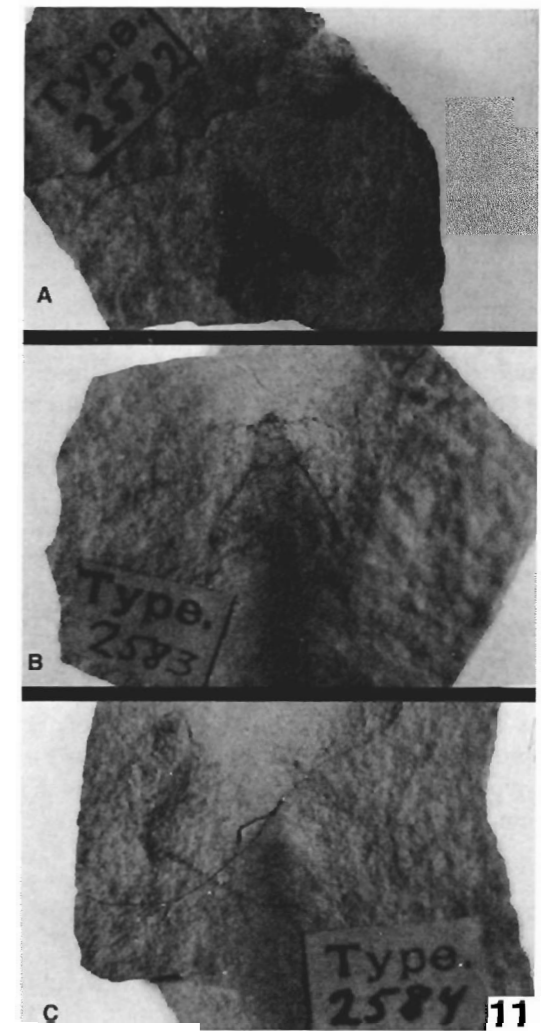


Fig. 11. Fossils from Florissant, Colorado (MCZC) placed in Elaphidiini by Wickham (1914). (A), (B) *Aneflaphus extinctus* (Wickham); (C) *Stenosphenus pristinus* Wickham.

(1929: 118-119), who coined the term "pseudo-segment" to refer to the modified eleventh antennomere. Most taxa examined have these pseudosegmental setae present.

Character 16.—Median pronotal callus: (0) present (Fig. 8, 12D, E); (1) absent (Fig. 12A-C, F-I). A median pronotal callus is a well-defined slightly raised region in the center of the pronotal disc with little or no punctation and pubescence. In some taxa, a central region is defined, but this is due to

elevations or rugosities surrounding it. Both states have a wide distribution in examined taxa.

Character 17.—Peripheral pronotal calli: (0) pronounced (Fig. 12D–F); (1) present but reduced (Fig. 19, covered with dense pubescence); (2) absent (Fig. 12A–C, G–I). The pronounced state (0) has well-defined areas around the central pronotal disc which are raised and devoid of punctation. Peripheral pronotal calli which are present but reduced (state 1) appear as raised, partially punctate regions around the central pronotal disc. Peripheral pronotal calli are absent (state 2) when there is no differentiation in protuberance and punctation of the regions around the pronotal disc. All states are widely distributed.

Character 18.—Posterior margin of procoxal cavities: (0) open (Fig. 18); (1) closed (Fig. 27). Closure of the procoxal cavities at the posterior margin of the prothorax is a function of the width of the apex of the prosternal process and the projection of the hypomerion. If both of these structures make contact, the procoxal cavities are closed posteriorly. If not, they are open.

Character 19.—Lateral margin of procoxal cavities: (0) open (Fig. 17); (1) closed (Fig. 24). The open state is recognized by a broad lateral exposure of the trochantin and its articulation with the antero-lateral region of the procoxa. The procoxae are closed laterally when the trochantin is hidden and the propleuron and prosternum are fused very close to the coxae. This character was a fundamental one used by Lacordaire (1869) to separate the sphaerionine "group" from the rest of Elaphidiini. In nearly all South American genera, the open state occurs. In most of the primarily North American genera and the provisional out-group taxa, the closed state is predominant.

Character 20.—Lateral pronotal tubercles: (0) acute (Figs. 12E, 41A); (1) rounded (Figs. 12E, 41B); (2) absent (Figs. 12A–C, G–I, 41C–E). Pronota are highly modified in many genera of Elaphidiini. Narrow and elongate lateral projections of the pronotum, ending in a sharp point are classified as acute; broad lateral protuberances which are not sharp at the apex are denoted as rounded; a pronotum without distinct lateral processes has state 3. Most of the taxa examined lack these tubercles. Only *Mallo-cera*, *Mephritus* Pascoe, *Nesostizocera floridana* (Linsley), *Nyssicus* Pascoe, *Orion*, *Phoracantha*, *Pseudoperiboeum* Linsley, *Rhomboidederes* Zajciw, and *Sphaerion* have acute pronotal tubercles. These are subject to sexual dimorphism in *Mephritus* and *Sphaerion*, with males generally having them less pronounced.

Character 21.—Transverse ridges on pronotal disc: (0) present (Fig. 12H); (1) absent (Fig. 12A–G, I). Only *Championa*, *Ironeus submetallicus*, *Metironeus* Chemsak, and *Stizocera plicicollis* (Germar) have transverse ridges on the pronotum.

Character 22.—Dorsal pronotum punctation: (0) absent to very sparse (Fig. 12G, H); (1) moderately dense (Fig. 12D); (2) confluent but not alveolate (Fig. 12A); (3) confluent and alveolate (Fig. 12B). State 0 has punctures separated by more than 10× their diameters; state 1 has rounded punctures separated by an average of 1–5× their diameters; state 2 has rounded punctures, the majority of which are in contact with one another, without alveolate partitions separating them; state 3 has elongate or trapezoidal-shaped punctures which are alveolate, with thin partitions separating them.

Character 23.—Prothoracic venter: (0) not striate; (1) striate. Ventral prothoracic striae occur only in *Rhomboidederes*.

Character 24.—Posterior margin of pronotum: (0) without medial callus (Fig. 12A–E, G–I); (1) with medial callus (Fig. 12F). The rounded callus at the base of the pronotum occurs only in *Nyssicus*.

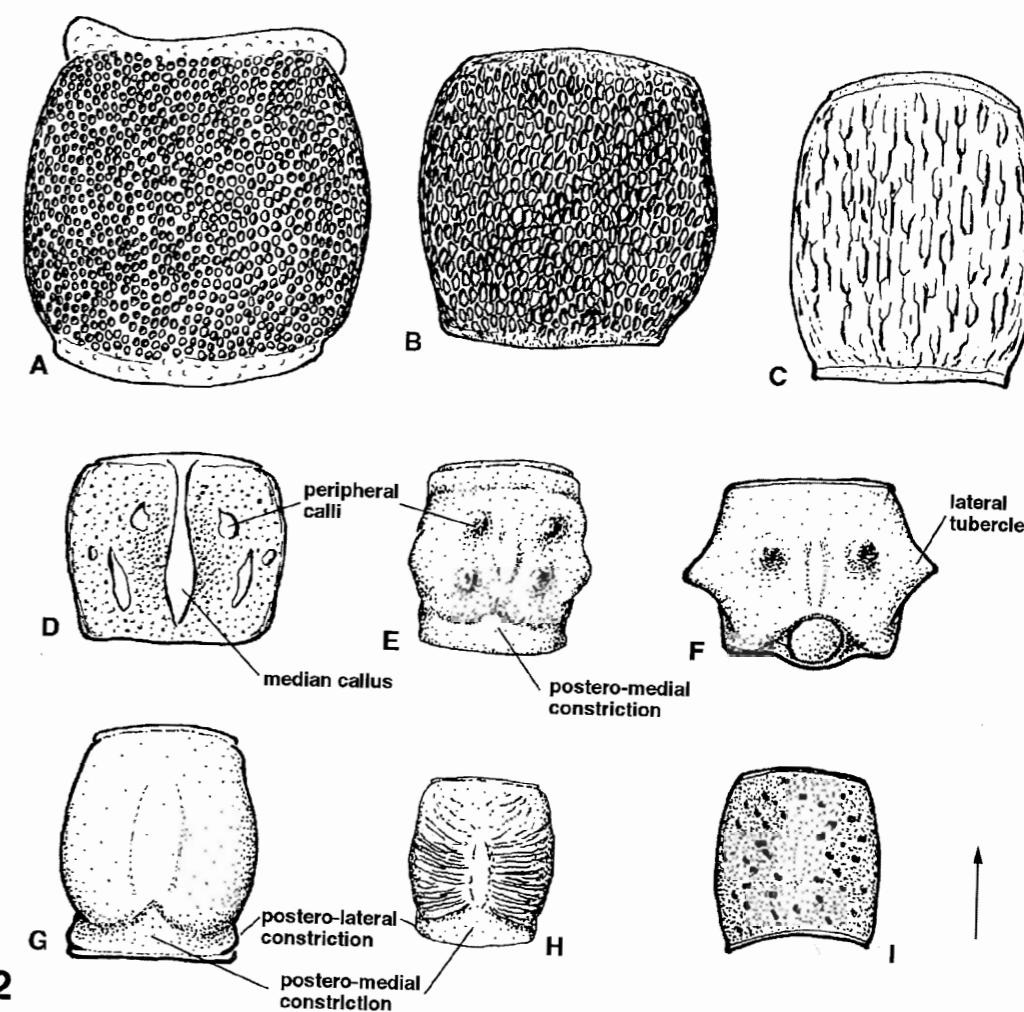


Fig. 12. Pronotal sculpturing, punctation, and calli, in dorsal view. Arrow indicates anterior. (A) *Nesiosphaerion insulare*; (B) *Anopliomorpha reticolle*; (C) *Elaphidionopsis fasciatipennis*; (D) *Parelaphidion aspersum*; (E) *Nesostizocera floridana*; (F) *Nyssicus topographicus*; (G) *Stizocera lissonota*; (H) *Ironeus submetallicus*; (I) *Parasphaerion granulatum*. Not drawn to scale.

Character 25.—Postero-medial pronotal constriction: (0) absent (Fig. 12A–D, F, I); (1) present (Fig. 12E, G, H). *Ironeus submetallicus*, *Nesostizocera*, and *Stizocera* have the pronotum constricted posteriorly with a small antero-medial extension of this constriction.

Character 26.—Postero-lateral pronotal constriction: (0) present (Fig. 12E, G, H); (1) absent (Fig. 12A–D, F, I). Only *Anoplocurius*, *Nephaliodes* Linsley, *Psyrassa* Pascoe, and *Stizocera* have a strong con-

striction of the pronotum at or anterior to the posterior sixth.

Character 27.—Sexual prosternal punctation (Fig. 42): (0) absent (Fig. 42A); (1) present (Fig. 42B). This is a sexually dimorphic character which, in males, is recognized as distinct patches of punctation anterior to the procoxae, and denser than surrounding punctation. Typically, these regions are surrounded by narrow, impunctate borders. In females, the prosternal punctation is non-differentiated. Both states are widespread.

Character 28.—Prosternal projection shape between procoxae: (0) linear, without expansions (Fig. 14); (1) broad and expanded apically only (Fig. 18); (2) broad and expanded laterally only; (3) broad and expanded apically and laterally. The linear prosternal projection which occurs only in *Anoplocurius*, *Terpnissa* Bates, and *Ectenessa* Bates, is recognized as a vertical planar projection lying between very narrowly separated procoxae. All other states have the prosternal projection broad and flattened horizontally between the procoxae. Most taxa have state 1, with a slight or strong expansion at the apex. *Eburia* Lepeletier and *Coleoxestia* have state 3, with expansions between the procoxae as well as apically.

Character 29.—Abruptly declivous prosternal projection (Fig. 44): (0) absent (Fig. 44A); (1) present (Fig. 44B). State 1 is present only in *Elaphidion* and *Eburia*. In some *Elaphidion* there is also a posteriorly directed process extending into the mesosternum.

Character 30.—Lateral mesocoxal cavities: (0) open to mesepimeron (Fig. 7); (1) closed to mesepimeron (Fig. 6). The states of this character are interpreted slightly differently from Linsley and Chemsak (1984, Fig. 1). When the open state is present, the mesosternum and metasternum do not contact one another laterad to the mesocoxae. This leaves an open space which allows contact between the mesepimeron and the mesocoxae. When the lateral mesocoxal cavities are closed, the coxae are completely surrounded by the meso- and metasternum. This character is usually difficult to interpret without clearing of the specimen since the point of contact is sometimes beneath the plane of the meso and metasternum. Both states are widely distributed.

Character 31.—Anterior margin of mesosternum (Fig. 35): (0) as in Fig. 35C; (1) as in Fig. 35D; (2) as in Fig. 35F; (3) as in Fig. 35E; (4) as in Fig. 35A, B; (6) as in state 2, but anterior margin abruptly directed posteriorly at sides. The mesosternum is

variously modified with regard to the anterior margin and mesosternal process between the mesocoxae. State 6 occurs only in the North American genera, *Anelaphus*, *Nesodes* Linsley, *Orwellion*, *Parelaphidion*, and *Peranoplium*. It is like state 2 (Fig. 35F) except for the anterior margin being abruptly directed posteriorly at the sides. State 3 occurs only in *Aposphaerion* Bates. The other states are widespread among the terminal taxa.

Character 32.—Mesosternum between coxae: (0) planar or slightly angled; (1) abruptly vertical. The abrupt vertical orientation of the anterior margin of the mesosternum is found only in *Championa*.

Character 33.—Mesosternal process width: (0) very wide; (1) narrow. The very broad mesosternal process, separating the procoxae by a distance greater than their diameter, is found only in *Anopliomorpha*.

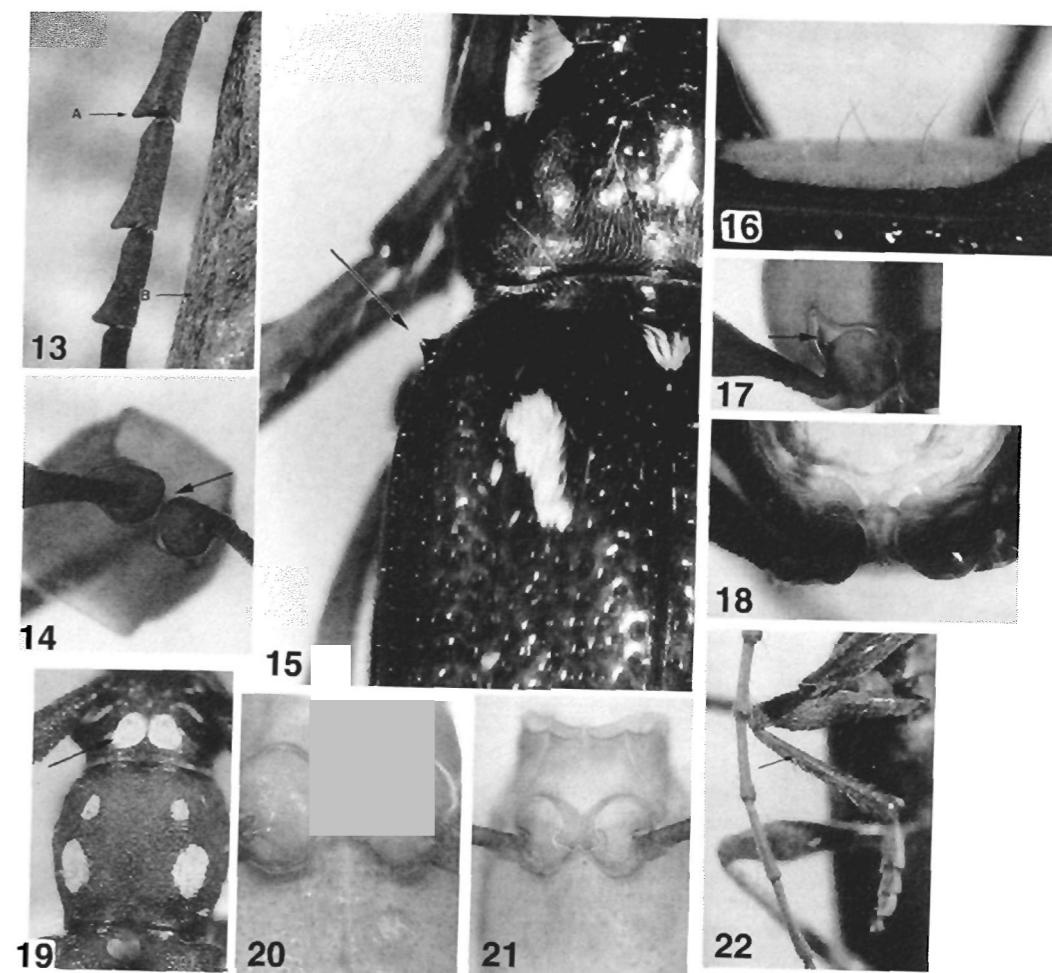
Character 34.—Mesosternal notch (Fig. 35): (0) present; (1) absent. The notch at the posterior margin of the mesosternum is absent only in *Ectenessa* and *Cordylomera*.

Character 35.—Mesonotal lateral projection orientation: (0) anteriorly oriented (towards head); (1) medially oriented between anterior and posterior margins of mesonotum (Fig. 36A–F); (2) posteriorly oriented (towards scutellum). All taxa examined have the lateral projections of the mesonotum medially oriented except for *Championa* and *Astromula* Chemsak and Linsley, which have them anteriorly oriented, and *Cordylomera* which has the arms posteriorly oriented.

Character 36.—Mesonotum lateral arm shape: (0) rounded (Fig. 36A–F); (1) acute and directed posteriorly. Acute lateral arms of the mesonotum arising medially but pointing posteriorly are only found in *Stenelaphus* Linsley.

Character 37.—Mesonotal median projection: (0) abruptly rounded (Fig. 36E, F); (1) absent or shallowly rounded (Fig. 36A–C); (2) very acute (Fig. 36D). The three states are widely distributed.

Character 38.—Mesoscutum pigmen-



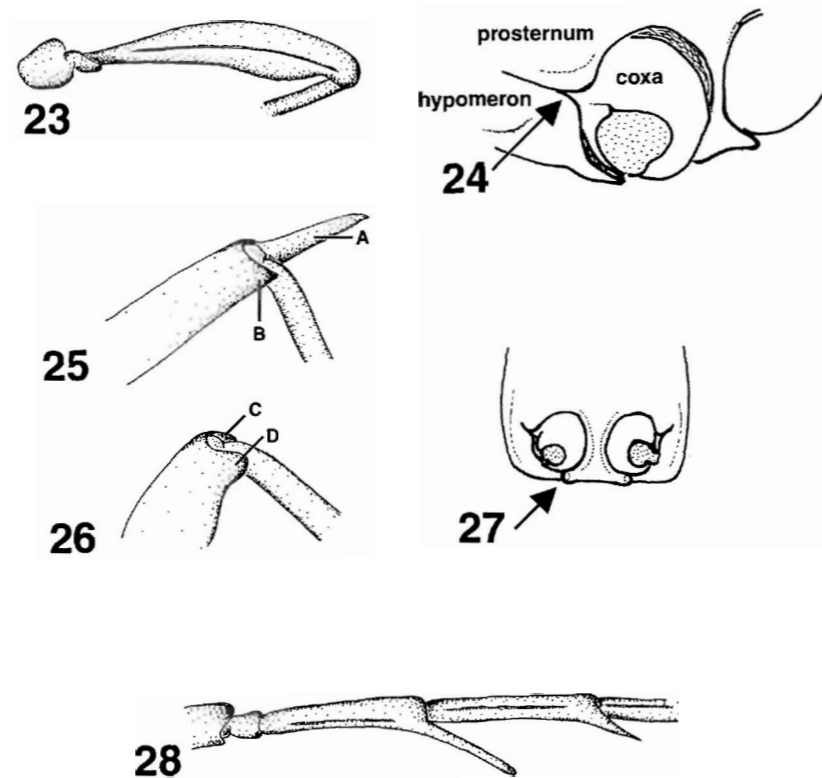
Figs. 13–22. Anatomical characters in Elaphidiini. 13, *Anelaphus obscurus*, dorsal view of left antenna and elytron, (A) laterally appendiculate antenna (lateral is to the left); (B) "typical" recumbent pubescence. 14, *Terpnissa listropterina*, oblique ventral view of cleared prothorax, showing linear prosternal projection. 15, *Elaphidion portoricensis*, dorsal view of elytron and pronotum, showing epipleural tooth. 16, *Stizocera poeyi*, lateral view of elytron, showing "flying hairs." 17, *Nyssicus topographicus*, ventral view of prothorax showing laterally open procoxal cavities. 18, *Anelaphus moestus*, posterior view of cleared prothorax, showing posteriorly open procoxal cavities and moderately expanded procoxal process apically. 19, *Linsleyonides chemsaki*, dorsal view of head and pronotum, showing post-ocular pubescence patches. 20, *Sphaerion* sp., ventral view of cleared pterothorax, showing mesocoxal projections from mesosternum absent. 21, *Castiale elegantula*, ventral view of cleared pterothorax, showing mesocoxal projections from mesosternum present. 22, ventral view of right legs and antenna showing linear antenna and tibial carina.

tion: (0) absent; (1) present on posterior half. The distinctive mesoscutum pigmentation occurs only in *Centrocerum*.

Character 39.—Scutellum basal constriction: (0) present (Fig. 36B, C); (1) absent (Fig. 36A, D–F). The constricted state is common in North American genera including *Anelaphus*, *Elaphidion*, *Eustromula*

Cockerell, *Orwellion*, and *Peranoplium* but also occurs sporadically in South American genera as well as the Asian *Allotraeus*. Most taxa examined lack the scutellar basal constriction.

Character 40.—Scutellum apex (posterior): (0) truncate; (1) rounded (Fig. 36C–F); (2) acute (Fig. 36B); (3) notched (Fig.



Figs. 23-28. Morphological characters in Elaphidiini. 23, *Tropimerus hovorei*, mesofemoral carina. 24, generalized laterally closed procoxal cavity. 25, metafemoral apices of *Pantonyssus nigriceps*. (A) spinose laterally; (B) dentiform mesally. 26, metafemoral apices of *Anelaphus moestus*. (C) rounded laterally; (D) rounded mesally. 27, *Megapsyrassa xestiodes*, ventral view of prothorax; arrow shows procoxal cavities closed posteriorly. 28, *Neoperiboem juanita*, base of antenna (first antennomere on left), showing blunt spine on antennomere 3.

36A). The rounded scutellum is widespread among most taxa examined; the acute state less so. The truncate scutellum occurs only in *Curtoemerus* and the notched state occurs only in *Meganeftus* Linsley.

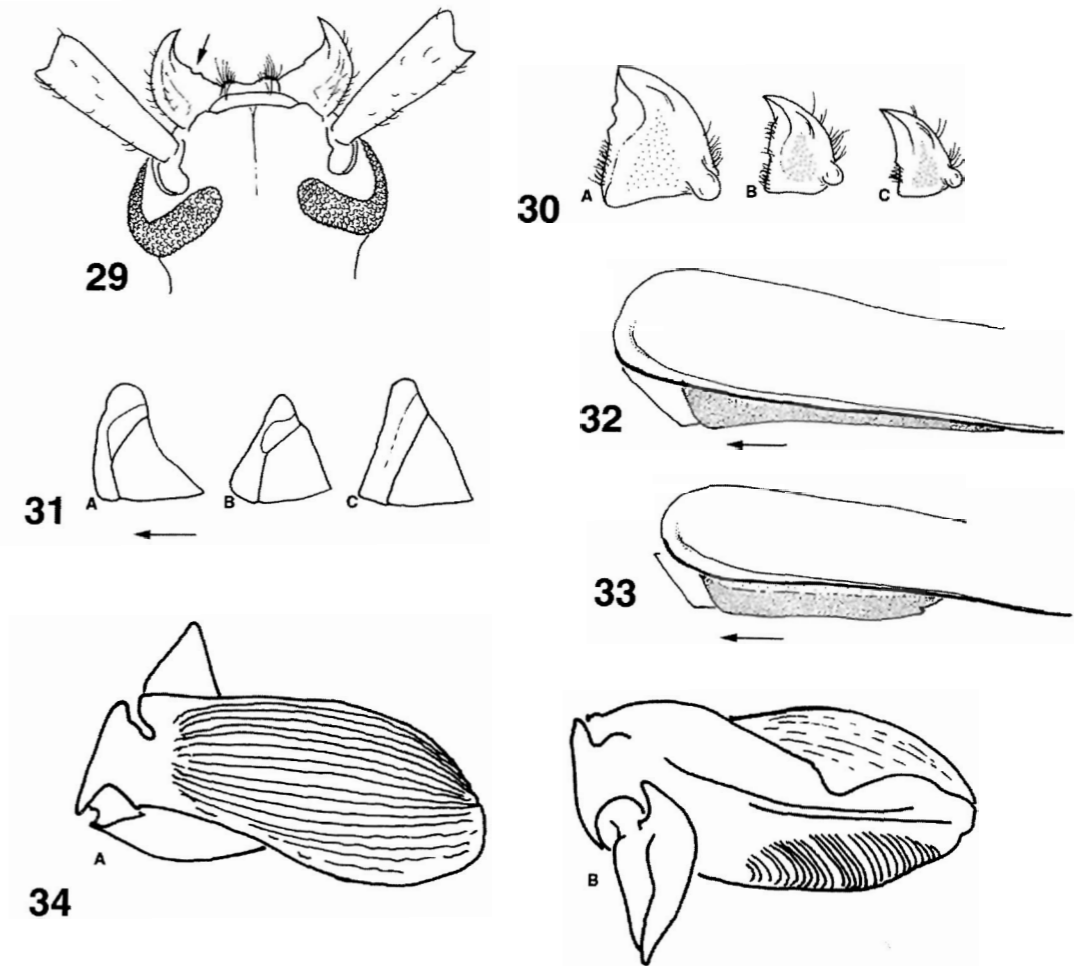
Character 41.—Basal width of scutellum: (0) approximately equal to width of mesonotum; (1) much wider than mesonotum. The wide scutellar base occurs only in *Neoperiboem*.

Character 42.—Junction of mesonotum and scutellum: (0) free dorsally; (1) completely fused. The fused condition occurs only in *Miopteryx*.

Character 43.—Lateral projections into mesocoxae from mesosternal process: (0) absent (Fig. 20); (1) present (Fig. 21). The presence of lateral projections is defined

both by rounded protuberances (condyles) of the mesosternum between the mesocoxae and corresponding concave depressions (acetabular excavations) on the coxae. As with most characters, clearing is necessary to accurately determine the state present. Both states are widespread in the examined taxa.

Character 44.—Mesepisternal carina (Fig. 31): (0) abruptly angled carina (Fig. 31A); (1) carina absent; (2) rounded carina (Fig. 31B); (3) straight, incomplete carina (Fig. 31C). The states of this character can only be seen with moderate clearing of the cuticle. State 0 is the most widespread. State 1 occurs only in *Anopliomorpha*, *Championa*, *Mephritus*, *Nyssicostylus*, *Nyssicus*, *Sphaerion*, *Terpnissa*, *Ectenessa*, and *Achryson*. State 2 occurs only in *Pseudo-*



Figs. 29-34. Morphological characters in Elaphidiini. Arrows indicate anterior. 29, *Elaphidion mucronatum*, dorsal view of head showing mandibular asymmetry. 30, Mandibular states, dorsal views of right mandible. (A) *Astromula nitidum*; (B) *Protomallocera hilairi*; (C) *Nephaliodes rutilus*. 31, Lateral view of mesothorax, showing mesepisternal states (arrow points to anterior). (A) *Anelaphus moestus*; (B) *Pseudomallocera auriflua*; (C) *Miopteryx spiniger*. 32, Lateral view of pterothorax, showing metepisternal-elytral junction in *Megapsyrassa huberi* (heavy stippling indicates region of metepisternum ventral to keel). 33, Lateral view of pterothorax, showing metepisternal-elytral junction in *Psyrassa* sp. (heavy stippling indicates region of metepisternum ventral to keel). 34, Metacoxal ridges in *Anelaphus moestus moestus*. (A) view of the anterior margin; (B) view of the posterior margin.

mallocera Zajciw. State 3 occurs only in *Atylostagma* White, *Miopteryx*, and *Hesperophanes* Dejean.

Character 45.—Shape of metasternal notch: (0) acute; (1) rounded; (2) blunt. The metasternal notch is the region of the metasternum that receives the antero-medial extension of the first abdominal ventrite. It is the angle of the sclerites on the inner, anterior margin of the posterior coxal cavities

(see Fig. 49) that determines the shape of this notch. If both sclerites come together at an angle of less than 45 degrees, then the notch is acute or blunt. An acute notch has a pointed apex; a blunt notch has a rounded apex. If both sclerites come together at an angle greater than 60 degrees, then the metasternal notch is rounded. The acute state is most widespread among the taxa examined. Only *Clausirion* Martins and Napp,

Eurysthea, *Stenosphenus*, *Terpnissa*, *Hesperophanes*, and *Cordylomera* have the rounded state.

Character 46.—Metasternal sulcus: (0) complete; (1) incomplete. The metasternal groove is an invagination corresponding to the internal metendosternite. The typical, complete condition is present when the groove runs anteriorly to near the plane at the posterior margin of the metacoxae (Fig. 49). The incomplete condition does not attain the coxae and typically extends anteriorly only half the length of the metasternum. The complete state is widespread. The incomplete condition occurs in many West-Indian genera not included in the analyses: *Linsleyonides*, *Nesanoplium* Chemsak, *Nesiosphaerion* Martins and Napp, and *Elaphidionopsis* Linsley.

Character 47.—Posterior notch of metepisternum (Fig. 38): (0) absent or subtle indentation (Fig. 38A); (1) narrow, shallow indentation (Fig. 38C); (2) wide and deep (usually extending at least one-third the width of the metepisternum at the posterior edge, below the keel) (Fig. 38B, D). This notch, if present, occurs on the posterior margin or postero-ventral margin of the metepisternum, and is most easily seen with some clearing of the cuticle. All states are widespread among the examined taxa.

Character 48.—Metepisternal notch projection: (0) absent; (1) small lateral bump present. If present, the projection is located in the region of the metepisternal notch, on the postero-ventral margin of the metepisternum. This is best seen by looking down the metepisternum from the anterior end. Of the specimens examined for the phylogenetic analysis, this projection was found only in *Sphaerion*. Subsequent examination of non-dissected *Mephritus* species has revealed a small protuberance in the same region of the metepisternum.

Character 49.—Metepisternal keel position: (0) dorsally positioned (Fig. 38B); (1) approximately midway positioned (Fig. 38A, C, D). The keel is the longitudinal ridge along the metepisternum above which

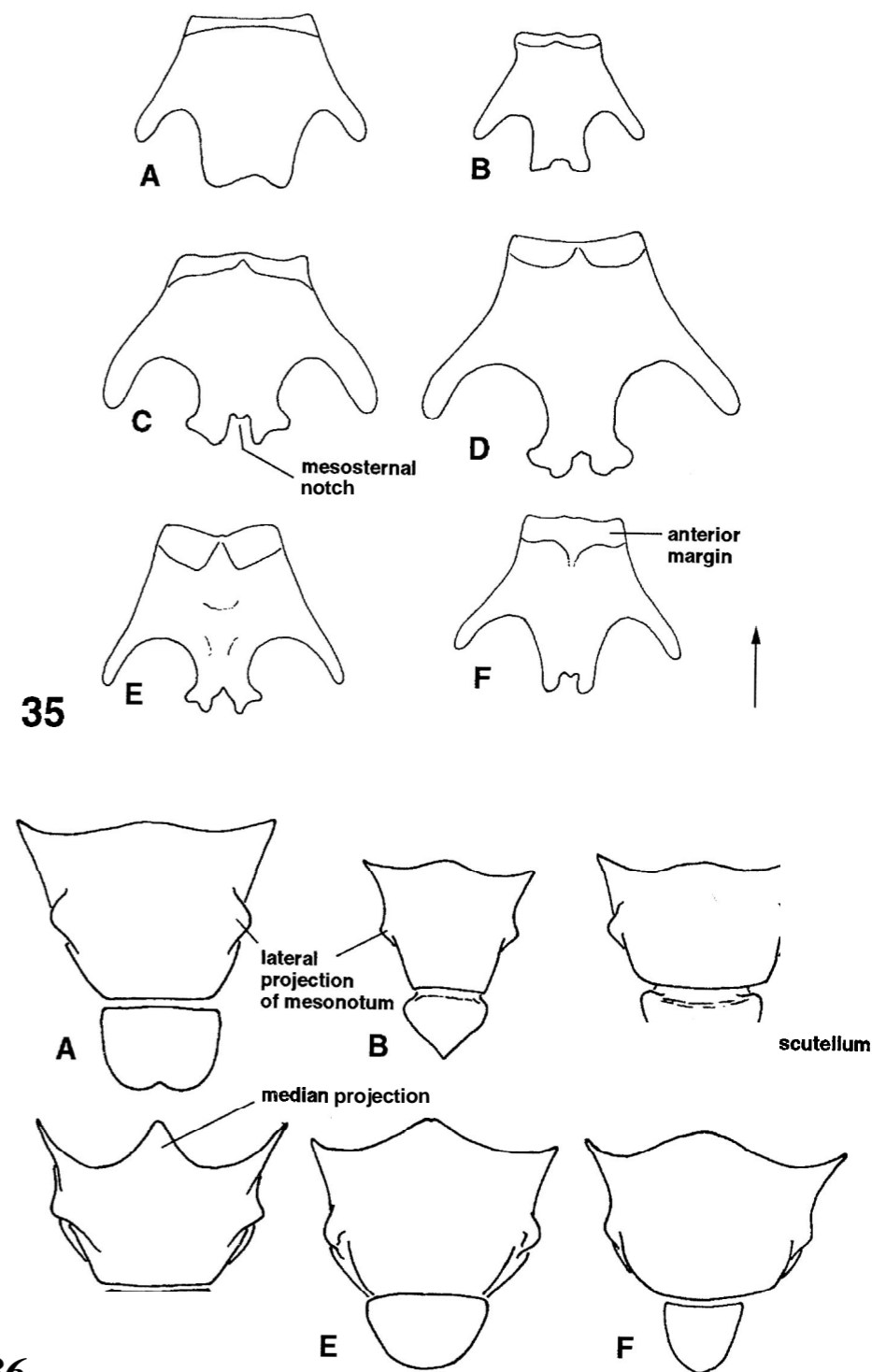
the cuticle is usually membranous, and below which it is more heavily sclerotized. Both states are widespread among examined taxa, although the dorsally-positioned carina is more common among provisional outgroup taxa.

Character 50.—Metepisternal sclerotization: (0) even sclerotization above and below keel; (1) Highly sclerotized ventrally below keel and membranous dorsally (Fig. 38A–D). State 1, differential sclerotization, is widespread among most taxa examined. Those taxa with even sclerotization above and below the keel include: *Appula*, *Atylostagma*, *Championa*, *Clausirion*, *Sphaerion*, *Terpnissa*, *Ectenessa*, *Neocompsa*, *Batyle* Thomson, *Hesperophanes*, *Coleoxestia*, and *Cordylomera*.

Character 51.—Mesal mesofemoral apices: (0) spinose (as in Figs. 8D, 9D); (1) dentiform (Fig. 25B); (2) rounded (Fig. 26D). Spinose femoral apices are acute, pointed processes extending beyond the tibial insertion and having an angle about the apex of less than 45 degrees. Dentiform femoral apices are pointed at the apex, do not extend much beyond the tibial insertion, and have an angle about the apex of greater than 60 degrees. Rounded femoral apices have a rounded apex and do not extend much beyond the tibial insertion. Dentiform and rounded states are widespread among the examined taxa. Those with spinose mesal mesofemoral apices include: *Atylostagma*, *Castiale*, *Elaphidion*, *Nyssicus*, *Phoracantha*, *Stizocera*, and *Eburia*.

Character 52.—Lateral mesofemoral apices: (0) spinose (as in Figs. 8C, 9C); (1) dentiform (as in Fig. 25B); (2) rounded (Fig. 26C). See state descriptions for Character 51. Dentiform and rounded states are widespread among the examined taxa. Those with spinose lateral mesofemoral apices include: *Appula*, *Castiale*, *Neomallocera*, *Pantonyssus* Bates, *Parastizocera*, and *Phoracantha*.

Character 53.—Mesal metafemoral apices: (0) spinose (Figs. 8D, 9D); (1) dentiform (as in Fig. 25A); (2) rounded (Fig.



35
Figs. 35–36. Morphological characters in Elaphidiini. Arrow indicates anterior. 35, Mesosternal variation, arrow indicates anterior. (A) *Miopteryx spiniger*; (B) *Conosphaeron concolor*; (C) *Elaphidion mucronatum*; (D) *Castiale elegantula*; (E) *Aposphaerion longicolle*; (F) *Appula lateralis*. 36, Mesonotal variation. (A) *Meganeflus fulvipennis*; (B) *Allotraeus sphaerioninus*; (C) *Parelapheidion aspersum*; (D) *Trichophoroides niveus*; (E) *Parastizocera procera*; (F) *Periboem acuminatum*.

INDEX

- acuminatum* Thomson. *Periboeum* 82
Adiposphaerion Martins & Napp 47. 48. 100
albisparsus Bates. *Trichophoroides* 95. 96
albomaculatus Champlain & Knull, *Linsleyonides* 65
alienus LeConte, *Stenelaphus* 90, 92
Allotraeus Bates 39
Ambonus Gistel 48. 49. 101. 103
Amethysphaerion Martins & Monné 49. 102
amictus Newman. *Mephritus* 68
Aneflomorpha Casey 34. 48. 52. 102. 103
Aneflus LeConte 38. 48. 51. 102. 105
Anelaphus Linsley 34. 48. 52. 102. 103
Anepsyra Casey 50
Anopliomorpha Linsley 48. 52. 101
Anoplocurius Fisher 53. 54. 98
Apoclausirion Martins & Napp 55. 99
Aposphaerion Bates 43. 55. 104
Appula Thomson 54. 55, 100
aspera Knull, *Gymnospyra* 59
aspersum Haldeman. *Parelaphidion* 78. 82
Astromula Chemsak & Linsley 54. 56. 105
Atharsus Bates 56. 99
atiaia Martins & Napp. *Stizocera* 93
atomarius Drury, *Enaphalodes* 59. 62
Atylostagma White 54. 57. 103
Aulacoscapus Linsley 72
auriflua Klug, *Pseudomallocera* 83. 86
aurivilli Melzer, *Nyssicostylus* 77. 78
aurivillii Linsley. *Trichophoroides* 95
Axestinus LeConte 38. 51
basicornis Pascoe. *Psyrassa* 87
bicolor Martins, *Minipsyrassa* 73
bimaculata Bates. *Micropsyrassa* 71
canotiae Fisher, *Anoplocurius* 53. 54
castaneum Chemsak & Linsley. *Sphaerionillum* 90
Castiale Pascoe 54. 57. 100
caymanensis Fisher. *Stizocera* 93
Centrocerum Chevrolat 54. 57. 104
Championa Bates 39. 54. 105
chemsaki Skiles, *Linsleyonides* 66
Clausirion Martins & Napp 54. 58. 104
clenchi Lane, *Hemilissopsis* 64
comptum Martins & Napp. *Clausirion* 54. 58
concolor Linsley, *Conosphaerion* 58. 59
Conosphaerion Linsley 58
Conosphaerion Linsley 58. 59. 101
Cordylomera Serville 39
cribricollis Bates. *Psyrassa* 36. 83. 87
Crocidastus Pascoe 49
Curtomerus Stephens 59. 60. 105
cyaneus Giesbert, *Tropimerus* 97
cyanipenne Audinet-Serville, *Sphaerion* 91
Cycliopleurus Hope 60
Cylindera Newman 60
Cylindrodera Gemrninger & Harold 60
Cyrtomerus Gemminger & Harold 60
decipiens Bates. *Trichophoroides* 95. 96
diabolicus Lameere, *Mephritus* 66
distinctus Newman. *Ambonus* 48
dozieri Fisher. *Stizocera* 93
duplex Bates. *Ironeus* 65. 66
Elaphidion Audinet-Serville 59. 60. 100. 104
Elaphidionopsis Linsley 59. 61. 95. 99
Elaphidium Agassiz 60
elegans Chemsak. *Championa* 39. 54
elegans Chevrolat, *Elaphidion* 36
elegantula Perroud, *Castiale* 54. 57
Elaphidionoides Linsley 52
erichsoni White. *Pantonyssus* 80
Enaphalodes Haldeman 59. 62. 104
Etymosphaerion Martins & Monné 59. 63. 105
Euristhea Lacordaire 63
Eurysthea Thomson 59. 63. 105
Eustroma LeConte 63
Eustromula Cockerell 59. 63. 102
Eutrichophoroides Linsley 38. 95
eximium Bates. *Anelaphus* 52
exornatum Newman, *Centrocerum* 54. 57
exoticum Martins & Napp. *Pilisphaerion* 84
extinctus Wickham, *Anelaphus* 10. 19
fasciatipennis Linsley. *Elaphidionopsis* 59. 61. 95
flavus Fabricius. *Curtomerus* 59. 60
floridana Linsley, *Stizocera* 93
fracticorne Wickham. *Elaphidion* 10
fuchsi Wickham, *Neaneplus* 71. 74
fulvipennis Bates. *Meganefus* 66. 67
gibbulum Bates. *Orwellion* 78. 79
glabra Schaeffer. *Atylostagma* 54
glauca Audinet-Serville, *Mallocera* 66. 67
globosus Knull, *Romulus* 89. 90
granulosum Martins & Napp. *Parasphaerion* 81
Gymnospyra Linsley 59. 64. 102. 103
Haplosphaerion Linsley 70
Hemilissopsis Lane 64. 101
Hemistizocera Linsley 36. 87
hesperus Chemsak, *Metironeus* 69
hilairei Gounelle, *Protomallocera* 85
hirta Kirby. *Paramallocera* 78
hoferi Knull, *Anelaphus* 48. 52
hovorei Chemsak. *Metironeus* 66
hovorei Giesbert. *Tropimerus* 95
Hypermallus Lacordaire 62
imbellis Casey, *Micraneflus* 66. 70
inornatum Chemsak & Linsley. *Anelaphus* 52
insulana Gahan, *Stizocera* 93
insulare White, *Nesiosphaerion* 71. 76. 95
insularis Linsley. *Nesodes* 77. 78
intricatum Galileo & Martins. *Piezophidion* 84
Ironeus Bates 36. 38. 65. 66. 105
jansoni Bates. *Trichophoroides* 95
jassuara Martins & Napp. *Stizocera* 93
hcordairei Lacordaire. *Paramallocera* 80
Lampracantha Thomson 79
Lampracanthus Thomson 79
Lampromerus Thomson 60
lateralis White. *Appula* 54. 55
Linsleyonides Skiles 65. 66. 98
lippus Germar, *Ambonus* 49
listropterina Bates. *Terpnissa* 95. 96
longicolle Bates. *Aposphaerion* 54. 55
lugens LeConte, *Stenosphenus* 90
maculatum Chemsak & Noguera. *Anelaphus* 52
magnipunctata Knull, *Gymnospyra* 64
Mallocera Audinet-Serville 66. 67. 99
marginatus Bates. *Miltesthus* 71. 72
Meganefus Linsley 66. 67. 102
Megapsyrassa Linsley 66. 68. 104
Mephritus Pascoe 66. 68. 100. 101
Metironeus Chemsak 66. 69. 101
Micraneflus Linsley 66. 70. 105
Micranoplium Linsley 66. 70. 105
Micropsyrassa Linsley 70. 71. 100
Miltesthus Bates 71. 72. 101
Minipsyrassa Martins 73. 104
Miopteryx Blanchard 71. 73. 100
moestus LeConte, *Anelaphus* 48
Morphaneplus Martins & Napp 71. 74. 105
Moureana Zajciw 89
Neaneplus Linsley 71. 74. 102
Neomallocera Martins & Napp 71. 74. 100
Neoperiboeum Linsley 71. 75. 101
Neotrichophoroides Linsley 38. 95
Nephaliodes Linsley 71. 75. 102
Nephalius Newman 91
Nesanoplium Chemsak 76. 95. 99. 104
Nesiosphaerion Martins & Napp 71. 76. 95. 104
Nesodes Linsley 77. 78. 103
Nesostizocera Linsley 36. 93
nigricauda Bates. *Atharsus* 56
nigricornis Bates. *Pantonyssus* 78
nigricornis Martins & Napp. *Apoclausirion* 55
nigripes Martins & Monné, *Amethysphaerion* 49
nitida Chemsak. *Psyrassaforma* 83. 88
nitidum Chemsak & Linsley, *Astromula* 54. 56
niveus Linsley. *Trichophoroides* 95. 96
notatus Olivier. *Stenosphenus* 93
Nyssicostylus Melzer 77. 78. 100
Nyssicus Pascoe 78. 79. 99
obliqua Audinet-Serville, *Eurysthea* 59. 63
obscurus LeConte, *Aneplus* 38. 48. 51
ocellicollis Zajciw, *Rhomboidederes* 89
opulenta Newman. *Neomallocera* 71. 74
Orion Guérin-Méneville 39. 78. 103
Orwellion Skiles 78. 79. 103
palpalis Bates. *Poecilomallus* 83. 85
Pantonyssus Bates 78. 80. 100
Paramallocera Aurivillius 78. 80. 103
Parasphaerion Martins & Napp 81. 99
Parastizocera Linsley 78. 81. 99
Parelaphidion Skiles 78. 82. 102. 104
patagonius Guérin-Méneville. *Orion* 39. 78
Peranoplium Linsley 34. 52
Periboeum Thomson 82. 83. 100
Phoracantha Newman 39. 104
phtisica Gounelle. *Stizocera* 93
piceum Chemsak. *Anelaphus* 52
Piezophidion Galileo & Martins 84. 105
pilicornis Fuchs. *Trichophoroides* 95
Pilisphaerion Manins & Napp 84. 100
pilosella Bates. *Micropsyrassa* 70
plicicollis Germar, *Stizocera* 90
Poecilomallus Bates 83. 85. 101
poeyi Guérin-Méneville, *Stizocera* 90. 93
polita White, *Atylostagma* 57
portoricensis Fisher, *Elaphidion* 36
pristinus Wickham, *Stenosphenus* 10. 19
procera Erichson. *Parastizocera* 78. 81
prolixus Martins & Napp. *Morphaneplus* 71. 74
Protaneflus Linsley 51
protensus LeConte, *Aneplus* 51
Protomallocera Martins & Napp 85. 100. 103
Protosphaerion Gounelle 83. 86. 103
Pseudaneflus Chemsak & Linsley 68
Pseudibidion Casey 87
Pseudomallocera Zajciw 83. 86. 98
Pseudoperiboeum Linsley 83. 87. 101. 102
Psyrassa Pascoe 36. 83. 87. 102. 103. 104
Psyrassaforma Chemsak 83. 88. 101
puberulum Fleutiaux & Sallé, *Nesanoplium* 76. 95
punctiventris Cazier & Lacey. *Stizocera* 93
quadrigutatus Swederus, *Nyssicus* 79
quadrisignatum Bates. *Sphaerionillum* 92
ravidus Gounelle, *Rhomboidederes* 83
rectilinea Casey. *Anefomorpha* 48
reticollis Bates. *Anopliomorpha* 48. 52
Rhomboidederes Zajciw 83. 89. 99
Romaleum White 62
Romulus Knull 89. 90. 104
rubristerna Martins & Napp. *Sphaerioeme* 89. 90
rubrum Martins & Napp. *Adiposphaerion* 47. 48
rutilus Bates. *Nephaliodes* 71. 75
simile Schaeffer. *Anelaphus* 52
sonoranus Casey, *Aneplus* 48
Sotenus Sharp 60
Sphaerioeme Martins & Napp 89. 90. 99
Sphaerion Audinet-Serville 90. 91. 101
Sphaerionillum Bates 90. 92. 105
Sphaerion Thomson 91
spinicorne Drury, *Elaphidion* 18. 59. 60
spiniger Blanchard. *Miopteryx* 71. 73
spurcus LeConte, *Anelaphus* 48. 52
Stenelaphus Linsley 90. 92. 103
Stenosphenopsis Linsley 93
Stenosphenus Haldeman 90. 93. 105
Stizocera Audinet-Serville 36. 90. 93. 100. 103