THE GENERA OF
ELAPHIDIINI THOMSON 1864
(COLEOPTERA: CERAMBYCIDAE)

BY

STEVEN W. LINGAFELTER
This work is dedicated to

Dr. Byron Alexander

with appreciation for his inspiring talent and dedication to teaching, research, and scientific illustration.
Abstract—A generic-level phylogenetic analysis of the tribe Elaphidini 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 Elaphidini. Phoracanthini Lacordaire 1869 is removed from Elaphidini and resurrected as a tribe with Phoracantha Newmann 1840 as the type genus. Cordylus Thomson 1834 and Allotracus Bates 1887 are not elaphidines and are tentatively retained to Phoracanthini. Champsiana Bates 1880, and Orion Guérin-Méneville 1844 are removed from Elaphidini 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 = Psyrrusa Pascoe 1866. Trichophoroides (Anelaphus) Linsley 1957b = Anelaphus Linsley 1936. Asetinina LeConte (1873) = Anelaphus LeConte (1873). The following 29 new combinations are proposed: Aneflus obscurus (LeConte 1873), Aneflus eximium (Bates 1885), Aneflus hoferi (Keull 1934b), Aneflus hornatum (Chemsak and Linsley 1979), Aneflus maculatum (Chemsak and Ogura 1993), Aneflus plecan (Chemsak 1962), Aneflus similis (Schaeffer 1908), Aneflus subdepressum (Schaeffer 1904), Aneflus nickeri (Casey 1924), Aneflus undulatum (Bates 1880), Psyrrusa cribricollis (Bates 1885), Stizocera aitaina (Martins and Napp 1983), Stizocera caymanensis (Fisher 1941), Stizocera dojieri (Fisher 1947), Stizocera floria (Linsley 1949), Stizocera insulana (Gahan 1895), Stizocera jasuara (Martins and Napp 1983), Stizocera jucunda (Gonoule 1909), Stizocera jucund (Guérin-Méneville 1838), Stizocera punctiventris (Cazier and Lacey 1952), Stizocera submetallus (Chemsak and Linsley 1968), Stizocera subradiata (Martins and Napp 1992), Stizocera vanzowelburgi (Fisher 1932), Stizocera wagneri (Gonoule 1913), Trichophoroides abipara (Bates 1872), Trichophoroides jansem (Bates 1885), Trichophoroides alini (Linsley 1961), Trichophoroides decipiens (Bates 1880), Trichophoroides plicicornis (Fuchs 1961). Diagnoses of all genera are presented with notes on distribution, diversity, and relationships. A key to genera of Elaphidini is presented.

LINGAFELTER. GENERA OF ELAPHIDINI

Introduction

The Elaphidini is among the most geographically 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, elaphidines are the most abundant cerambycids attracted to lights. As currently defined, elaphidines 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 Elaphidini. I developed a list of explicitly defined characters and states for all elaphidine 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 Elaphidini (and similar taxa with metally spined antennae) is provided for their identification.

TAXONOMIC HISTORY

Thomson (1864) proposed the "Division" Elaphidiontidae to include ten genera. This family group name was based on the genus Elaphidion Audinet-Serville. Elaphidiontidae has been used since 1930, but Ivi (1985) indicated Elaphidion should be the appropriate name of the tribe. The basis of Ivi'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 latinated with the nominative singular termination, -on. Thus the stem is Elaphid and the tribal suffix, -idae must be added. Forming Elaphidini (following Ivi = Ilius 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, Callidopini, and Methini. Thomson further characterized the tribe Eubetrica, originally proposed by Blanchard (1845), as including many other currently recognized elaphidine taxa including Eubetrica White, Centrocerus Chevron, Ambonus Gistel, Spheortroct Au- din-Serville, Periboeum Thomson, Appu- la Thomson, Stizocera Audinet-Serville, Mallocoera Audinet-Serville, and Eurythrae Thomson. Thomson (1864) defined the Elaphidini as having body convex, eyes coarsely faceted, femora slightly clavate, and elytral spines spinose. These characters separated Elaphidionidae from its Eubetrica which had body subdepressed, eyes without apical spines, and femora clavate. La- cordaire (1869) proposed the groups Hes- pérophanes (including taxa which are currently in Elaphidini and Hesperophanini, characterized by the non-globose anterior coxae, externally open intermediate coaxal cavities, and generally unspined antennae), Eubritae (mainly consisting of taxa with eburneous elytral calli but identified primarily on the basis of externally-closed intermediate coaxal cavities), and Phoracan- thioides (including taxa currently in Elaphidini and Phoracanthini, characterized by spined but non-carinate antennae, intermediate coaxal cavities open externally, procoxa- l cavities not angulate externally), and Sphérionides (including nearly all of Thom- son's Eubritae, characterized by spines and carinate antennae, anterior coaxal cavities angulate externally, and intermediate coaxal cavities open externally). The variability of the characters above
that the distinction of Sphaerionini from not satisfactorily closed or open in closely related species of the anterior coxal cavities may be either able characters were the non-carinate useful character. He felt that the most Sphaerionini as junior synonyms. The "elaphidiine" group is most concentrated "elaphidiine" species (Chemsak, et al. 1925); Anelaphus, Elaphidion, Par-elaphidion Skiles, Enaphalades Haldeman) are attracted in great numbers to brown sug- ar 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 Tropinomer Giesbert (1987), and Stenophanes Haldeman (Giesbert and Chemsak 1989) are commonly encountered on flowering trees. Anelomorphophetus (LeConte) adults have been reported feeding in large num- bers on Karwinskia blossoms (Tumbow and Wappes 1981). Adults of Anelaphus albifasciatus Linell have been reported feeding on new growth of Oponasa (Raske 1972).

T Wig-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 di- tantly related Oncideres. 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 Elaphidion including Pyrrhus Pascoe (Champain, et al. 1925); Anelomorphophetus Casey (Craighead 1923); and Anelaphus Linsley (Craighead 1950), although in these groups the girdling is internal and done by the larve. Larval hosts are not known for most spe-

in bark of dead branches. The larvae either feed for some time under the bark, or im- mediately enter the wood, feeding and de- veloping within the heartwood. Larval de- velopment takes 1-3 years, correlated with the size of the beetle. A pupal cell is created in the region be- tween the bark and sapwood at the end of larval development. Pupation occurs in ei- ther late summer to early fall, or early spring. Adults do not emerge until spring or summer, regardless of when pupation oc- curs.

It is assumed that adults of most elaphi- dines (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, Enaphalades Haldeman) are not represented in numbers to brown sug- ar bantan 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 Tropinomer Giesbert (1987), and Stenophanes Haldeman (Giesbert and Chemsak 1989) are commonly encountered on flowering trees. Anelomorphophetus (LeConte) adults have been reported feeding in large num- bers on Karwinskia blossoms (Tumbow and Wappes 1981). Adults of Anelaphus albifasciatus Linell have been reported feeding on new growth of Oponasa (Raske 1972).

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dissected for examination of the full range of phylogenetically important characters. Omission of taxa is probably very common in phylogenetic analyses, and most extinct taxa have an undiscovered or absent fossil record, or insufficient information can be gleaned from their fossil record. The Elaphidini 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 Elaphidini, *Anelaphus extinctus* (Wickham) and *Stenophora pristina* 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 elaphidini 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 elaphidini 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, phylayria, hind wings, and genitalia were disarticulated. The wings, and in some cases, genitalia, were placed directly into vials of 50% glycerin/50% of 10% hydroxyl peroxide solution for 10–30 minutes and then transferred to the glycerin vial. The remaining body parts were partially cleared in 10% hydroxyl 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 were used as exoskeletal features or cuticular processes visible through dissection microscopy with fiber optic illumination and magnification less than 20x. Additional characters could only be revealed effectively through the use of Nomarski interference contrast microscopy. Presumably homologous characters among different species and discrete variable states were identified and coded in the data matrix.

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

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characters examined in this study follows.

Characters not used in analyses or key.—Genitalia of many genera of Elaphidines 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, genitalia characters were not included in the phylogenetic analyses. Since the key was intended to be practical and not require dissections, genitalia 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 definitive 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 punctation 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.—Ommatidia 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...
finely faceted eye appears smooth. This character has been used since Lacordaire (1869) for classification of Cerambycidae. Because ommatidial 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 ommatidial size to be consistent within a species. Virtually all traditional elaphidini taxa have coarsely faceted eyes. Those with finely faceted eyes include: Championa Bates, Irenes Bates (in part), Sphaerionidae; Lincapelter, Others of Elaphidini.

Table 2. Character state matrix for taxa of Championa Bates. See Table 2. Continued.
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 Apalinus, Mallocera, Miltesthus Bates, Nyscostylus Melzer, Protomalacoma Martins and Napp, and Sphaeront 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 mandible viewed from mesal, biting surface). State 1, shared by Peranoplus and Anelaphus, is characterized by having widely separated dorsal and ventral planes of the subapical incisor region (distinctly more than one-third width 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 palp in the speciose, primarily North American Elaphidiinae outgroup including Anelaphus, Peranoplus, and Elaphidion. Most other taxa examined possess these sensilla on the labial palp.

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 Championia, the digitiform patches occurred towards the 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 Sagus 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 Curomerus Stephens, which has greatly expanded palp. Most taxa in other Cerambycidae tribes (and other subfamilies) have unexpanded terminal maxillary palpomeres.

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

Character 9.—Mesal antennal spines: (0) absent (Fig. 13); (1) present and acute (Figs. 8B, 9B, 45, 46); (2) present and blunt (Fig. 28). Nearly all traditional elaphidine taxa possess mesal antennal spines on at least the third antennomere. Some preliminary outgroup taxa lacked these spines except for Allotaxa and Cordylomera. Anopolocuris Fisher, Aexitinus (Fig. 45), Curomerus, Elaphidion elegans, Eurythenia Thomson, Microphila Linsley, and Morpheus Martins and Napp lack these spines. Some Anoplomorph Case species, Centrocerus Chevolot, Microsymbrassa Linsley, Neoperiboeum Linsley, and most Elaphidion aethius 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 pinched at apices (Fig. 45C); (2) fiddle 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 Aneclus, Aexitinus, Micranthia, Neaefus, and Coleosoma Aurivillius have the apices greatly expanded.

Character 12.—Antennal carinae: (0) absent (Fig. 14); (1) single or double carinate (Fig. 45B). Elaphidion antennae 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.
This character, like orommatidal structure, has been used historically to separate Sphaerodatta (carninae present) from the rest of Elaphidion (carninae absent) (Lacordaire 1869; Linsley 1936; Linsley 1961b). Linsley (1936) acknowledged, however, that this character was not absolute in that the carinula are absent in some species of Elaphidion. I have found antenal carinulae to be widespread in Elaphidion, with no regional pattern. Carnae were absent from all provisional outgroup taxa examined, except Neo-compassa Martins.

Character 13. — Antennal segmentation: (0) 12 antennomeres; (1) 11 antennomeres. Most species of Aneflus and all Aneflus, Pseudosegmentation Martins and Monné, and Pseudosegmenta Chemak have antennae distinctly 12-segmented. Many additional taxa (including some Aneflus species) have the eleventh segment constricted, superficially appearing 12-segmented (Fig. 8B), but this is not the case (see discussion of Character 15).

Character 14. — Length of third antennomere of male: (0) approximately length of pronotum; (1) about half length of pronotum (this state also present in females) (Fig. 4A); (2) approximately two-thirds length of pronotum (Figs. 8, 10B). This character is sexually dimorphic. Generally, males have longer antennae than females in Elaphidion. This character is particularly evident in the length of the third antennomere. For this reason, size-comparing females of genus "a" with males of genus "b" would be inappropriate.

Character 15. — Pseudosegmental setae on terminal antennomere: (0) present (Fig. 4B); (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 (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 punctuation 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 cells: (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 cells which are present but reduced (state 1) appear as raised, partially punctate regions around the central pronotal disc. Peripheral pronotal cells 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 prothorax and the projection of the hypomeron. 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 mesothorax and its articulation with the antero-lateral region of the prothorax. The procoxae are closed laterally when the trochantin is hidden and the propleuron and prothorax are fused very close to the coxae. This character was a fundamental one used by Lecordaire (1869) to separate the sphaerionitte "group" from the rest of Elaphidini. In nearly all South American genera, the open state occurs. In most of the primarily North American genera and the provisional outgroup taxa, the closed state is predominant.

Character 20.—Lateral pronotal tubercles: (0) acute (Figs. 12K, 41A); (1) rounded (Figs. 12E, 41B-E); (2) absent (Figs. 12A-C, G-I, 41C-E). Pronotal tubercles are highly modified in many genera of Elaphidini. Narrow and elongate lateral projections of the pronotum, ending in a sharp point are classified as acute; broad lateral protruberance which are not sharp at the apex are denoted as rounded; a pronotum without distinct lateral processes has state 0. Most of the taxa examined lack these tubercles. Only Mallophora Megaphritis Pascoe, Neostizicora forfata (Linsley), Nyssicus Pascoe, Orus, Phoracantha, Pseudoderboeckia Linsley, Rhomboides E. J. Bates, and Sphaerianthus have acute pronotal tubercles. These are subject to sexual dimorphism in Megaphritis and Sphaerianthus, with males generally having them less pronounced.

Character 21.—Transverse ridges on pronotal disc: (0) present (Fig. 12H); (1) absent (Fig. 12A-C, G-I); (2) present (Fig. 12A-C, G-I). Only Champioma, Neostizicora submetallica, Metriornis Chermshe, and Stizicora plicicollis (Germain) have transverse ridges on the pronotum.

Character 22.—Dorsal pronotal punctation: (0) absent to very sparse (Fig. 12G-H); (1) moderately dense (Fig. 12D); (2) confluent but not alveolus (Fig. 12A); (3) confluent and alveolate (Fig. 12B). State 0 has punctures separated by more than 10 X their diameters; state 1 has rounded punctures separated by an average of 1-5 X 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 trapezoid-shaped punctures which are alveolate, with thin partitions separating them. Anoplolepis Linsley, Anoplolepsis Fisher, Conopphorina Linsley, Symoypopus maguiquunchata (Knutti), Micropysurus bimaculata (Bates), and most Peraphorini species have confluent, alveolate punctation. The other states of this character are more widespread.

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

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

Character 25.—Postero-medial pronotal constriction: (0) absent (Fig. 12A-D, F-I); (1) present (Fig. 12E, G, H); (2) absent (Fig. 12A-D, F-I). Only Anoplolepis, Nephilolepsis Linsley; Prayaus Pascoe, and Stizicora have a strong constriction of the pronotum at or anterior to the posterior sixth.

Character 26.—Sexual pronotal 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 pronotal 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 Ectenesia 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 Lepeltier and Coloxeisia have state 3, with expansions between the procoxae as well as apically. 

Character 29. —Abruptly declivitous 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 lateral to the mesocoxa. This leaves an open space which allows contact between the mesepimeron and the mesocoxa. 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. 35E; (3) as in Fig. 35E; (4) as in Fig. 35A; (5) 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, Neoderod Linsley, Orrellion, Paraphidion, 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 Anoplomorpha.

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

Character 35. —Mesonotal lateral projection orientation: (0) anteriorly oriented (towards head); (1) medially oriented between anterior and posterior margins of mesosternum. All taxa examined have the lateral projections of the mesosternum medially oriented except for Champlong and Astromula Chemsak and Linsley, which have them anteriorly oriented, and Cordylomera which has the arms posteriorly oriented.

Character 36. —Mesonotal lateral arm shape: (0) rounded (Fig. 36A-F); (1) acute and directed posteriorly. Acute lateral arms of the mesosternum arising medially but pointing posteriorly are only found in Steinelaphus 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 pigmentation: (0) absent; (1) present on posterior half. The distinctive mesoscutum pigmentation occurs only in Centrocerus.

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, Orrellion, and Peranoplium but also occurs sporadically in South American genera as well as the Asian Allophorina. Most taxa examined lack the scutellar basal constriction.

Character 40. —Scutellum apex (posterior): (0) truncate; (1) rounded (Fig. 36E-F); (2) acute (Fig. 36B); (3) notched (Fig.
36A). The rounded scutellum is widespread among most taxa examined; the acute state less so. The muncato scutellum occurs only in Curtomerus and the notched state occurs only in Megasperissa 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 Neoperiboeum. The rounded scutellum is widespread among most taxa examined; the acute state less so. The muncato scutellum occurs only in Curtomerus and the notched state occurs only in Megasperissa Linsley.

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 mesoscutae 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 mesoscutae and corresponding concave depressions (metasternal 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.—Mesepimeron 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 Anoplophora, Championa, Mephritus, Nycteaestuctus, Nyctea huberti, Sphaeriion, Terpnissa, Ecenesus, and Achryson. State 2 occurs only in Pseudooxycnemus, Zajciv, and Metepisternum.

Character 45.—Shape of metasternal notch: (0) acute; (1) rounded; (2) blunt. The metasternal notch is the region of the metapleurum 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.

Character 46.—State of scutellar notch: (0) acute; (1) rounded; (2) blunt. The scutellar notch is the region of the scutellum that has the point of the pronotum. It is the angle of the sclerites on the inner, posterior margin of the pronotum.

Character 47.—State of notum: (0) approximately equal to width of mesonotum; (1) much wider than mesonotum.

State 0 is the most widespread. State 1 occurs only in Anoplophora, Championa, Mephritus, Nycteaestuctus, Nyctea huberti, Sphaeriion, Terpnissa, Ecenesus, and Achryson. State 2 occurs only in Pseudooxycnemus, Zajciv, and Metepisternum.

Character 48.—State of mesocoxal cavities: (0) open posteriorly; (1) closed posteriorly. 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 Anoplophora, Championa, Mephritus, Nycteaestuctus, Nyctea huberti, Sphaeriion, Terpnissa, Ecenesus, and Achryson. State 2 occurs only in Pseudooxycnemus, Zajciv, and Metepisternum.

Character 49.—State of metasternal notch: (0) acute; (1) rounded; (2) blunt. The metasternal notch is the region of the metapleurum 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.
Eurythrea, Stenophanes, Ternipissa, 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, Neiosphaerion 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 Mephitrus 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 condition 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, Atylossigma, Championa, Clastriion, Sphaerion, Ternipissa, Ectenusa, Neocompsa, Batyle Thomson, Hesperophanes, Colecostia, and Cordylomera.

Character 51. — Metasomal mesofemoral apexes: (0) spinose (as in Figs. 8D, 9D); (1) dentiform (Fig. 25B); (2) rounded (Fig. 26D). Spinose mesofemoral apexes are acute, pointed processes extending beyond the tibial insertion and having an angle about the apex of less than 45 degrees. Dentiform mesofemoral apexes 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 mesofemoral apexes 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 mesofemoral apexes include: Atylossigma, Castiale, Elaphidion, Nyssicus, Phoraantha, Sticocera, and Eburia.

Character 52. — Lateral mesofemoral apexes: (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 apexes include: Appula, Castiale, Neonallocera, Pantosytonius Bates, Parasitocera, and Phoraanatha.

Character 53. — Metasomal metatibial apex: (0) spine (Figs. 8D, 9D); (1) dentiform (as in Fig. 25A); (2) rounded (Fig. 26D).