A Reclassification of the Genera of Scolytidae (Coleoptera)
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A Reclassification of the Genera of Scolytidae (Coleoptera)

Stephen L. Wood

ABSTRACT.—A taxonomic revision of the genera of Scolytidae (Coleoptera) in the world fauna is presented. Included are 215 valid genera and 273 invalid generic and subgeneric names. The type-species for each genus-group name was examined, including the type-specimen of the type-species in those taxa where a holotype, lectotype, or neotype has been designated—with the exception of four contemporary genera, the type-series of which are lost, and six fossil genera for which no effort was made to locate the types. Taxonomic keys to the families of the Curculionoidea, and to the subfamilies, tribes, and genera of Scolytidae are presented. Descriptions and citations of the original validations of the two subfamilies and 25 tribes of Scolytidae are included. For each genus-group name there is a citation of its original validation, type-species, and synonymy. For each valid genus there is an indication of its distribution, type-species, and synonymy. For each valid genus there is a designation of its feeding and mating habits, and citations of published keys for the identification of species.

Of general interest to coleopterists is a review of the status and position of the families Platypodidae and Scolytidae within the Curculionoidea, including several characters not previously presented. These two families are entirely distinct from one another and from Curculionidae. The phyletic position of Platypodidae and Scolytidae is near the more primitive families of Curculionoidea and quite remote from specialized Curculionidae.

Because of their immense economic impact on world forests, forest products, and certain aspects of agriculture, considerable attention has focused on the Scolytidae. Although the literature is filled with reports of the economic ravages and of efforts made to manipulate their populations, comparatively little attention was given to other aspects of their study prior to 1960. Since then, there has been a virtual explosion of information about many other facets of their existence.

Although advances in basic communication involving nomenclature and classification normally preceded the expansion of knowledge in other groups of organisms, this was not the case with the Scolytidae. There appear to be several reasons for this delay. The sheer number of species and the urgency to do something with the management of populations compelled local foresters to act. The unavailability of trained taxonomists apparently caused practical foresters to enter the fields of naming and identifying species to meet their own limited needs. With two pre-1960 exceptions, taxonomic work on Scolytidae was done by senior foresters who lacked a fundamental interest or training in the study of diversity, phylogeny, or evolution. These exceptions were Chapuis, who produced a classical work on Platypodidae (Chapuis 1865) and was starting to work on Scolytidae (Chapuis 1869) before jurisdictional problems arose, and Hagethorn, whose brief career (1904–1912) ended tragically. The unwillingness to accept and apply the concept of evolution and to abandon the typological (morphological) species concept by more recent influential workers also delayed progress.

The present study had its origin in a conversation with C. D. Michener, at Logan, Utah, in August 1949, during which he suggested a reclassification of the genera of Scolytidae in

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the world fauna as an appropriate subject for my doctoral dissertation. Fortunately, for me and for science, a more limited topic was chosen, but the suggestion was never forgotten and has remained a lifelong objective. In 1981, when I was asked by colleagues to finalize a comprehensive world catalog of Scolytidae, completion of the generic study became mandatory and urgent. Although this presentation is a bit premature, its basic objectives are achieved. More thoughtful selection of illustrations and greater detail in their presentation would have been helpful to the user.

The Scolytidae are among the more difficult insects to classify; yet their tremendous economic importance is so great that immediate and precise identification is demanded by those industries threatened by the activities of these insects. Although my attraction to the Scolytidae was to their fundamental structure, diversity, ecology, and behavior from theoretical and other points of view, as knowledge began to accumulate, my rural background and religious philosophy made me sensitive to the economic interests of others and to a need for me to assist them with what I had learned. Another need was also paramount. Among the great frustrations in learning are those resulting from errors that have been transmitted from one generation to the next and, once learned, must be unlearned and corrected before progress can continue. Biological nomenclature and classification have been profoundly impeded by this problem. Therefore, the primary objectives of this study are (1) to review the holotypes or syntypes of the type-species of all named genera and subgenera to make certain that they are correctly placed in appropriate genera, then find the correct generic names for them, and review as many species as possible and group them in those genera, and (2) to devise a scheme of classification such that others can identify those genera.

In an attempt to estimate the number of species remaining to be named from America north of Mexico, White (1975), in his example using Scolytidae, recognized 592 species in 1970 and projected that there would be 650 named by the end-point year of 2040, when 100% would be known. That estimate was made prior to publication of my monograph (Wood 1982). In the monograph, numerous species were placed in synonymy and others were named or they extended their distributions into the United States and Canada, leaving about the same total number of species and projection as before. Meanwhile, more than half of the scolytid fauna of Mexico and Central America was named from 1960 to 1982. This rapid expansion of the fauna south of the United States made a projection for the larger area meaningless at the present time.

Few attempts to classify the higher categories of Scolytidae on a worldwide basis have been published. Perhaps the first contribution worthy of note was that of Ferrari (1867), who listed and described the genera of Tomi- cides (my Scolytinae with Scolytini deleted). There was no attempt to actually classify the genera by Ferrari. Eichhoff (1879a) published a classical monograph of this same group in which he presented keys and descriptions to all known genera and species. His family
Tomicini included 40 genera that were distributed among the subfamilies Crypturgidae (Crypturgus, Dolurgus, Aphanarthrum, Tricteninus, Pycnarthrum), Cryptophoridae (Pityophthorus, Eikelophus, Taphrogyrus), Tomicidae (Thamnurgus, Xylocieptes, Tomilts, Lepicerus, Dryocestes), Hylocuridae (Hylocurus), Micracidae (Micracus), Arauptidae (Arapus), Hexacolidae (Hexacus), Xyleboridae (Cocotropus, Xylocotes), Pityophthoridae (Pityophthus, Eidophalus, Triarmocerus, Cryptopthalmus, Pycnarthrum), Cryphalidae (Liaphratus, Hypoborus, Triarmocerus, Cryphalus, Glyptodentus, Stephanoderes, Cosmoderus), Prohlechilidae (Prohlechilus), Xylactonidae (Xylactonus, Scolytogenes), Pityophthoridae (Pityophthus, Eidophalus, Triarmocerus, Cryphalus, Glyptodents, Stephanoderes, Cosmoderus), Tomicidae (Thamnurgus, Xylocieptes, Tomicus, Lepicerus, Dryocotes), Hylocuridae (Hylocurus), Micracidae (Micracus), Arauptidae (Arapus), Hexacolidae (Hexacus), Xyleboridae (Cocotropus, Xyleborus, Premnobius, Gnathotrichus), Xylotgodidae (Trypodendron), Corthylidae (Corthylius, Bmychyspartus, Anchonocerus, Phthonius, Trypocranus, Pterocoryllus), and Amphicranidae (Steganocranus, Amphicranus).

Hagedorn (1910a, b) treated 115 genera and 1,234 species in the entire family worldwide. He divided Scolytidae (Ipidae, in his usage) into four non-Linnean subfamilies, based on the detailed structure of the mouthparts, that contained the tribes indicated: Pilidentatae (Phloeotrupinae), Spinidentatae (Eccoptogastrinae, Diomerinae, Crypturginae, Hylocuriinae, Hylesininae, Ipiniae, Cryptiphinae), Saeidentatae (Xyloctoninae, Crypturginae, Phloeotrichinae, Hylcsininae, Xyloctoninae, Cryptiphinae), and Mixodentatae (Spongicerinae).

Hopkins (1915a, b), in two papers, (a) reclassified the subfamilies and tribes of Scolytidaceae and (b) reclassified the genera and species of Cryptiphinae. He elevated the group to superfamily rank, Scolytidae, and recognized four families within it (Ipiniae, Scolytidae, Scolytoplatypodidae, and Platypodidae). His Ipiniae included the subfamilies Cryptiphinae, Ipiniae, Micracinae, Webbinae, Xylocitoniinae, Crypturginae, Phloeotrichinae, Hylesininae, and Phloeoborinae. His Scolytidae included the subfamilies Coptonotinae, Hexacolinae, Bothrosteninae, Camptocerinae, and Scolytinae. His Scolytoplatypodidae included the subfamily Scolytoplatypodinae, and Platypodidae the subfamilies Platypodinae, Genycerinae, and Chapuisinae. It appears to have been the intention of Hopkins to follow his basic classification with a series of papers treating in detail the various divisions of his classification, but only one paper was published. Hopkins (1915a) reviewed the subfamily Cryptiphinae, in which he included 48 genera that are currently distributed (below) among 17 tribes Cryptalini, Dryocoteini, and Xyleborini.

Wood (1978) reviewed 15 major published classifications of the higher categories of Scolytidae, including all of those cited above, and presented a revised and expanded classification of subfamilies and tribes and tentatively assigned 404 nominate genera and subgenera to his 25 tribes. That classification was adapted to his monograph of the North and Central American Scolytidae (Wood 1982), which listed 1,433 species in 94 genera. The present contribution is an expansion of that classification to the genus level for the entire world.

**REVIEW OF CHARACTERS**

**Characters Shared by Platypodidae and Scolytidae**

In the early stages of this study, I was thoroughly convinced that Platypodidae could be no more than a well-marked, primitive subfamily of Scolytidae. Shared characters that led to this premature conclusion included: (1) clearly formed preapical sutures extend from the anterior end of the median gular suture to or near the anterior tentorial pits; these sutures are reinforced internally by a massive internal inflection of the cuticle that occurs nowhere else in the Curculionoidea; (2) the mandible lacks the horizontal cylinder that rotates on the anterior and (heavily reinforced) posterior condyles, with its cutting edge apical, instead, the posterior condyle is in a different position, the axis of the mandibular hinge is transverse, and the cutting edge is mesal (as in Anthribidae and Nemonychidae); (3) the rostrum is short to nonexistent; (4) the tibiae totally lack corbels, but they share a common basic structure and are armed on the apical and lateral margins by a characteristic series of spines; (5) the eyes are essentially flat against the head; (6) the antennae are mostly of the same basic geniculate type, with some members of several primitive tribes having a short scape (little if any longer than the pedicel); (7) the visible abdominal sterna 1 and 2 are weakly connate, except all are free in all primitive genera of Platypodidae; (8) the elytral interstriae 10 ex-
tends to near the apex in all Platypodidae and in some primitive representatives of virtually all tribes of Scolytidae; (9) the larval characters are basically the same except as noted below; and (10) they share the same basic ecological niche.

Characters Not Shared with Other Curculionoids

Curculionoidea, excluding Anthribidae, Nemonychidae, Platypodidae, and Scolytidae, share a unique mandibular character in which the basal half forms a cylinder that rotates on a horizontal axis between the two articulating condyles (Fig. 8). The hypostomal area adjacent to the posterior condyle is enlarged and strengthened to accommodate a new mode of action; the cutting edge is apical and usually takes the form of a large cusp on the side of the basal cylinder. In the four families identified above, the mandibular condyles are closer together, the oblique action is more like that of a hinge, the cutting edge is mesal, the mandible ends in an acute point, and the hypostomal area is minimal.

The Anthribidae and Nemonychidae have an adult labrum. It is lost in all other Curculionoidea; however, in most primitive tribes of Scolytidae (most Hylesininae, Ctenophorini, etc.) there is an epistomal lobe that resembles a small, fused labrum and is probably homologous to it (Fig. 1). In Platypodidae the epistomal lobe is more generally present, and in Tesserocerus and Chaetastes (Fig. 2) a suture separating this lobe from the epistoma is evident in some species. Comparable structures are unknown in the remainder of the Curculionoidea.

In general, beetles have two gular sutures that are separated by a median gular sclerite. In Nemonychidae (Fig. 3) and some Belidae (Fig. 3B, and Crowson 1967) two gular sutures are clearly indicated from the margin of the foramen magnum to the point of invagination of the tentorium (posterior tentorial pit) where they end. In Anthribidae, the entire tentorial structure is lost and the gular sutures are usually reduced to little more than lateral irregularities on the margin of the foramen magnum. In Belidae there is variation from two widely separated gular sutures that end in two separate posterior tentorial pits (Fig. 3B) to convergence to a single median pit, with consequent reduction in size of the gula, to formation of a single median gular suture of variable length (Fig. 3C). The allies of Belidae (Aglycyderidae and Oxycorynidae including Rhopalotria) share at least part of this same variability. The only other known members of the Curculionoidea that share in similar variability are members of the neotropical scolytid genus Gnathotrupes. Of the 23 species of
Gnathotrupes examined for this character by me, 5 had two complete gular sutures that extended to and were continuous with the pregular sutures, 8 had the pregula more or less normal. Most Platypodidae (Fig. 4) have an unusually large pregula and a short to very short median gular suture.

Pregular sutures are totally absent in all curculionoids, except for Platypodidae (Fig. 4) and Scolytidae (Fig. 5-G) and for their partial presence in females of two (unidentified) Australian Belidae (Fig. 3C). In these two belids the pregular sutures extend only from near the anterior tentorial pits to near the point of antennal articulation; they are not represented from the area of antennal articulation to the anterior end of the median gular suture (the point marked externally where the tentorial apparatus invaginates). The pregular sutures illustrated by some writers on Curculionidae (Hopkins 1911:Fig. 1) do not exist; they represent irregular undulations in the cuticle that serve to strengthen the posterior (or ventral) wall of the rostrum and do not qualify as sutures in any acceptable usage of that term.

 Mouthparts have been used extensively in fundamental divisions of the Curculionoidea (Crowson 1967). For example, in Anthribidae and Nemonychidae the maxillary lacinea and

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Fig. 3. Diagrams of the ventral surface of the head of (A) Cimberis atteloboides (Nemonychidae), (B) Belua sp. (Belidae, from Australia), and (C) an unidentified female Belidae from Australia. Note the convergent postgular sutures and remnants of pregular sutures from the level of the antennal insertion to (or toward) the anterior tentorial pits. gp = gular suture, ptp = posterior tentorial pit.
Fig. 4. Posterior aspect of head of a female of Doliopygus chapuisi (Duvivier) (Pb typodiJa cl. Note the very short median gular suture and the prominent progbular sutures.

galea form separate elements (Ting 1936:Fig. 78). The only other curculionoids sharing this character are the Tesserocerini (Platypodidae) (Fig. 6), Attelabidae, and Rhyynchitidae (Ting 1936:Fig. 78). Similarly, the Anthribidae and Nemonychidae have a 4-segmented maxillary palp (Crowson 1967, Ting 1936). This character is shared by all Attelabidae (Crowson 1967, Ting 1936), some Rhyynchitidae, and one Platypodidae (Austroplatypus) (Browne 1971a).

The costate lateral margins of the pronotum in primitive tribes of Scolytidae (Diamerini, Ctenophorini, Scolytini, etc.) is another indication of primitive origin of this family within the Curculionoidea.

The tibial structure of Platypodidae and Scolytidae is unique. It appears to have been derived from a structure resembling that of Prototylaster (Fig. 7), in which the median member of three apical spines became the terminal mucro of Platypodidae and the mesal spine became the terminal mucro in Scolytidae (Wood 1973a). The lateral margin is armed by one or more spines in primitive tribes; these may be replaced in specialized groups by socketed denticles (teeth) of setal origin (Wood 1978). The tibial structure of Scolytus and Campocercus is a specialized deviation from the basic scolytid structure that only superficially resembles the cossonine tibia. Similar structure occurs in Histeridae, Bostrichidae, Brentidae, or other coleopterous groups having a long history of occupancy of insect tunnels bored in wood. The tibial spines of Araucarini (Cossoninae) that have been suggested as ancestral to those of Scolytidae (Kuschel 1966) also are of independent origin; in fact, the scolytid denticles to which they were compared are socketed and bear no structural similarity to them whatever.

The elytral locking mechanism is basically the same throughout the Curculionoidea, except that it is radically modified in Attelabidae and Rhyynchitidae in an obvious specialization (Wood 1978, and unpublished drawings). A minor departure occurs in Scolytidae (Corlymbi) (Wood 1978).

Visible abdominal sternae 1 and 2 are entirely free in all primitive genera of Platypodidae but are weakly connate in the higher Platypodidae, all Scolytidae, and in most higher Curculionoidea.

The larvae present an enigma. Except in the most primitive genera, the frons and clypeus are usually fused in Platypodidae (Browne 1972), as in Nemonychidae (Crowson 1967), thus making them easily distinguishable from those of Scolytidae. However, characters have not yet been found that distinguish some Scolytidae from some Curculionidae (Viedma 1963). The difficulty may come more from reduction and simplification to accommodate small size than from real differences. Browne (1972) reported urugomphi-like structures in two species of Platypodidae; if correct, this is the only known occurrence of these structures in the Curculionoidea.

DISCUSSION

Scolytidae and Platypodidae as Families

A position within the Curculionoidea is universally accepted for Platypodidae and Scolytidae, except for Scheld (1909), who gave them superfams status without explanation. For more than a century, it was traditional to list Platypodidae and Scolytidae as separate families next to Curculionidae until Crowson (1967:164) combined both families with Curculionidae, primarily on the basis of the absence of convenient larval characters that could separate them from that family. How-
Fig. 5 A–F. Head structure of Curculionidae (Stenocelis, Rhynochus) and Scolytidae (Hylurgops, Ips): Stenocelis brevis (Boh.) (Curculionidae), A, lateral, B, dorsal, and C, caudal, with internal tentorial and associated structure indicated by broken lines. Hylurgops rugipes (Mannerheim), D, lateral, E, posterior, F, dorsal, internal structure as above.
Fig. 5 G-I. *Ips woodi* Thatcher, G, ventral, H, lateral; *Rhyncolus knoeltzani* Thatcher (Curculionidae), I, ventral. Abbreviations: ai = antennal insertion; aps = apodeme formed internally by pregular suture; dat = dorsal arm of tentorium, dfm = dorsal margin of foramen magnum; c = cervical membrane attachment; gs = gular suture; mgs = internal apodeme formed by the median gular suture; mtp = median tentorial pillar that invaginates from the combined posterior tentorial pits; pg = pregula; pap = paired apodermal plates that branch dorsad from mgs and bears the tentorial apparatus at its anterior extremities; pmp = postgula; ps = pregular sutures; ptb = posterior tentorial bridge; ptpp = posterior tentorial pit.

Fig. 6. Maxilla of Platypodidae: *Periommatus bispinus* Strohmeyer (left); *Chaetastes tuberculatus* (Chapuis) (center); and *Tesserocerus insignis* (Saunders) (right). Note the separate galea and lacina. Re-drawn from Strohmeyer (1914: pl. 1).

ever, following more than 30 years of study of the comparative anatomy of the Curculionoidea, I find that position untenable and suggest that the relationship of Platypodidae and Scolytidae to Curculionidae is remote, at best, and warrants much closer examination. Platypodidae and Scolytidae universally share with one another: (1) well-developed pregular sutures that are reinforced internally by massive apodemal inflections of the entire cuticle,
extending from the posterior tentorial pit (at the anterior end of the median gular suture) to or near the anterior tentorial pit adjacent to the anterior articulation of the mandible (Figs. 4-5), and (2) a primitive mandible that is articulated and functions (about as in Anthribidae and Nemonychidae) in a manner entirely different from that of higher curculionoids (Fig. 8).

In view of these universally present primitive characters, relict retention of other ancestral features in one or more genera of these two families takes on added significance. For example: (1) The platypodid genus *Australplatypus* clearly has a 4-segmented maxillary palpus (Browne 1971a) (known elsewhere only in Anthribidae, Nemonychidae, Attelabidae, and some Rhynchitidae). (2) The platypodid tribe *Tesserocerini* has the maxilla clearly divided into separate laciniar and galeal elements (Fig. 6); elsewhere in the Curculionoidea this character is shared by the same four families (cited here in No. 1). (3) An adult labrum within the Curculionoidea occurs only in Anthribidae and Nemonychidae; however, an epistomal lobe resembling a fused labrum is widely represented among primitive Scolytidae (Fig. 1) and is usually present in Platypodidae (in *Tesserocerus* and Chaetastius, Fig. 2, it is even separated from the epistoma by a suture). (4) A complete gula, with two gular sutures continuous with the pregular sutures, is present in at least five Gnathotrupes (Scolytidae) species (Wood 1973a), and the pregula is greatly prolonged in eight other species of this genus, the pregula is greatly enlarged and the median gular suture is short to very short in most Platypodidae (Fig. 4). (5) In most Platypodidae and many scolytid Hylesinini, Scolytini, Mi-
cracini, etc., the scape is very short, little if any longer than the pedicel and definitely not geniculate, and in other groups (some Phloeotribus, some Micracini, etc.) the club is poorly formed, very little imagination is needed to see the possibility of independent origin of the geniculate, clubbed antenna from that of other curculionoids. (6) The costate lateral margins and concave pleura of scolytid Diameserini, Ctenophorini, and some Scolytini occur elsewhere in the Curculionoidea only among the most primitive families. (7) The platypodid-scolytid tibiae totally lack corbels. Their lateral margins bear true spines in Platypodidae and some primitive Scolytidae. These are replaced in all higher Scolytidae by socketed denticles of setal origin that occur nowhere else in the Curculionoidea. Although most characters are shared by some members of each group, a sharp demarkation remains. For example, the male spiculum gastrale is undeveloped in Platypodidae, but it is well-developed in Scolytidae (Wood 1982); tarsal segment 1 is greatly elongated in all Platypodidae (Fig. 9), except for Protoplatypus and Scolytotarsus, but it is intermediate in Protophylastes and Coptonotus (These four genera contain a total of five rare, tropical species). The shape and structure of the head, eye, antenna, pronotum, scutellum, elytra, and tibiae are almost equally distinctive. Details of platypodid be-
behavior are too poorly known to add conclusive supporting evidence. The higher Platypodidae appear to have been the most primitive segment of this phyletic line to take up the woodboring ambrosial habit, which drastically affected their morphology; this habit appears to have arisen independently in at least eight tribes of Scolytidae (Hyorrhynehini, Phloeosinini, Scolytini, Scolytotaplotypodini, Xyletorini, Xyleborini, Crysphalini, Cortylini) (Wood 1982).

The Platypodidae universally lack socketed tibial denticles (derived from setae) (Figs. 7, 9); these structures are present in all higher groups of Scolytidae (Fig. 10) but are lacking in at least some genera of several primitive tribes. In all primitive genera of Platypodidae visible abdominal segments (sterna) 1 and 2 are free; in the higher Platypodidae and in all Scolytidae they are weakly connate. The posterior half of elytral interstriae 10 is universally present in Platypodidae; it is present in primitive members of most tribes of Scolytidae (Fig. 12), but it is lost in the higher members of almost all tribes (Fig. 11). The apical protibial mucro of Platypodidae appears to have been derived from the middle apical spine of a tibia resembling that of Prototyphlastes (Wood 1973a); it appears to have been derived from the inner (mesal) spine in Scolytidae (Fig. 7). In larval Platypodidae (except Prototyphlastes and Sceliflanus) the elytrus is fused to the frons (Brown 1972); in Scolytidae it is a separate sclerite. The list could go on, but the above should indicate a close relationship between the two families and the limited overlap of many characters.

Subfamilies and Tribes

A review of characters usable in classification of the higher categories of Scolytidae was presented by Wood (1978). Several trends were reported in that study: (1) the primitive head is more or less truncate on its posterior face, the dorsomedian area is progressively prolonged caudad in specialized groups (Figs. 13-14, and Wood 1982: Fig. 14); (2) the primitive frons is convex in both sexes (in the higher Hylesiniinae the male frons is variously impressed and the female frons is usually convex); the reverse is usually found in the Scolytinae; (3) the primitive eye is oval, entire, and finely faceted; specializations include elongation, emargination (including complete division into two parts) (Fig. 15), and enlargement of facets (apparently correlated with nocturnal flight habits); (4) the antennal scape primitively may have been short, little longer than the pedicel; it is elongate or triangular in most groups; (5) the antennal funicle primitively contains seven segments, and there is a more or less orderly reduction to a minimum of one segment as specialization increases; (6) the antennal club varies from almost nonexistent (three movable segments no longer than those of the funicle in primitive Phloeotribus) to a simple cone-shaped structure with transverse sutures to large and
strongly flattened or obliquely truncate, with or without sutures; it is probably the most variable major structure found throughout the family; (7) the prothorax may have (a) the coxae widely separated in primitive groups to fully contiguous in specialized ones; (b) the pleuron concave, with the lateral margins acutely costate in primitive genera (Figs. 11-12), to convex, with the lateral margin unmarked in specialized genera; (c) the pronotum longitudinally straight in dorsal profile and unarmed by crenulations in primitive groups to strongly arched and armed by crenulations or asperities in specialized ones;

(8) the basal margins of the elytra tend to be costate primitively, with the Hylesininae becoming procurved and crenulate (Fig. 16), the Scolytinae transversely straight and longitudinally rounded (Fig. 17); (9) several complex changes occur in the meso- and metathorax that will be discussed below; (10) the male tergum 8 is visible and pubescent in most groups (Fig. 22), but it is telescoped beneath 7 and without pubescence in Carphodicticini, Ipini, Dryocoetini, Xyloterini, and Xyleborini; (11) the venter of the abdomen has (a) segments 3 and 4 (visible segments 1 and 2) free in all primitive Platypodidae but weakly connate in the higher Platypodidae and all Scolytinae and (b) limited specialized groups in which specialized features are very impor-
Variations in rye shape (left to right): shallowly sinuate (*Hylostes crenatus* Fabricius); narrowly and shallowly emarginate (*Euproctus caucasia* Lindeman); strongly sinuate or broadly, shallowly emarginate (*Phloeosinus baco* Obril); deeply emarginate (*Phloeosinus thase* Perrin); completely, equally divided (*Polygraphus poligraphus* Linnaeus); and completely, unequally divided (*Sphacotorytes globosus* Blandford).

*Figs. 16-21.* Thoracic structure of Scolytidae: 16, elevated crenulations (arrow) on procurred basal margins of elytra of *Phloeosinus scabrosus* Eichhoff; 17, weakly subcostate basal margins of elytra in *Scolytodes plumeriae* Wood; 18, metatergum of *Hylastes nigricus* Mannerheim, arrows mark intersegmental line (left) and scutocostal suture (right); 19, metapleuron of *Hylastes nigricus* Mannerheim, upper arrow marks pleural suture; lower arrow marks anterior end of groove that receives costal margin of elytra; 20, ventral aspect of prothorax, arrow marks acutely elevated precoxal ridge (or costa); 21, metatergum of *Euapogocera dentipes* Blandford, pn = postnotum, is = fused intersegmental line, ss = scutocostal suture (compare to Fig. 18).

Most of the above character states are utilized in the following key to subfamilies and tribes to indicate phyletic trends in the family, subfamily or tribe in which they are involved. However, two of them are sufficiently complicated and important that elaboration is appropriate. These occur on the metathorax and the tibiae.

Three primary characters of the metathorax show important features that exhibit phyletic
trends. First, in Cureulionoidea generally, including Platypodidae and primitive Scolytidae, the pleural suture follows a zigzag course from the pleural wing process ventrad to the point where the costal margin of the elytron touches the body. It then turns abruptly caudad to a point just before reaching the posterior limits of the segment, where it turns mesad and continues to the pleural coxal process. On the metepisternum at the anterior or first angle (below the pleural wing process) a carina or small, flattened spine is present that fits into a small groove on the inner (costal) margin of the elytron just behind the humeral angle. This character state within Scolytidae is best seen in the Hylastini (Fig. 23, parts 43-44) and in some Hylesinini. The trend is for the suture to progressively straighten out whereas the metepisternal spine remains stationary but becomes more remote in position from the changing suture (Fig. 23, part 42).

The matching groove on the elytron moves somewhat dorsad and caudad, suggesting that the costal margin of the elytron extends farther ventrad than primitively. In Cryptalinini the metepisternal spine is considerably reduced in size, and its function in locking the elytra in closed position is partly assumed by a new diagonal groove on the metepisternum (Fig. 31). In Corhyulini, the spine is entirely lost and the groove is enlarged and extends to a more ventral position (Figs. 23, part 47, and 32). The result is that the closed elytron in this tribe now covers all but a small anterior portion of the metepisternum.

A second significant feature of the metathorax involves progressive changes in position of the sextosentellar suture. In Cureulionoidea generally, Platypodidae, and primitive Scolytidae (Hylastini and Hylesinini are examples), this suture reaches the margin of the scutellar groove near the anterior limits of the groove and continues parallel to and very near its lateral crest for about two-thirds of the length of the groove, then the suture curves abruptly lateral to follow its usual course to the posterior margin of the segment (Fig. 23, part 43). In more advanced tribes this suture progressively straightens out, meeting the marginal crest of the groove only briefly, if at all (Fig. 23, part 41).

The third significant metathoracic feature that is usable in phylogeny occurs only in the Hylesininae. A significant feature of insect flight is the intersegmental line between the metathorax and its postnotum (derived primitively from the interior portion of the first abdominal segment but functionally part of the thorax), which must flex with each stroke of the metathoracic wings. This suture is present in all insects, including Platypodidae, Scolytinae, and primitive Hylesininae (Fig. 23, parts 43, 45). In the more advanced Hylesininae, the median two-thirds of this intersegmental line is lost by complete fusion of the postnotum to the metatorax (Fig. 23, part 41). This fusion is progressive, leaving a weak suture primitively, but it is totally obliterated in advanced groups of this subfamily.

The tibiae exhibit remarkable variation in constant, conservative patterns that are valu-
Fig. 23. Diagrams of terga and pleura of Scolytidae: 41, metatergum and 42, pleuron of Chryses hickorae LeConte, arrow points to remnant of intersegmental suture in 41, to metepisternal spine in 42. 43, metatergum and 44, pleuron of Hylastes nigrinus Manscerheim, arrows as above; 45, metatergum and 46, pleuron of Cnemotrupus panamensis (Blandford), arrows as above; 47, pleuron of Pityphthorus creatensis Wood, metepisternal spine is lost and is replaced by a small groove (arrow). Abbreviations: is = intersegmental suture, ms = metapleuron, mn = metepisternum, ps = postnotum, pn = pleural suture, s = metepisternal spine (part of locking mechanism for elytra), sg = scutellar groove, ss = scutellum sutures.

able in following trends in phylogeny. Apparently, the primitive model from which the tibiae of Platypodidae and Scolytidae were derived resembles that of Protolyastes (Fig. 7). The protibia of Protolyastes is slender, with three rather small spines at the apex and
a very minute spine on the posterior face immediately basad from the tarsal insertion. Comparative studies (Wood 1973, 1978) suggest that the mesal (inner) apical spine became the apical spine in Platypodidae (Figs. 7, 9). The middle spine in Scolytidae is bent lateral and is a major, identifiable element that projects beyond the level of the tarsal insertion in one or more members of several tribes (Hyorrhynechini, Diamerini, Bothrostenini, Philoeotribini, Philoeotribini, Hypoborini, Polygraphini, Scolytini, Ctenophorini, Scolytopylatypodini). All tibial spines in Platypodidae (Fig. 9), Hyorrhynechini, Scolytini (Fig. 7), and, apparently, Ctenophorini (Fig. 7) are true spines. In all higher Scolytidae these spines are either intermixed or replaced by socketed denticles of setal origin (Fig. 10). The patterns of possession and replacement within the family suggest that socketed denticles had an early monophyletic origin within the Scolytidae, with differential survival of this character in the posterior, and do not suggest polyphyletic origins.

Many other characters that are not mentioned above are useful in classification and phylogeny in more limited groups. Several of these are employed in the keys.

Conclusions

As stated above, the traditional place of Scolytidae in classification has been as a family next to the Curculionidae. However, as Curculionidae became fragmented into several families, the position of Scolytidae within the Curculionoidea changed. The traditional position in classification has been next to the Curculionidae; however, close examination suggests that such a placement is based on superficial resemblance, not on fundamental structure. As indicated above, the Curculionidae have two gestural sutures that extend from the anterior tentorial pit (adjacent to the anterior articulation of the mandible) to meet the anterior end of the median gular suture occur only in these two groups. These sutures are reinforced internally by massive apode-

mes. Remnants of regular sutures found in females of two species of Belidae extend from the anterior tentorial pit toward the anterior insertion and never converge or approach the gular suture (or sutures). (2) In these two families, the mandibles come to an apical point and have the cutting edge mesal as in Nemonychidae; furthermore, the articulating condyles are comparatively close together, with the posterior one more nearly lateral in position, and the hypostomal area behind the posterior condyle is minimal in size to almost nonexistent. In most Curculionoidea, except for these two families and Nemonychidae and Anthribidae, the basal half of the mandible forms a horizontal cylinder that rotates on the two condyles, and the cutting edge of the mandible is apical; the posterior condyle is posterior in position and is supported by an enlarged hypostomal area. (3) The subcostal habit in which mated pairs enter vital host tissues to oviposit is shared by Platypodidae, Scolytidae, and some Cossoninae (Curculionidae); however, the mode of excavation and several structural features (gular area, tentorium, mandible, etc.) indicate that the latter group exhibits an evolutionary parallelism, not a fundamental relationship. (4) Six genera (Protohylastes, Coptocotus, Scolytotarsus, Prototypatus, Mecopelma, Schedlarius) are structurally and biologically intermediate between the Platypodidae and Scolytidae and could be placed in either family. The characters, reviewed in this paragraph, with primary stress placed upon true regular sutures, indicate a fundamental close relationship between Platypodidae and Scolytidae that is not shared with other groups.

A second point of significance has to do with the position of Platypodidae and Scolytidae within the Curculionoidea. Their traditional position in classification has been next to the Curculionidae; however, close examination suggests that such a placement is based on superficial resemblance, not on fundamental structure. As indicated above, regular sutures are shared, in part, only with females of two species of Belidae, and the mandibular-hypostomal structure is shared only with Anthribidae and Nemonychidae. These indications suggest a relationship of Platypodidae and Scolytidae to the segment of Curculionoidea having two gular sutures, rather than
one. However, close inspection of Belidae discloses at least three genera with only one median gular suture and an elongated postgula, and an entire segment of Oxycoeridae (Rhopalotria) with one gular suture and a postgula of variable size. Furthermore, one genus of Scolytidae (Gnathotrupes) contains at least five species with a complete gula connecting pregular and postgular elements, and at least eight more in which the connection is almost complete. In many Platypodidae, the pregula is enlarged and is scarcely separated from the postgula. Because such a situation does not occur elsewhere among those curculionoids having one gular suture, wisdom suggests that a search be continued for additional clues to phyletic relationships.

A movable labrum occurs among curculionoids only in Anthribidae and Neonomychidae. Remnants of a labrum are found in many primitive Scolytidae (particularly Hylesini), and a fused labrum, complete with a transverse suture, occurs in Platypodidae (especially Tesselnerini). I am unaware of similar remnants in other curculionid families.

A 4-segmented maxillary palpus occurs in Australoplatypus (Browne 1971a:49), a feature restricted to only the most primitive curculionoids (see family key below).

A lacina separate from the galea is characteristic of all Tesserocerini (Platypodidae); this is another feature that is restricted to the most primitive curculionoids (see family key below).

The antenna has been used extensively in the classification of curculionoid families, particularly character states of orthocerous vs. geniculate, apex filiform vs. clubbed (or capitate), etc. In no curculionoid are segments 1 and 2 without some degree of enlargement; furthermore, in many of those traditionally referred to as geniculate, the scape is not longer than it is in some Anthribidae. In a large segment of Platypodidae and many Scolytidae, the scape is short, little if any longer than the pedicel, and often it is broadly triangular in shape. In virtually all curculionoids (except most Anthribidae), the three apical segments of the antenna are at least slightly enlarged; although the literature generally states otherwise, a few Anthribidae have an abruptly enlarged club. In the genus Phloeotribus (Scolytidae), the club is usually sublamellate, with the three segments freely movable upon one another (Fig. 16). In primitive members of this genus (socioe, rhododactylus, etc.) the three segments are no longer or wider than are the funicular segments and are as movable. I see no possibility that the Phloeotribus antenna could have been derived from a solid club of the type found in most other Scolytidae. Since this is the only deviant character found in this genus, could it not be a relic reminder that the scolytid club was derived on an independent, parallel line from a common ancestor, and not from other curculionoid groups having clubbed antennae?

Much has been said and written of the similarity of the titiae between Scolytus (Scolytidae) and many Cossoninae (Curculionidae) in curculionoid family classifications. However, it has never been pointed out that similar titiae occur in Histeridae, Brenthidae, and other coleopterous families containing groups with a long history of subcortical existence. Within the Scolytidae, the Scolytus titia is unique and apparently does not represent a truly primitive condition. The truly primitive character state of the titia on this phyletic line occurs in Protogenastes, with Platypodidae and Scolytidae derived along separate phyletic lines from the basic structure.

Larval characters, thus far, have not been very helpful in answering questions about scolytid phylogeny. In fact, reliable means have not yet been found for separating all Scolytidae from all Curculionidae (Viedma 1963, Lekander 1968). Whether this is due to the absence of characters or to the lack of diligence in the search for characters among groups not found in Europe needs to be answered. Primitive larval Platypodidae have the frontal sutures extending to the articulating membrane of the mandibles, a fact not previously noted. Browne (1972) suggested that structures found on two platypodid larvae could be relics of urogomphi. If so, this is the only evidence of the existence of urogomphi in the Curculionoidea. Larval Scolytidae and Platypodidae are easily separated from each other by the separate (Scolytidae) or fused clypeus and frons (Platypodidae). It is of interest that this same character separates larval Neonomychidae and Anthribidae (see family key below).
Lower Jurassic curculionoids with a long rostrum have been referred to the Curculionidae by Crowson (1983), although they bear a very strong resemblance to Belidae or, perhaps, Eobeltidae. Arnoldi (1977) named the extinct family Eobeltidae from 14 species that were placed in 7 tribes in 4 subfamilies, taken from Upper Jurassic deposits of South Kazakhstan (Karastan) in the USSR. In this family the head is similar to modern Belidae except that it is more broadly oval and the rostrum is shorter, as in some modern male Bremthidae. The mandibles are large, with a single apical point and a mesal cutting edge as in modern Nemonychidae. The antennae attach either to the middle or near the apex of the rostrum and are orthocerous, with the three apical segments slightly enlarged but not forming a definite club. Arnoldi did not mention gular sutures or a labrum. The body resembled modern Belidae except that the lateral margins of the prothorax were acutely elevated as in modern Oxyctridae and the elytra were much less strongly sclerotized than in modern Belidae.

From the above, two fundamental conclusions emerge. First, the Platypodidae and Scolytidae are very closely related to one another and, in fact, they intergrade to a limited extent. At the same time, these two families are quite distantly related to other families in this superfamily. Second, in spite of the apparent absence of larval characters, there are enough discordant adult characters to conclusively demonstrate that the Platypodidae-Scolytidae, as one unit, do not belong to and probably are not even closely allied to Curculionidae. It is my contention that their peculiar sutures (and accompanying internal apodemes) prevented elongation of the rostrum and forced them into an entirely different mode of existence from other curculionoids (parent adults had to bore into vital host tissues to oviposit because they had no rostrum and, consequently, could not follow the curculionid habit of using the rostrum to form oviposition pits). They could have been derived in the Jurassic from a short-rostrumed Eobeltidae-like ancestor that had fully formed peculiar sutures. Belidae and related families, and all other curculionoids having one gular suture, branched off later or from other segments of Eobeltidae or its derivatives. Rostrum length among Jurassic curculionoids was diverse, varying from short and broad (Arnoldi 1977) to long and slender (Crowson 1983). The presence of obvious, sophisticated scolytid tunnels in Lower and Middle Cretaceous conifer bark suggests that the Platypodidae-Scolytidae phylectic line had its origin at least in Upper or Middle Jurassic. The exact phylectic positions of known Jurassic and Cretaceous "curculionid" fossils are difficult to determine, because details of labrum, mandibles, gular sutures, etc., are not sufficiently well preserved to permit analysis. I seriously doubt that any true Curculionidae existed prior to the Cretaceous.

Habits and Classification

Although the Platypodidae are established above as a family, separate from Scolytidae, they are significant because they represent the first major paraphyletic branch from the platypod-scolytid line of specialization. Their adoption of the xylomycetophagous habit appears to have accelerated their structural and biological deviation. Only the intermediate genera Protoplatypus, Mecopelmus, and Schedarius lack the ambrosial habit (Protohylastes, Scolytotarsus, and Coptonotus are unknown biologically). Schedarius (monogamous) and Protoplatypus (polygamous) place their eggs in sealed niches; all other known platypodids are monogamous and distribute the eggs loosely in the parental galleries or carry them on the female from. Mecopelmus makes a cave-type nuptial chamber (without oviposition galleries) in the cambium region of its host and deposits the eggs in clusters therein, and the larval form independent mines in the cambium at least for the latter part of their development. Protoplatypus forms stellate or radiate tunnels, with a central nuptial chamber in the cambium region, and the eggs are placed in regular, alternate, sealed niches along the linear egg galleries, the larval form independent mines throughout their development. Schedarius is xylophagous (Wood 1957a), places its eggs in randomly organized niches that are sealed with frass, and the larval form long, independent mines that wander aimlessly through the wood. An obvious association with fungi is apparent in the vicinity of adult and larval activity, although no mycelial growth in the
In my review of characters usable in distinguishing subfamilies of Scolytidae (Wood 1978), only one significant character gap was found that was supported by numerous features. These characters are summarized in the key to tribes below. The presence or absence of pronotal asperities, the ambrosial habit, and several features used traditionally by past workers to separate multiple subfamilies of Scolytidae either have no value in characterizing subfamilies or have no value in phylogeny. For these reasons, only two subfamilies were recognized. Because the Hylesininae are structurally and biologically less diverse and their specializations more conservative, they are treated here as more primitive than the Scolytinae.

Tribes of Hylesininae

In general, the Hylesininae are phloeo­plagous. Exceptions include the twig- or small-branch (pith)-boring mycetophagous Hyorrhynchini (all three genera), Bothrosternini, and Hylaeops (Phloeo­sinini, last half of larval stage only), xylophagous Dendroisius and three known species of the large genus Chremaneus (Phloeosinini); the mycetophagous Cnestis, Eupagioceerus, and Sternodothrus (Bothrosternini); and the spermophagous Pagiocerus (Bothrosternini) and one species of Phlocosilus (Phlocosil­sini). The usual mating system in this subfamily is monogamy, with the female initiating the new parental gallery. Departures from this system include (a) apparent male haploidy (arhenotocous parthenogenesis accompanied by consanguineous polygyny) in Saeus (Hyorrhynchini); (b) monogamy, with male initiation of parental galleries in some Phloeosinus and Olo­nthogaster (Phloeosinini); and (c) heterosangunines (superficially resembling harem) polygyny in at least two species of New Guinea Olo­nthogaster (Phloeosinini), and in all Carphothor­sus and many Polygraphus (Poly­graphini).

These basic habits appear to be correlated with (1) a conservative evolutionary departure from the ancestral structure; (2) a more com­ pact (stout) body; (3) the body compaction that appears to have resulted in the development of a row of coarse crenulations on the basal margins of the elytra (their function is evidently to add resistance when a predator attempts to pull from a tunnel the beetle that is blocking the entrance), and (4) the straightening of the pleural suture. The compaction of the body apparently also had an effect upon the mechanism of flight and permitted fusion of postnotum 2 to the metathorax. Although use of these characters requires further study and refinement, a definite trend from the Hylastini-Hylesinini to Phlo eosinini is indicated.

There appears to be a gradual transition in characters from the Hylastini to Hylesinini to Tomcini. The Hyorrhynchini and Phrixosomi­mini appear to be relics of an earlier radiation of primitive stock and are quite unrelated to the other three tribes. The remaining hylesinine tribes have the postnotum partly to entirely fused to the metanotum and fall into three units. The first includes the Old World Diamerini and New World Bothrosternini that probably contain the most primitive species of this subfamily. Their prosternal, pronotal, and basal of elytral structure is much more primitive than the Hylastini-Hylesinini. Their antennal structure is much more similar to Coptonotus-Protophylastes (Platypodidae), although the Hylastini-Hylesinini club is probably more similar to the ancestral structure.

The second tribal unit within the more highly evolved segment of this subfamily includes the Phlocosirini and Phlooeosinini. Tidal structure of at least a few representa­tives of each suggests an ancient origin. Ex­cept for the aberrant structure of the antennal club of Phlocosirini, they probably could not be separated from one another at the tribal level. They include species bearing the greatest departures from the primitive forms in the pleural and scutocutellar suture patterns. The absence of socketed protorial teeth in Aricerus and the movable segments in the antennal club suggest that Phlocosirini is the more primitive of these two tribes.

The Polygraphini and Hypodorinini are obvi­ously specialized ancient groups that are unrelated to one another but of uncertain affinity to other groups. The superficial appearance of the body form of Poly­
Graphini suggests a relationship to Tomicus, but the prothorax structure of Serrastus suggests a much more ancient origin of this group. The Hypophorini could be a specialized paraphyletic line that branched from the Phloeosorini.

Tribe of Scolytineae

The tribes of Scolytinae are easily clustered into five major groups on the basis of several anatomical characters. The most primitive, composed of Scolytini, Ctenophorini, and Scolytoplatypodini, share primitive prothorax structure without socketed denticles, a 6- or 7-segmented antennal funicle, a head without a caudal extension of the dorsal occipital area, rather widely separated procoxae, etc. This group contains members (Cnemonyx, Scolytodes) with the greatest structural similarity of all Scolytinae to primitive Platypodidae (Protoplatypus, in this instance) and to Hylciniinae. In fact, some Cnemonyx (galeritus and its allies) have coarse crenulations on the basal margins of the elytra; also, Protaphylastes was thought to be allied to Pseudohylesinus (Tomicini) until the legs and antennae were studied. The Ctenophorini habits include phloeophagy, xylophagy, and mycophagy; monogamy and polygyny (heterosanguineous only); egg chambers of the cave, linear and radiate types; and deposition of eggs in loose clusters in parental chambers or in individual niches sealed by frass. The monogamous, xylomyctophagal Scolytoplatypodini appear to be a specialized Old World geographical replacement of the Ctenophorini. The Scolytini are monogamous (except for a few bigynous Scolytus) and phloeophagous (except for the xylomyctophagous Camptocerus). Cnemonyx (Scolytini) and Scolytodes (Ctenophorini) could have been derived from a common ancestor. Physyx (Tomicophorini) could easily be placed as a primitive tribe of Hylciniinae on both anatomical and biological bases.

The second cluster of tribes within the Scolytinae includes the Micracini and Caciophorini. Advances include a more efficient body form (cylindrical compaction), slightly extended dorsal occipital area of the head, reduction of funicular segments to six (rarely five), universal occurrence of pronotal asperities, common occurrence of xylophagy and bigyny, etc. Xylomyctophagy and males normally associated with more than two females are unknown. Scalelike prontal and elytral setae are a common occurrence. The evolutionary connection between this group of tribes and the more primitive Scolytini-Ctenophorini-Scolytoplatypodini is remote; however, a connection to the more advanced Xyloctonini-Cryphalini is clearly evident.

The third cluster of tribes within the Scolytinae includes the Carphodicticii, Ipini, Dryococtini, Crypturgini, Xyletorini, and Xyleborini. In this group, male abdominal tergum 8 is reduced in size and telescoped beneath 7, as in the female. In addition, the procoxae are almost always contiguous, the occipital area of the head attains its greatest prolongation, the obliquely truncate antennal club is developed and exploited, both heterosanguineous and consanguineous polygyny are common, and xylomyctophagy is universal in two tribes. Carphodicticii and some Dryococtini are obviously very primitive, but their connection to other primitive Scolytinae is remote and not reflected in the modern known fauna. The basal margins of the elytra are elevated and costate in Dendrodicticus (Carphodicticii) as in some Hylciniinae.

The fourth cluster of tribes within the Scolytinae includes Xyloctonini and Cryphalini. In these tribes the procoxae are entirely contiguous, and the antennal club is flat, with the sutures on the posterior face moderately displaced toward the apex. The small metepisternal spine that functions in locking the elytra in the closed position is reduced and partly replaced by a small groove (Fig. 31). Segmentation of the antennal funicle is reduced, ranging from a maximum of seven to a minimum of three. Monogamy is the general habit, with consanguineous polygyny universal in four genera of Cryphalini (Cryptocarenus, Hypothenemus, Trischidia, Periocrypha). There appears to be a close connection between Micracini and this group of tribes. The antennal locking mechanism also suggests a remote connection between this group and the Corthylini (Figs. 23, 31-32).

The final cluster of tribes includes the Corthylini. The flattened antennal club, with the sutures equal on both sides, the unique elytral locking mechanism, tibiae, eyes, elytra, etc.,
characterize this unique tribe. Phyloophagous is almost universal in the primitive half of the tribe, xylomycetophagy in the advanced half. Both monogamy and heterosanguineous polygyny are common. Consanguineous polygyny apparently occurs in three species of Araptala. There may be a remote phylogenetic connection to the Cryptaliini.

Geographical Origin of Tribes

For a discussion on this topic to have any semblance of objectivity, certain premises must be established. First, it is assumed that continental drift did occur and, due to that phenomenon, South America and Africa were either connected at their southern ends or were at least close enough to permit faunal exchange by island-hopping until earliest Tertiary. At that time, Australia was close enough to the southern end of South America to permit at least limited faunal exchange. Second, it is assumed that South America was an island during most of the Tertiary. In addition to the assumed connection to Africa in earliest Tertiary, South America was connected to North America in early Tertiary and again in late Tertiary either by a land bridge, as presently exists, or by a series of islands that were close enough to permit faunal exchange. Third, it is assumed that faunal exchange between Africa, Europe, and Asia has been no problem except as it has been affected by climate. Fourth, it is assumed that climate has fluctuated as evidenced by fossil remains of magnolia trees in Alaska and of tropical forests where the Sahara Desert is now located. Finally, it is assumed that scolytid beetles have had habits throughout their history that were essentially as seen at present. That is, groups presently restricted to tropical forests have always been so restricted, and groups now in more temperate climates have been able to occupy cooler climates for a long time.

In the first column of Table 1 are listed all tribes of Scolytidae presently recognized in the world fauna. From each tribe, those genera were selected that now are restricted to tropical climates. If those genera are now represented in both Africa and South America or if they have a very closely related geographical replacement genus on both continents, but are not found outside the tropics elsewhere, then those tribes were considered to have a pre-Tertiary origin (Table 1, column 2). If the tribe at that time was local in distribution and was represented on only one land mass, it was not included as pre-Tertiary even though it could have been present. A faunal connection from South America to Australia was regarded as early Tertiary, not just pre-Tertiary. It is noted (1) that 6 of 11 tribes of Hylesininae and 7 of 14 tribes of Scolytinae are judged on this basis to be of pre-Tertiary origin, and (2) that the only pre-Tertiary group containing species with the xylomycetophagous habit is Xyleborini. (Hylesinini is excluded, because its only xylomycetophagous genus, *Hyleps*, has not yet fully adopted that habit.) This does not mean that other xylomycetophagous groups were not present, but only that, if they were present, they were local in distribution (on only one land mass) at that time. It is further noted (3) that all tribes judged as pre-Tertiary were phloeophagous except for Xyleborini and part of Micracini. This suggests that xylephagy and xylomycetophagy are of comparatively recent origin.

The significant point is that the family Scolytidae was a well-established, diversified group by the beginning of the Tertiary. The fossil engravings of scolytids in coniferous bark from Upper Cretaceous illustrated by Brongniart (1877) and described from Lower Cretaceous by Blair (1943) are evidence of a much longer family history of the group than is usually recognized. It is probable that the beetles that made those engravings were much more similar to the Ctenophorini or, possibly, *Protoplatypus* than to modern Hylesininae.

Phylogeny

As stated above, the Platypodidae-Scolytidae group are members of the Curculionoidea. Within that superfamily, they form a distinctive unit that is characterized by the presence of fully developed pregalvular sutures. Because the only other known pregalvular sutures within the Curculionoidea are the apical remnants found in females of two species of Belidae, the possibility of an ancient common ancestor should be examined. Three genera of Belidae and an entire segment of Oxyco- rytnidae (*Rhopalotria*), a supposed derivative
Table 1. Estimated age of the tribes of Scolytidae, based on genera known to be restricted to tropical areas. Tribes are considered pre-Tertiary if a tropical genus or a close geographical replacement genus occurs in Africa and also in South America (Column 3). More recent postseparation (of Africa and South America) distribution is added as indicated (Column 4).

<table>
<thead>
<tr>
<th>Tribe</th>
<th>Pre-Tertiary</th>
<th>Ancient origin</th>
<th>Distribution added after early Tertiary</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hylastini</td>
<td>0</td>
<td>Holartic</td>
<td>No change</td>
</tr>
<tr>
<td>Hylesini</td>
<td>+</td>
<td>Old World</td>
<td>South America (from Africa), North America (from Asia)</td>
</tr>
<tr>
<td>Tomocini</td>
<td>a. Xylechinini</td>
<td>+</td>
<td>South America</td>
</tr>
<tr>
<td>b. Dendroctonini</td>
<td>+</td>
<td>Worldwide</td>
<td>Worldwide</td>
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<td>Prioxysmini</td>
<td>+</td>
<td>Africa-South America</td>
<td>No change</td>
</tr>
<tr>
<td>Hygroscyphiini</td>
<td>0</td>
<td>Oriental</td>
<td>No change</td>
</tr>
<tr>
<td>Diaperini</td>
<td>0</td>
<td>Africa</td>
<td>Southern Asia to Australia</td>
</tr>
<tr>
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<td>0</td>
<td>South America</td>
<td>North America</td>
</tr>
<tr>
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<td>South America</td>
<td>Australia (from South America); North America to Eurasia, from South America.</td>
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<td>Africa-South America</td>
<td>Ancient to Eurasia; modern to North America</td>
</tr>
<tr>
<td>Hypobmuti</td>
<td>+</td>
<td>Worldwide (or Africa-South America)</td>
<td>Relicts</td>
</tr>
<tr>
<td>Polygraphini</td>
<td>0</td>
<td>Africa</td>
<td>Europe and Asia, then to North America</td>
</tr>
<tr>
<td>Scolytini</td>
<td>0</td>
<td>South America</td>
<td>North America then to Eurasia</td>
</tr>
<tr>
<td>Scylcomyctotriphini</td>
<td>0</td>
<td>South America</td>
<td>North America</td>
</tr>
<tr>
<td>Misraeni</td>
<td>+</td>
<td>South America-Africa</td>
<td>South America-Africa</td>
</tr>
<tr>
<td>Catopomini</td>
<td>0</td>
<td>North America</td>
<td>No change</td>
</tr>
<tr>
<td>Carphodactilini</td>
<td>+</td>
<td>?</td>
<td>South America-Southern Asia</td>
</tr>
<tr>
<td>Iponi</td>
<td>+</td>
<td>South America-Africa</td>
<td>Worldwide</td>
</tr>
<tr>
<td>Dryocotini</td>
<td>+</td>
<td>Africa</td>
<td>Worldwide</td>
</tr>
<tr>
<td>Crypturgini</td>
<td>0</td>
<td>Africa</td>
<td>North America, Eurasia</td>
</tr>
<tr>
<td>Xyleterini</td>
<td>0</td>
<td>Asia</td>
<td>North America</td>
</tr>
<tr>
<td>Xyleborini</td>
<td>+</td>
<td>Africa-South America</td>
<td>Worldwide</td>
</tr>
<tr>
<td>Xylogumbini</td>
<td>0</td>
<td>Africa</td>
<td>Asia</td>
</tr>
<tr>
<td>Cryptophilli</td>
<td>+</td>
<td>Africa-South America</td>
<td>Worldwide</td>
</tr>
<tr>
<td>Cortelyphonini</td>
<td>0</td>
<td>South America</td>
<td>Worldwide (African segment)</td>
</tr>
</tbody>
</table>

Marked (+) present in recognizable form prior to the beginning of the Tertiary or on more than one land mass. Marked (0) if represented at the beginning of the Tertiary by a local representative or a precursor that was present on only one land mass.

of Belidae, have only one gular suture, not two as in other members of the Belidae-Oxycoenidae-Aglycydidae (Proterhinidae) group. Because such a placement would be a radical departure from the traditional position of Platypodidae-Scolytidae within the Curculionoidea (which has been next to the Curculionidae), additional supporting evidence was sought. The following summary of information presented in the above sections was found. A functional, but degenerate, adult labrum occurs in Curculionoidea only in Anthribidae and Nemognychidae. Rudiments of a labrum are well marked in many Platypodidae and obscurely indicated in some primitive Scolytidae, but they are not indicated in other curculionoids known to me. Anthribidae and Nemognychidae have a maxillary lacinia separate from the galea; this character is shared by Platypodidae (Tesserocerini), Attelabidae, and Rhynchitidae; the lacinia and galea are fused in all other curculionoids. Most of those curculionoids having two gular sutures have a segmented maxillary palp; Attelabidae, some Rhynchitidae, and one Platypodidae share that character. In Anthribidae, Nemognychidae, Eobeldia (fossil), Scolytidae, and Platypodidae the mandible is apically pointed, the cutting edge mesal, the clylides are closer together and differently positioned, and the apical part of the hypostoma is of minimal size. In all other cur-
culionoids, the basal half of the mandible forms a cylinder that rotates on a horizontal axis between the condyles, the dentate cutting edge is distal and moves through a different arc, and the hypostoma is enlarged to give greater strength to the posterior clypeole. Whereas the preponderance of adult characters support the suggested relationship, larval characters have not been found that separate some Curculionidae from some Scolytidae. The larvae of Platypodidae and Scolytidae are easily separated; however, it is by the same primary character that Anthribidae and Nemognatidae larvae are separated (see key to families below). Obviously the Platypodidae-Scolytidae are not part of the Curculionidae and occupy a more primitive position in phylogeny. Exactly where they branch from the main curculionoid stem is not yet clear, but it could be from an Eobeliidae-like ancestor.

Within the Platypodidae-Scolytidae, three major phyletic units are evident. The smallest and most distinctive paraphyletic line is the Platypodidae (about 1,000 species). They lack socketed tibial denticles, have the terminal, protibial micro modified from the middle one of three apical spines (as compared to Protokylastes), always have the posterior half of elytral interstriae 10 present, always have a primitive mechanism for locking the elytra in closed position, lack a spineum gastrost, and contain members having the primitive characters cited in the above paragraph. The Scolytidae contain partial or complete departures from these characters. As indicated above, six rare tropical genera (containing a total of seven species) are intermediate between these families.

The other two major phyletic lines include the Hylesininae (about 2,000 species) and the Scolytinae (about 4,000 species). Although the most primitive members of the family undoubtedly are members of the Scolytinae, that subfamily also contains far more and greater specializations than do the Hylesininae. Because the Hylesininae are less diverse and depart less drastically from the primitive form, they are considered more primitive and paraphyletic; the Scolytinae are more specialized and contain the major evolutionary thrust of the family. Hylesininae evolution appears to have been oriented toward a body type that is subspherical to take advantage of the row of circumalveolous on the bases of the elytra, scolytine evolved toward cylindrical compartment that is more effective in deeper host tissues where the ambrosial habit was exploited.

Progress toward a more nearly spherical body form in Hylesininae was accompanied by straightening out (somewhat) the scutocutellar and pleural sutures on the metasternum. This apparently modified the mechanism of flight such that refection between the metasternum and its postnotum was no longer necessary and that the intersegmental line (membrane) was lost, at least in the median area. Accompanying that change were: a reduction in the number of segments of the antennal funicle from seven to as few as three and changes in the antennal club from cone-shaped, with simple, transverse sutures, to flattened and with or without sutures in numerous combinations. The primitive mating system was monogamy, with the female initiating the new parental gallery. Limited departures from that system include male-initiated monogamy and heterosanguineous polygyny (many Polygraphini) and consanguineous polygyny (Smales in Hyorrhynchini). A recognizable phyletic sequence appears to progress from the primitive Hylastini through the Hylesinini to Tomicinae. Hyorrhynchini and Phrinosomini appear to have been derived independently on separate lines from the same basic stock as that group of tribes. Among those tribes with a fused postnotum, Bothrosternini and Diamerini appear to be geographical replacements of one another that arose from a common ancestor that was much more closely allied to the Ctenophorini-like ancestor of Scolytinae than to the immediate ancestral stock of the Hylastini-Hylesinini-Tomicinae. Although the Phloeotribini and Phloeosomini are closely related to one another, they (as one unit) were probably derived from the Bothrosternini-Diamerini ancestral stock independently from the unrelated Polygraphini and Hypoborini. Differentiation of phyletic lines in the Hylesininae has progressed slowly, consequently, they are difficult to detect. In general body habitus, Protokylastes (Platypodidae) resembles primitive Hylesininae very closely, but the legs and antennae do not. Pycnarthrum (Ctenophorini)
would be placed in Hylæsininae except for its legs. A primitive relationship of Hylæsininae to primitive Scolytinae and Platypodidae is clearly indicated in these genera.

Among the Scolytinae, the Ctenophorini, Scolytini, and Scolytotaphypodini are closely related to one another and were almost certainly derived from a common Ctenophorini-like ancestral stock. The Ctenophorini more nearly resemble Prototypalatus (Platypodidae) than do other members of this subfamily. Some Cerambycidae (allies of galerita, Ctenophorini) have circulations on the basal margins of the elytra as in Hylæsininae. The four remaining clusters of tribes were probably derived from a Ctenophorini-like ancestor in the following pattern. Although there is no clear primitive connection to an ancestral group, Micracini and Catopinini are anatomically and biologically allied to one another. An advanced member of Micracini probably gave rise to the Xylecotini-Cryphalini group, then a Cryphalini-like member gave rise to the Corthylini. The remaining tribes, Carphodicticini, Ipini, Dryocoetini, Crypturgini, Xyleterini, and Xylelorini (listed in ascending order of anatomical and biological complexity) were probably derived from another Micracini-like ancestor along the same (one) phyletic line of descent. Active major evolutionary thrusts appear to be in progress within the Dryocoetini, Xylelorini, Crypturgini, and Corthylini, which combined contain more than half the living species of Scolytidae.

METHODS

Although this project was conceived in 1949, serious work on it was not started until 1955. From 1955 to 1965, comparative anatomical studies were made of representatives of more than 100 selected genera of Curculionoidea, in addition to more than 60 genera of Scolytidae and Platypodidae. As the patterns of evolution began to emerge from those studies, a major effort was made to collect specimens and to gather behavioral and ecological data on species not previously known to me. More than 2,000 species of Scolytidae and 300 species of Platypodidae were collected from North and South America, Europe, Asia, Australia, and New Guinea. In addition, visits were made for the purpose of studying types and comparing them to other museums in the United States, Canada, Mexico, Venezuela, England, Austria, Finland, USSR, India, Japan, Australia, and Papua-New Guinea. There visits included stays of a month or more at the British Museum (Natural History), the Schell Collection (both at Lienz with Schell in 1965 and at Vienna in 1983), and the Forest Research Institute, Dehra Dun, India (where more than 40,000 Indian specimens were sorted to species in addition to studies of the types). It is estimated that well over 400,000 specimens of Scolytidae and Platypodidae were examined. From these museums not visited in person by me, types and other specimens were obtained for study through loan. Except as noted below under Incertae Sedis, all existing type-species for all named genera and subgenera were examined and, where type-specimens have been designated, the type-specimen of those species were also studied. The basis for recognition is given under each species and synonym below.

Except at Helsinki (Finland), Leningrad and Moscow (USSR), Bulolo (Papua-New Guinea), and Sydney (Australia), where local museum equipment was used, the studies were made using an American Optical Company stereoscopic microscope, model 25, equipped with an ocular grid, at magnifications of 10, 40, 80, and 160X. All measurements were made at 10X and excluded the head (in measurements of body length). Authentic specimens of the type-species of several genus-group names assigned to the Scolytidae were not examined during the course of this study. These species fall into two categories: (1) those for which the types or other authentic specimens could not be found and are presumed lost, and (2) fossil species.

The types of four genera could not be found. These included:

1. Allarthrum Hagedorn (1912:355), based on A. kolbci Hagedorn (1912:355), from Peterhafen, Deutsch New Guinea. The type(s), 1.5 mm in length, was deposited in the Kgl. Zoolog. Museum Berlin but cannot now be found. The illustration of the antenna (Hagedorn 1912:Fig. 5) is of a Cryphalus species. It is provisionally listed as a synonym of Cryphalus.
2. *Bufonius* Eggers (1919:231), based on *B. obscurus* Eggers (1919:231) from Amani, Ost-Africa. The unique holotype, 1.5 mm, was lost with the Hamburg Museum in 1944. The antennal funicle was described as 2-segmented, the club elongate, with three transverse sutures; the scutellum was not visible, the basal margins of the elytra were sharply rounded, and the elytral sculpture was pronounced and unique. Except for the absence of cremulations on the basal margins of the elytra, this genus would be placed in Hypoborini. A more detailed knowledge of the fauna of East Africa is needed before it can be correctly placed in classification.

3. *Tusaphorus* Eggers (1920b:119; preoccupied, renamed *Tapholthorus* Wood), based on *T. africanus* Eggers (1920b:119) from Deutsche-Ostafrika. The unique holotype, 3.0 mm, was lost with the Hamburg Museum in 1944. The antennal scape was elongate, the funicle was 5-segmented, the club was flattened, with a suture near the apex, and the frons was impressed above the eyes. This genus almost certainly is in the Dryococtini, possibly near *Tiarophorus* or *Xylepites*.

4. *Pseudomicracis* Eggers (1920a:36), based on *P. elaeis* Eggers (1920a:36) from Dares-Salaum, Ostafrika. The unique female holotype, 1.5 mm, was lost with the Hamburg Museum. The frons was impressed, the antenna was similar to *Micracis*, the scape was triangular, with long hair on the outer angle, and the sutural apex of the elytra mucronate. Because only one known genus bears the combination of characters described by Eggers, his name is associated with those African species previously referred to the American genus *Micracis*. As such, this genus is recognizable and is treated below under the name *Pseudomicracis*.

Of the six fossil genera that have not been previously placed in synonymy under older names of modern genera, four are from Baltic amber, one is from Burmese amber, and one is from sedimentary deposits. These include:

1. *Carpohorites* Scheld (1947:32) was based on *C. kelibacii* Scheld (1947:32) and *C. posticus* Scheld (1947:33), both from Baltic amber (*Carpohorites* was a lapsus calami). From the descriptions, I see no reason to separate these species from *Carpohorites*; however, I have not examined the specimens.

2. *Hylescierites* Scheld (1947:29) was based on *H. granulatus* Scheld (1947:30) from Baltic amber. From the photograph of the holotype and the original description, I see no reason for separating this species from *Hylurgus*.

3. *Taphramites* Scheld (1947:41) was based on *T. gnathotrichus* Scheld (1947:42) from Baltic amber. From the description, it appears that this species should be placed in Dryocoetini, probably in or near *Dryocoetes*. I have not examined the specimen.

4. *Xylechinites* Hagedorn (1907:120) was based on *X. aniceps* Hagedorn (1907:120) from Baltic amber and was redescribed and illustrated by Scheld (1947:30–32). The descriptions and photograph of the holotype indicate that this species is a Tomicini near or in *Xylechminus*. I have not examined the specimen.

5. *Cryphalites* Cockerell (1917:368) was based on *C. rugosissimus* Cockerell (1917:368) from Burmese amber. Because no usable characters were included, the original description gives no clue as to where this species should be placed. It is assumed that Cockerell was correct in assigning it to Cryphalini. I have not examined the specimen.

6. *Xyleborites* Wickham (1913:26) was based on *X. longipennis* Wickham (1913:26) from the Wilson Ranch near Florissant, Colorado. The author indicated that this species, 2.2 mm in length, resembled *Xyleborus pubescens*. Essential characters were not described. The specimen was not examined by me.

*Pityophthorides* Wickham (1916:18) and *Adipocephalus* Wickham (1916:16) are not considered to be members of the Scolytidae.

**Systematic Section**

Although some obvious unanswered questions remain as to the exact position of Platypodidae and Scolytidae within the Curculionoidea, the following key is presented for the identification of families. The presence of complete pregaular sutures and the mandibular structure of Platypodidae and Scolytidae are obviously more primitive than the absence of these sutures and the specialized mandibular structure of Belidae and Oxycoorynidae, but the single gular suture and presence of larval epipharyngial rods are more advanced than...
the two gular sutures and absence of the rods in Belidae. The long subsectional history and very small body size of Platypodidae and Scydtyidae have had an obvious effect on their anatomy that complicates interpretation of their position in phylogeny.

This key to families of the Curculionoidea is tentative. A thorough reexamination of the Belidae-Agryaeididae-Ocyporididae groups is needed to determine the significance of single vs. double gular sutures, the precise position of character gaps that separate families, etc. Another area of concern is the section of the key in couplets 11 and 12. Characters to separate these three taxa are weak, but, in view of the large number of species to be classified herein, perhaps the recognition of these three families is justified. Among more than 130 genera of Curculionidae (in the sense used here) dissected by me, I saw three possible divisions of this family. These included (1) the Cossoininae-Rhynchophorinae, (2) the broadnose weevils, and (3) all others. It is recognized that some equally distinct groups may exist that were not seen by me, but a thorough comparative anatomical study should precede their recognition. Following my study, I seriously doubt that even one-third of the 75 or more subfamilies that have been recognized within Curculionidae will survive this rank; most are worthy of no more than tribal status.

Key to the families of Curculionidae

1. Adult: two gular sutures present or rudiments of them evident (only one gular suture and a postgula present in several Belidae and Rhopalodidae of Ocyyporidae); maxillary palp 4-segmented; abdominal segments free (except 3-6 connate in Anthribidae); antennae usually orthoconous, scape little longer than succeeding segments, club loosely 3-segmented. Larva: epipharyngeal rods absent; maxillary palp 3-segmented, rarely 2-segmented; thoracic legs present; frontal sutures reaching articulating membrane of mandible; two folds in each abdominal tergum

2. Adult: one gular suture extending from minute postgula at margin of foramen magnum to posterior torcular pits (usually where base of rostrum meets head); maxillary palp 1- to 3-segmented (4-segmented in one Platypodidae, some Byntheridae, and all Atte­labidae); abdominal segments free or partly connate in some groups; antennae frequently geniculate; a definite club usually present (or thoracous in Bruchidae; intermediate in Phyceidae, Apionidae, some Platypodidae; and one Sci. "ystidae). Larva: epipharyngeal rods present; maxillary palpi 1- or 2-segmented (4-segmented in Brethidae and Byntheridae); thoracic legs absent (present in Bruchidae and Phyceidae); frontal sutures not reaching articulating membrane of mandible (except Brethidae, Apionidae, Phyceidae, some Platypodidae); two to four folds in each abdominal tergum

3. Adult: labrum distinct and separate (except absent in Bruchidae of Anthribidae); maxillary palp flexible, lamina forming a distinct element (see also Rhynchaenidae and Tenebrionidae in Platypodidae). Larva: mandibles with a distinct nola

4. Adult: labrum fused or lost, maxillary palp rigid; maxilla without a separate lacinia. Larva: mandibles without a distinct nola

5. Adult: gular sutures rudimentary, represented only at margin of foramen magnum or totally lost; tentorium largely or entirely obsolete; proventriculus developed; lateral margins of pronotum acute (rounded in Bruchidae); inner margin of elytra with a flange near costal margin; cavities of mesoscutae broadly closed outwardly by sternum, visible as abdominal stria 1-4-4 (one). Larva: clupeus distinct from froms, or head deeply retracted; mandibles without ventral process in addition to nola (includes the distinct subfamilies Bruchelinae, Anthribidae)

6. Adult: gular sutures extending from margin of foramen magnum to posterior torcular pits; tentorium present; proventriculus indistinct; inner margin of elytra without a flange near costal margin; mesoscutae not or imperfectly closed outwardly by sternum; abdominal sterna free. Larva: clupeus usually fused to fossae, head not deeply retracted into prosoma; mandibles with a ventral process in addition to nola

7. Adult: gular sutures longer, extending to posterior torcular pits; partial prepupar sutures occasionally present in female near apex of rostrum; at least three genera with large postgula and short median gular suture; antomae filiform or nearly so, inserted laterally remote from base of rostrum; inner margin of elytra with a flange near costal margin; wing with five anal veins in main group complete to base; tarsi normal, pseudotetramerosus; lateral margins of pronotum transversely rounded. Larva: maxillary palpiger well developed, thoracic spiracle intersegmental

8. Adult: gular sutures usually short (a large postgula and one median gular suture in some Osyyporidae), externally visible near foramen magnum or else lateral margins of pronotum acute; antennae inserted at or near base of rostrum; either antennal club or tarsus pseudotetramerosus; inner margin of elytra with...
out a flange near costal margin; wings with fewer than five anal veins or else bases of elytral veins incomplete. Larva: maxillary palpiger usually not evident; thoracic spiracle in mesothorax 5

5(4). Adult: tarsi pseudot inhibitorous, segment 2 bilobed; antennal insertion at base of rather short rostrum; antenna filiform, not clubbed; pronotum distinctly well developed. Larva: maxillary palpiger not distinct 6

6(3). Adult: pseudot inhibitorous, segments 2 and 3 bilobed; antennal club 2- or 3-segmented; (a) large postgula and at least a partial median plate out of transversely at least Rho-
patori}a; lateral margins of pronotum acute; antennal insertion at base of long rostrum, on ventral face; proventriculus poorly developed. Larva: palpiger distinct. Oxycoyiidae

b) Larva: palpiger distinct. Agyroidesidea (Protothynidae)

7(6). Adult: proventriculus present and reinforced internally by massive apodermal ridges; rostrum short to nonexistent; tibia armed on apical or lateral margins by a series of spines and/or socketed teeth of setal origin; corbels never present; hypostomal area small, never armed by a large spine, posterior mandibular clypeus more anterior in position; axis of mandibular hinge oblique to transverse, cutting edge on mesal margin (Fig. 8: some members of Tesseroncerini) with a separate lacina 7

8(7). Adult: proventriculus absent, with no indication of supporting internal apodermal structure (longitudinal ridges giving rigidity to rostrum are not reinforced internally and should not be confused with true proventricular sutures); rostrum variable, long to very short, lateral margins of tibia unarmed (except for simple spines in some Cassuonidae); corbels commonly present; hypostomal area larger, commonly armed by a large spine, posterior mandibular clypeus more posterior in position (Fig. 8); hinge parallel to body axis, cutting edge on apical margin, separate lacina never present (except some Attelabidae) 8

9(8). Adult: tarsal segment 1 elongate, usually longer than 2-5 combined (except shorter in Protostylus, Protostylus, Coptostylus, Scolytinaee); tibia armed on apical and/or lateral margins by one or more spines, never by socketed denticles, apical spur formed by middle apical spine (as compared to Protostylus); male scutellum gastrale absent; antennal club solid, unmarked by sutures (clearly indicated in Coptostylus); head about as wide as pronotum; pronotum with distinct lateral constriction near middle; when visible, scutellum usually reduced, decollate, usually with not more than apex attaining (flush with) elytral surface; metepisternum very elongate, its anterio margin straight, its anteroventral angle neither displaced caudad nor extended ventrally; mesepimeron flat, vertical; mesepisternum moderately to greatly enlarged, varying from flat to inflated; eyes convex, never truly emarginate; pronotum never armed by apicities. Larva: elytra finely to fusc in all except primitive genera; frontal sutures reaching articulating membrane of mandible or not... Platypodiidae

10(9). Adult: tarsal segment 1 about equal in length to 2 or 3; tibia armed on apical and/or lateral margins either by spines or socketed denticles (compared to Protostylus structure), male scutellum gastrale present; antennal club variable, with or without sutures; head narrower than pronotum; pronotum almost never with constriction near middle; when visible, scutellum usually flush with elytral surface, often flattened; metepisternum stout to elongate, its anterior margin usually procurred, its anteroventral angle displaced slightly caudad and distinctly extended ventrally; mesepimeron flat, oblique; mesepisternum smaller, decollate cephalad, eyes more nearly flat against head, often emarginate to divided; pronotum often separate. Larva: clypeus distinct, separate from fusc; frontal sutures never reaching articulating membrane of mandibles... Scolytidae

9(8). Adult: labial palp inserted ventrally on mentum; head frequently constricted behind eyes; antennae never geniculate, inserted dorsally or laterally at base or middle of rostrum, club absent to moderately distinct; proventriculus without sclerotized plates. Larva: frontal sutures reaching articulating membrane of mandibles...

10(9). Adult: labial palp inserted apically; antenna straight or geniculate, inserted laterally at middle or near apex of rostrum, club 1- to 3-segmented, lose to compact, small to large. Larva: frontal sutures either reaching or not reaching articulating membrane of mandibles...

11(10). Adult: maxillary palp 4-segmented, galea and lacina distinct; mandibles often dentate on outer margin; labial palp 1- or 3-segmented (rarely absent); elytra with a scutellary strid; submarginal suture short, laterally reeased; hind wing usually with four anal veins, radial cell well developed; sterna 3-6 freely free, 3-4 connate in some, 3-6 connate in most; ep piece of male tegmen simple, setose; malphigian tubules grouped three on each side of alimentary canal; more than two ovaries in each ovary. Larva: legs absent, two or more sterna present on each side of head; antennae usually 2-segmented, maxillary palps 2- or 3-segmented; abdominal terga with two folds... Attelabidae
objc

Family Scolytidae Latreille

Scolytus Latreille [1807, 273, Type-genus: Scolythus Graeffy 1782, see also China 1992]

The family Scolytidae is comprised of a group of more than 6,000 small to minute species. Whereas the preponderance of species are tropical, a few of them reach the northern and southern limits of tree distribution near the polar regions. They are unique in that loosely pair-bonded adult parents bore into subcortical tissues of their host (usually) before mating or oviposition occur. Eggs are variously placed in the galleries, and the larvae either expand the parental mines or form individual galleries while the parents defend the outer entrance to the tunnel. Thus, the beetles are essentially internal plant parasites that spend virtually their entire lives secreted within the tissues of the host. The ephemeral habitat they occupy is the unforthright, weakened, or dying tissue of woody plants; only one generation is completed in each host unless a large tree that is succumbing progressively is involved. Because of the very brief period this habitat is open to them, efficient means of locating a host, recruiting a population to subdue it, and overcoming host resistance are mandatory. This is accomplished through sensitivity to odors emitted by trees under stress, by a complex system of pheromones, and by mutualistic relationships with fungi. Several of the most efficient species, with respect to meeting these challenges, compete with man for timber and horticultural resources and present a very real threat to human economy. Most woody plants, a few herbaceous plants, and many fruits and nuts are infested by these insects. The adjustments they have made in their mating systems, utilization of food resources, and adaptive radiation form a classic example of biological diversity.

Key to the Subfamilies and Tribes of Scolytidae
(Modified from Wood 1978)

1. Each basal margin of elytra procurred and armed by a series of marginal crenulations (Fig. 16) (or less commonly by a continuous elevated costa in some Bothrasternini, Diacmeini, Polygraphini), usually with a subcortical emargination between them; scutellum usually small and rounded or depressed, absent in some groups; pronotum weakly if at all declivous on anterior half, usually unarmed

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strike; notosternal suture well developed and usually extending almost to anterior margin; hind wing with three or fewer anal veins, radial cell not evident; sternum 3-4 connate and much longer than 3-6; cap piece of tegmen bifurcate. Larva: rudimentary, segmented legs present; sternum absent; antenna 1-segmented; maxillary palp 3-segmented; abdominal terga with three to four folds... Apionidae developed. Larva; frontal sutures extending geniculate then trochant er, long, cylindrical, with projecting setae; proventriculus poorly developed. Larva: median area on posterior part of head overlapped by prothorax; maxillary palp 2- or 3-segmented, two basal sensillae on labrum; frontal sutures complete but indistinct; abdominal terga with two folds... Rhyynchitidae

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Adult: maxillary lacinia usually fused to galea, palpi 2- or 3-segmented; metepimeron carinate, fitting flange on inner margin of elytra near humeral angle, metepimeron not carinate; antenna straight or geniculate, clubbed or not. Larva: posterior part of head free in median area; maxillary palp 1- to 3-segmented; no basal sensilla on labrum... 11

11(10). Adult: abdominal tergum 8 longitudinally grooved for reception of inwardly raised elevation near apex of elytra; tergum 8 bearing a pair of spiracles; maxillary palp 3-segmented, but largely retracted into palpifer; antenna not geniculate. Larva: rudimentary, segmented legs present; maxillary palp 2-segmented; 3 sterna present... Rhyynchitidae

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Adult: abdominal tergum 8 not grooved, spiracle absent; maxillary palp 2- or 3-segmented, usually not retracted into palpifer... 12

12(11). Adult: either antenna not geniculate, or if geniculate then trochanters long, cylindrical, femur remote from costa, attached to apex of trochanter; ventral surface of mentum usually with projecting setae; proventriculus poorly developed. Larva: frontal sutures extending to articulating membrane of mandibules; abdominal terga with two kids... Apionidae

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Adult: antenna usually geniculate; trochanters triangular, femur attached to side of trochanter, sometimes almost touching costa; ventral surface of scutum without projecting setae; proventriculus usually well developed. Larva: frontal sutures not reaching articulating membranes; abdominal terga with two to four folds... Curculionidae
but crenulations sometimes present on intersegmental areas; head usually visible from above, somewhat wider; protibia usually wider; scales or deeply divided setae a common feature (subfamily HYLESIININAЕ)

2. Basal margins of elytra forming a straight, transverse line across body (Fig. 17), unarmed, rarely (some Scolytini, Cryptophorini, Creophilini) with a weakly elevated continuous line; scutellum usually large, flat (rarely absent or highly modified in some Xyleborini), pronotum weakly to strongly dehiscent on anterior half and usually armed by many asperate crenulations, particularly on median half (Figs. 31, 46, 52); head usually partly or entirely concealed from dorsal aspect, somewhat narrower; protibia usually narrower; scales or deeply divided setae an uncommon feature (subfamily SCOLYTIDAE).

3. Scutellar area of metasternum and its postnotum separated by a suturelike intersegmental membrane (Fig. 23, pts. 43, 45); posterior part of scutocutellar suture strongly curved mesad to a point near crest of scutellar groove then continuing cephalad parallel to this costa for about two-thirds of metasternum length (Fig. 23, pt. 43) (except much less in Phrynocosini and Hylorhynchinae); metamereal suture descending subvertically from pleural wing process to metepisternal groove formed to receive corresponding costal groove and flange of elytron then abruptly angled and continued caudad along this groove to a point near pleural coxal process (Figs. 18, 23 pt. 44); scutellum visible; funicle 6- or 7-segmented or if 5-segmented (Sueus) then eye divided, male frons not impressed, and antennal club symmetrical

4. Scutellar area of metasternum and its postnotum completely fused on at least median third, intersegmental suture usually obsolete (Figs. 21, 23 pt. 41); scutocutellar suture less strongly curved, approaching costa of scutellar groove more gradually and continuing cephalad parallel to it for less than half length of metasternum (Fig. 23, pt. 41) (it never reaches margin of this groove in some groups; metameral suture sometimes as described above, but more commonly running a more direct route from pleural wing process to pleural costal process, often remote from locked position of costal margin of elytra for most or all of its course (Figs. 21, 23 pt. 41); scutellum either not visible or if visible then funicle 5-segmented and male frons impressed (Bothrosternini with 6-segmented funicle but with a distinctive protibia, Fig. 24)

5. Scutellar area of metasternum and its postnotum separated by a suturelike intersegmental membrane (Fig. 23, pts. 43, 45); posterior part of scutocutellar suture strongly curved mesad to a point near crest of scutellar groove then continuing cephalad parallel to this costa for about two-thirds of metasternum length (Fig. 23, pt. 43) (except much less in Phrynocosini and Hylorhynchinae); metamereal suture descending subvertically from pleural wing process to metepisternal groove formed to receive corresponding costal groove and flange of elytron then abruptly angled and continued caudad along this groove to a point near pleural coxal process (Figs. 18, 23 pt. 44); scutellum visible; funicle 6- or 7-segmented or if 5-segmented (Sueus) then eye divided, male frons not impressed, and antennal club symmetrical

6. Prothorax: procoxal area rather large, its lateral margins strongly, sharply elevated from anterior margin to coxal (Fig. 20); crenulations on elytral bases usually poorly developed; antennal funicle 7-segmented, club conical, segment 1 often as long as others combined, head somewhat prolonged, subrostrate, frons never sexually dimorphic; eyes

7. Prothoracic: procoxal area rather large, its lateral margins strongly, sharply elevated from anterior margin to coxal (Fig. 20); crenulations on elytral bases usually poorly developed, antennal funicle 7-segmented, club conical, segment 1 often as long as others combined, head somewhat prolonged, subrostrate, frons never sexually dimorphic; eyes
Fig. 25. Mesal aspect of elytral base: A-B, *Pseudophylinus nebulosus* (LeConte), groove nearest pubescent surface continues to base without interruption (ignore the tiny grains of frass trapped in the groove in A); C, *Philonthus cristatus* (LeConte), groove near base interrupted by a series of interlocking nodules and cavities.

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entire, rather short; Northern Hemisphere, except introduced elsewhere; in Neotropics

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Prothoracic precoxal piece small, short, its lateral areas elevated or not; evolutions on elytral bases more conspicuously elevated, forming a definite row (except confused in *Dactylopleura*); antennal funicle variable; 5- to 7-segmented, club weakly to moderately flattened; head less distinctly rostrate, male funicle usually impressed, eye oval to elongate, entire to feebly emarginate

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5(4). Pronotum asperate on anteroventral areas (except *Hylastinus*); prothoros with elevated costate ridge from costa to anterior margin (weaker than in Fig. 20); antennal funicle 6- or 7-segmented, mesal surface of elytra at base of suture immediately behind scutellum with an interlocking series of nodules and cavities (Fig. 25-C); this lock interrupts groove and flange of suture (not visible when elytra in locked position); worldwide

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Hylastini

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Anteroventral areas of pronotum unarmmed; precoxal costa on prothorax absent; funicle 5- to 7-segmented; mesal surface of elytra at suture with interlocking groove and flange continued to base without a series of nodules or cavities immediately behind scutellum (Fig. 25-A-B); worldwide

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Tomocini

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6(3). Protibia armed on outer apical margin by several asperate denticles of approximately equal size; procoxae contiguous; funiscapes not sexually dimorphic; antennal scape elongate, suture 1 of club partly septate; pronotum never armed by asperities. America, Africa

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Phrictosomini

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Protibia with outer apical angle produced into one conspicuous spine reaching level of tarsal insertions, outer margin without any socketed teeth, procoxae rather widely separated; male funicle broadly impressed (except in dwarfed Sues); female funicle convex; antennal scape either long or short, club asceptate; pronotum either with or without asperities in anteroventral areas; southeast Asia

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Hyrrhyynchini

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7(6). Lateral margins of pronotum usually subacutely elevated, costaate (as in Fig. 12); mesepimeron moderately to very large, its dorsal portion usually grooved for reception of elytral base; scutellum shield under base of elytra large, extending posteriorly beyond visible scutellum (Fig. 26); scutocutellar suture remote from costa of scutellar groove to its base; outer apical angle of protibia often with only one major recurved spine (Fig. 7); Africa, southeast Asia to Australia

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Diamerini

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8(7). Outer apical angle of protibia with a curved bifid process, meson- and metafemur with one or two (usually smaller) curved spines on outer apical angle extending beyond level of spine on inner apical angle (Fig. 34); pronotum smooth or longitudinally striate; funicle 6-segmented; lateral prosternal area usually subacutely elevated from costa to anterior margin; anterior coxae rather widely separated; precoxal in elytral bases rather small or (rarely) replaced by a continuously elevated costa; eye entire

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Bothrosternini

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Protibia armed by several teeth of about equal size (except *Aricerius* in *Philonthini*), none of them extending be-
1986 WOOD: GENERA OF SCOLYTIDAE 31

Fig. 26. Diagram of Sphalerotrupes globosus Blandford, with elytra removed, showing enlarged scutellar plate that lies below the base of the elytra.

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Fig. 27. Antenna of Phloeotribus: A, rhododactylus (Marsham); B, curcumanus Börner.

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9(9). Scutellum visible, elytral bases notched for its reception; tarsal segment 3 stout, usually somewhat bilobed (except slender in Chrysomelinae); mesal surface of elytra at suture immediately behind scutellum with a series of interlocking nodules and cavities (Fig. 25-C) .............................................. 10

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10(9). Scutellum obsolete, elytral bases only slightly if at all emarginate at suture (Fig. 17); tarsal segment 3 slender; mesal surface of elytra at suture usually without a special lock, groove and flange extend to base at position of scutellum (degenerate in Fig. 25-A-B) ........ 11

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10(9). Antennal club constricted at sutures and movable at intersegmental lines (Figs. 16, 27); Holarctic, Neotropical, and Australian Phloeotribini

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11(10). Eye emarginate or entirely divided; pronotum never armed by asperities; crenulations at bases of elytra more widely distributed, extending lateral beyond interstriae 5 (Fig. 10); funicle 5- or 6-segmented; scutocutellar suture passing near and parallel to costs of scutellar groove on anterior fourth of metanotum; Northern Hemisphere and Africa Polygraphini

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12(11). Eye sinuate or entire; pronotum armed by a few scattered or clustered asperities; crenulations at bases of elytra restricted to area between suture and interstriae 5; funicle 3- to 6-segmented; scutocutellar suture remote from costa of scutellar groove on anterior fourth of metanotum; almost worldwide Hypoborini

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13(12). Metepisternum visible throughout its length, slightly more than its dorsal half covered by elytra when in locked position, either with a conspicuous groove for reception of costal flange throughout its length or else groove represented at its anterior end by a denticulation or costal remnant near anterior end of metepisternum (Fig. 23, parts 42, 44, 46); antennal club varying from flat to obliquely truncate (Fig. 29) .............................................. 14

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14(13). Metepisternum largely covered by elytra, its groove for reception of costal flange obsolete, a small, transverse callosity (Cryphaliini, Fig. 31) or a small transverse groove (Corthylini, Figs. 23, part 47, and 32) at anterior end of metepisternum; antennal club strongly flattened; antennal club never obliquely truncate .... 24

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15(14). Lateral margins of pronotum subacutely elevated, basal margins of elytra usually finely elevated; pronotae rather widely separated except contiguous in Xyloctoninae; protibia

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16(15). Lateral margins of elytra subacutely elevated, basal margins of elytra usually finely elevated; pronotae rather widely separate except contiguous in Xyloctoninae; protibia
Figs. 28-32. Scolytidae parts: 28. *Ips* woodi (Thatcher), ventral aspect of prothorax showing contiguous coxae, left coxa removed (ignore the plant fiber between the coxae); 29, obliquely truncate antennal club of *Dryococcus confusus* Swaine; 30A, posterior face of prothorax of *Scolytodes poppinus* Eggens showing unsocketed spines on lateral margin, B, enlargement of spines 1 and 2; 31, dorsal aspect of posterolateral area of prothorax of *Cryphalus refocollis* Hopkins, with left elytron removed to expose anterolateral area of metathorax (arrow points to the groove that is partially replacing the metepisternal spine); 32, left pleuron of *Coriolus panamensis* Blandford, with elytron removed, upper arrow points to pleural suture, lower one to the groove that has entirely replaced the metepisternal spine.
with prominent outer apical process recurved (Fig. 7: Scolytodes), usually extending beyond tarsal insertion, posterior tibia tapered on apical third and armed by several small socketed denticles; funicle 6- or 7-segmented; tarsi often retractible into tibial grooves .... 15

Lateral and basal margins of pronotum rounded (except Coetacea); procone subcuneous (except most Mieracini and a few Xylocerini; prothorax with outer apical angle incompletely marked by several small socketed denticles; funicle 2- to 6-segmented; tarsi not retractible (except in Eucacotypetra). 17

15(14) Eye divided or nearly so by a very deep emargination; antennal club flat, usually enlarged, with sutures strongly preserved, abdomen conspicuously ascending toward apex (not always clear in Chthonotom); tarsi always retractible into tibial grooves, Africa and southern Asia .................. Xylocotini

Eyes entire to shallowly sinuate on anterior margin; antennal club flat, usually smaller, more slender, sutures variable, if present, abdomen horizontal; tarsi retractible or not .... 16

16(15) Antennal club with one or more sutures indicated by grooves, setae, or setae scopulae; scutellum large, flat: America: mostly phloemophagous, never mycetophagous .............. Chthonophorini

Antennal club unmarked by sutures; pronotum with sides strongly concurred on posterior half, scutellum absent (a small scutellum present in Scolytoplatyphus congonga); Africa to Asia and New Guinea; mycetophagous ............. Scolytoplatyphodini

17(14) Procoxae moderately separated; prothorax with sides parallel, armed by denticles only on apical margin or posterior face; funicle 6-segmented (5-segmented in one African genus); female funicle rarely concave; male rarely concave (except two Pseudothydas); Africa and America, one species in Asia .... Mieracini

Procoxae contiguous (except Carphodicticiini, some Xylocerini); prothorax much wider apically, armed on lateral margin by several denticles; female funicle rarely concave (a few Dryocoetia); male often concave; funicle 5- to 5-segmented, 6-segmented in Tarusphorus. 18

18(17) Male funicle strongly excavated, epistermite armed by a pair (usually) fused horseshoe-shaped processes on inner surface (Fig. 47); funicle 5-segmented, club often small and feebly flattened; eye small, entire; pronotum with summit near basal margin, projecting back over scutellum in some species; western United States and Mexico ............... Caecopini

Not fitting above combination of characters .... 19

19(18) Mesop- and metathoracic tibiae more slender, more abruptly narrowed on apical fourth, lateral and apical margins armed by fewer, coarser teeth; eye sinuate to shallowly emarginate (divided in Tairophorus, Dryocoetia, Africa); pronotum sometimes with a raised line on basal or lateral margin; peculiar area not depressed; series of similar size and body form (except male dwarfed and deformed in Coccytops and Oecopemus) habits varied but never woodboring or mycetophagous .... 20

If eye completely divided into two parts and antennal funicle 4-segmented then male funicles deeply excavated and male equal in size to female; if eye emarginate (or if divided and antennal funicle 5-segmented) then male dwarfed, deformed, and flightless and female meso- and metathoracic tibiae expanded to just beyond middle then at least arately tapered to apex, its apical two-thirds on outer margin armed by a row of numerous small, closely set teeth of equal size, these usually supplemented in same row by submarginal hair on posterior face; male pronotum highly modified, peculiar area depressed (except Premacolinus); woodboring, mycetophagous ............. 23

20(19) Pronotum rather strongly, laterally constricted on posterior half, anterior half not declivous and never armed by asperities; anterior coxae moderately separated; anten­ nal club strongly flattened, marked by two sutures, sutures on posterior face almost equal to those on anterior face; South America and India to Ceylon (Sri Lanka) .................. Carphodicticiini

Pronotum not constricted, sides straight to arcuate, anterior half usually declivous, usu­ ally armed as anterior or nonmycetophagous; anten­ nal club obliquely truncate or with sutures on posterior face; strongly displaced toward apex (case with sutures obsolete) .... 21

21(20) Eye shallowly sinuate (shallowly emarginate in some: Acnosphotonicini), its lower half distinctly narrower than above; prothorax with 5- to 6-segmented club, antennal club rarely obluscate truncate (Pityotus, Orthodontia), pro­ coxae contiguous, intercalary piece longitudi­ nally emarginate to truncate, never complete; elytra moderately subulate to elaborately excav­ ated, with lateral margin usually armed by tubercles or spines; pronotum more strongly declivous on anterior third; asperities usually larger; worldwide .......... Ipini

Eye sharply, rather deeply emarginate (sinuate in Deropria), lower half usually almost equal in width to upper half; prothorax usually with four or more distinctly separated, elytral declivity flattened to convex, unornamented by spines or large tubercles; pronotum either evenly arched from base to anterior margin or less strongly declivous on anterior third, asperi­ ties, when present, usually fine and abundant (a few exceptions) .... 22
Antennal funicle 4- to 6-segmented, club either obliquely truncate or with sutures on posterior face strongly displaced toward apex; anterior half of pronotum more strongly declivous and rather coarsely asperate (unarmed in Tiarophorus); worldwide. . . . . . . Dryocosetin

Subfamily Hylesininae

Hylastes LeConte [1876:387, Type-genus: Hylastes, Fabricius, 1803]

Most previous classifications have recognized the Hylesininae as a major division of the taxon treated here as Scolytidae, however, there has been variability in the taxonomic rank assigned to it. Most of the distinguishing characters employed previously are not found consistently throughout the group and, consequently, have little or no taxonomic value.

The most consistent and reliable character available for the recognition of this subfamily is the procured basal margins of the elytra that are armed by a row of cremulations, and the scutellar notch between them. The heavier, more coarsely armed tibiae are distinctive but less reliable as a distinguishing feature. The more primitive Bothrosternini, Diamesini, and a few other isolated examples lack the specialized elytral cremulations and have the basal margins elevated along a continuous costa reminiscent of some Platypodidae. This same character also occurs in Dendroidicteop (Carphodicticici) and, in a greatly reduced form, many Scolytini, Ctenophorini, and Cryphalini. On the other hand, a few Cryphalini (allies of galeritis, Scolytini) have fully formed basal cremulations that suggest an affinity with the Hylesininae. Even though the demarkation between subfamilies is not as sharp as some would like, the division of subfamilies is simple and the characters are reliable.

Tribe Hylastini

Hylastes LeConte [1876:387, Type-genus: Hylastes, Fabricius, 1803]

DESCRIPTION.—Frons not sexually dimorphic; eye oval, entire, antennal scape elongate; funicle 7-segmented; precoxal ridge on prothorax strongly, acutely elevated; protibia very broad, with rather numerous lateral socketed teeth; scutellum visible; cremulations at base of elytra poorly developed, usually not forming a definite row; declivital interstriae 10 sometimes present (Scierus), declivital sculpture usually simple; vestiture usually includes scales (some exceptions); scutocutellar suture parallel to costa of scutellar groove for two-thirds length of pronotum; metapleural suture descending subvertically from pleural wing process to metepisternal groove (this groove interlocking with groove on costal margin of elytron) then continuing caudad along this groove to a point near pleural coxal process; tarsal segment 3 wider than 1 or 2.
Biology.—All species are monogamous. They breed in coniferous hosts, usually at the base or in the roots of large trees, although some species prefer the lower surface of prostrate logs that are in contact with the ground. Parental galleries are monoramous or biramous, usually entirely in the phloem, but exposed on peeled bark. Eggs are placed in niches and are sealed in with frass. Larval mines are comparatively long and wander irregularly in the phloem. The species are not aggressive, usually preferring unthirfty or felled trees after they have been attacked by other bark beetle species, except a few species of *Hylastes* have been reported to kill seedlings in nursery stock. Their role in the primary destruction of roots is unstudied.

Taxonomy.—Members of this tribe are the most common fossil Scolytidae in Baltic amber (Oligocene). They are not always clearly separable from the Hylesini to which they are obviously closely related phylogenetically, and they appear to be of ancient origin in the family. Their specialized habits apparently have resulted in evolutionary parallelism and superficial similarity of appearance with certain Cossoninae (Curculionidae), resulting in an erroneous supposition that the two groups are closely related. The generic limits within the Hylastini are not sharp. Individual variation within species and the similarity of species within genera make specific identification in the group rather difficult. They are strictly holarctic in distribution, if introductions to southern Africa, New Zealand, and Australia are ignored, and they are confined to the Pinaceae.

Key to the Genera of Hylastini

1. Anterior coxae rather widely separated by an intercoxal piece, its width at least equal to half width of a coxa; striae 9 and 10 both independently continued at least to level of abdominal sternum 4; elytral vestiture sparse, recumbent, yellow, hair- or bristle-like, never including scales; general surface of elytra and pronotum dull; body color reddish brown; North America: *Abies, Cedrus, Pinus*; 2.7-4.3 mm


   *Hylurgops* LeConte [1876:389, Type-species: *Hylastes pinifex* Fitch = *Hylurgops rugi-
penins pinnflex (Fitch), subsequent designation by Hopkins 1914:123. Synonyms: Hylo-
sinutes Germar 1813:15, Type-species: Hylo-
sinutes electrinus Germar, monobasic; Hyla-
sinutes Hagedorn 1907:117, Type-species: Hy-
lastites schellenici Hagedorn, monobasic; Mygelophilites Hagedorn 1907:118, Type-spe-
cies: Mygelophilites dubius Hagedorn, mono-
basic; Hylascierites Scheidl 1947:29, Type-
species: Hylascierites granulatus Scheidl, monobasic]. Distribution: 7 species, 2 with
subspecies, in North America; 2 in N Africa;
18 nominate species in Europe and N Asia; 7
nominate fossil species including 1 from
North America and 6 in Baltic amber (Oligocene). All are monogamous and breed
in phloem tissues of Pinaceae; most are in
roots, butts, and stumps of standing hosts,
some in logs, and at least one may occur in
smaller material. Keys: Wood (1982:82) for
North America, Pfeffer (1944) for Europe and
N Africa, Tsai and Huang (1964b) for China,
Murayama (1963) for NE Asia. 

Hylastites Erichson [1836:47, Type-species:
Bostrichus ater Paykull, subsequent designa-
tion by Westwood 1835:39 and Thomson
1859:146]. Distribution: 16 species in North
America; 1 in Jamaica; 17 nominate species
in Europe and N Asia; 1 in N Africa; 1 in the
Canary Islands; fossil species include 2 from
Baltic amber (Oligocene), 1 from Miocene of
Colorado. All are monogamous and breed in
phloem tissues of Pinaceae; most are in
roots, butts, and stumps of standing hosts,
some in logs, and at least one may occur in
smaller material. Keys: Wood (1982:93) and Blackman
(1941) for North America, Pfeffer (1944) for Europe,
Murayama (1963) and Tsai and Huang (1964a) for NE Asia.

Tribe Hylasinini

Hylasinini Erichson [1836:46, Type-genus: Hylasinus
Fabricius, 1801]

Phloeoborus Fabelius [1966:257, Type-genus: Phloeo-
tripes Erichson, 1836 = Phloeoborus Erichson, 1836]

Phloeophagus Fabelius [1893:426, Type-genus: Phloe-
oborus Erichson, 1836]

Dactylyphagus Blandford [1893:426, Type-genus: Dactyl-
lyphagus Chapuis, 1869]

Hylastinidae Nixdorff [1912h:273, Type-genus: Hylasti-
nus Bedel, 1888]

Alisiphagini Murayama [1963:i, 29, Type-genus: Alisiph-
agrus Swaine, 1918]

DESCRIPTION.—Frons obscurely to deeply
and extensively impressed in male, female flat
to variously convex; eye oval to elongate, en-
tire to feebly sinuate on anterior margin; an-
tennal scape very short to very elongate, fun-
nicle 6- or 7-segmented (except 5- to 7-
segmented in Hylasinopsis), club conical to
moderately flattened, symmetrical or nearly
so, two or more sutures indicated, except su-
tures absent in Dactylyphagus; procoxae nar-
rowly to moderately separated, precoxal ridge
on prothorax moderately to very strongly,
acutely elevated; pronotum armed by a few
aspteries, except absent in Hylasinus; meta-
cutellum area separated from postnotum by a
distinct suture; mesal surface of sutural
groove of elytra just behind scutellum inter-
rup ted by a series of interlocking nodules and
cavities; tarsal segment 3 usually wider than 2,
often bilobed.

BIOLASCT.—All species are monogamous.
All are phloecophagous except the xylophagous
Phloeoborus and Dactylyphagus. Parental gal-
eries are hiramous or, if a well-developed
turning niche is present, they may be mono-
ramous. Eggs are deposited in niches and are
sealed in with frass. Larval mines usually fol-
low a definite course away from the parental
mine and rarely cross one another. Phloe-
oborus and Dactylyphagus appear to have a
symbiotic relationship with fungi, but not in a
mycetophagous sense (old parental mines are
stained black and wood adjacent to larval
mines is discolor ed and in a more advanced
state of decay).

TAXONOMY.—The occurrence of this tribe
in the Eocene and its almost worldwide distri-
bution suggest an ancient origin. The strictly
nenropical Phloeoborus and ethiopian (ex-
cept for two oriental species) Dactylyphagus
suggest that these unique but related genera
were derived from a common ancestral
African stock at or before the time of separa-
tion of South America and Africa. The remain-
ing American Hylasinini include representa-
tives of Hylasinus and Alisiphagrus, both of
which occur in Asia and appear to have
reached North America in comparatively re-
cently. The one Hylasinus in South Amer-
ica (antipodus Scheidl) is quite similar to liv-
ing Australian species and was apparently
derived from Australian stock anciently. This suggests that *Hylesinus* is very old.

The African genera *Hylesinopsis* and *Rhopoloselion* appear to be comparatively young, and they are now going through a period of rapid evolutionary change. It could easily be argued that they should be grouped into a single genus and also that both should be fragmented into many small genera. However, it appears that only a small fraction of the African species have been discovered. It is anticipated that when more species are known most of the apparent character gaps will have disappeared, leaving only two major clusters of species.

*Hylesinus* and *Ficicus* have been grouped into one genus by most workers. However, when all species are examined, it is apparent that two distinct clusters of species are formed on both anatomical and biological (host choice) bases. Since these two cannot be combined without also including a third cluster of species (*Alniphagus*), I have elected to recognize all three as genera. *Alniphagus* appears to be more nearly allied to *Ficicus* than to *Hylesinus*.

The three clusters of genera mentioned above, together with the comparatively unrelated *Hylesinopsis, Kissophagus, Peteobius, Cryptocerus, and Neopteleobius*, appear to represent remnants of a previous phyletic radiation that took place anciently. Although they cluster conveniently into one tribe, the extinction of intermediate forms makes comments on phylogenetic relationships difficult at this time.

**Key to the Genera of Hylesinini**

1. Antennal club subcylindrical to strongly flattened, with three sutures clearly indicated, funicle 6- or 7-segmented (5-segmented in some *Hylesinopsis*), posterior face of prostigma flattened to weakly convex, smooth, punctures with their lateral margins feebly or not at all tuberculate, lateral margin armed by socketed teeth, female pronotum never with a visible mycetangium; smaller, *phloeophagous* species, rarely larger than 5.0 mm.

   - Antennal club subcylindrical, elongate, at least 1.5 times as long as wide, sutures freely procurred; eye shorter, less than 3.0 times as long as wide (3.3 in *Hylesinatus*); interstriae 10 never represented on posterior third of elytral length; body usually more slender.

   - Antennal club rather strongly flattened, stouter, less than 1.5 times as long as wide; sutures weakly to rather strongly procurred (if almost straight, then scutellum not visible), some species appear to have four or more sutures; eye elongate, at least 4.0 times as long as wide, interstriae 10 often narrowed and carinate on posterior third of elytra; body usually stouter; Africa.

2. Frons convex in both sexes, not sexually dimorphic, sometimes marked by a line, median carina; antennal funicle 6-segmented (except 7-segmented in *Hylesinatus* which lacks pronotal asperities).

   - Male funicle moderately to very strongly impressed, female funicle convex (or impressed in *Neopteleobius*), median carina absent or poorly represented; antennal funicle 7-segmented (except 6-segmented in *Neopteleobius*); pronotal asperities always present.

3. Frontal rectangle (Fig. 1) conspicuously longer than wide; pronotum unarmed by asperities; antennal funicle 7-segmented; elytral ground vestiture of short, rather stout hair (not subplumose); Europe to W Asia, introduced almost worldwide; herbaceous to shrubby legumes; 0.5-5.5 mm.

4. Hylesinus

   - Frontal rectangle conspicuously wider than long, pronotum armed on anterolateral areas by a few fine asperities; antennal funicle 6-segmented, elytral ground vestiture of either plumose or scalelike setae.

5. Frons with a fine, long, median carina, elytral ground vestiture of abundant, short, plumose setae of uniform color; pronotum more slender, 0.95 times as long as wide; Europe, Africa, W Asia; *Forestia*.

6. Peteobius

   - Frons without a carina, elytral ground vestiture of abundant scales, their margins entire, usually forming patterns of light and dark color; pronotum stouter, less than 0.85 times as long as wide; Europe, North Africa, W Asia; *Ululus*; *Sorbus*, etc.

7. Cryptocerus

   - Male funicle very strongly, extremely excavated to well above upper level of eyes; male declivity truncate and armed above and below by large, blunt processes; apical segments of male funicle each ornamented by one or more very long, coarse setae; Africa (Nigeria to Tanzania), *Piptoselis*; 2.5-2.3 mm.

8. Male frontal impression less profound, rarely extending above eyes; declivity convex, one or more interstriae sometimes elevated and armed by smaller tubercles.

9. Female funicle 6-segmented; male and female funicle impressed, strongly in male, moderately in-
Fig. 34. Alshipagus aspericollis (LeConte), dorsal aspect (After Bright 1976: 207).

908. Male frons weakly, very shallowly emarginated; protibia armed by five socketed teeth, outer apical angle only moderately abrupt; antennal club more nearly subcircular; setae in elytral ground vestiture subshimmer; Japan to W North America (Fig. 34). *Alnus*, 2.1-3.4 mm

\[ \text{Alshipagus} \]

— Male frons moderately to extensively excavated; protibia armed by no more than four socketed teeth, outer apical angle abrupt; antennal club more strongly flattened, its apex less narrowly rounded; setae in elytral ground vestiture undivided, abundant to absent, Australia to Japan and China; Ficus, rarely other hosts; 1.6-5.0 mm

\[ \text{Ficus} \]

10(2). Pronotum subtriangular, scutellum small to absent; funicle 7-, 6-, or 7-segmented; striae often impressed, punctures usually larger; Africa, 1.3-3.0 mm

\[ \text{Neopteleobiinus} \]

— Pronotum subquadrate, scutellum rather large; funicle 6-segmented, striae usually weakly impressed, narrow, punctures fine to obsolete; Africa, 1.5-4.5 mm

\[ \text{Rhopalopelus} \]

11(1). Antennal club with two sutures (often obscure); female prosternum with a large mycetangium ornamented by hair; metatarsus retractile into tibial groove; Central and South America, 3.0-16.0 mm

\[ \text{Phloeoborus} \]

— Antennal club unmarked by sutures; female pronotum with a median, transverse, slitlike mycetangium on anterior third; metatarsus not retractile, tibial groove absent; Africa, SE Asia, Philippines; 0.6-14.0 mm

\[ \text{Dactylipalpus} \]

\hline

9. Male impression not extending above upper level of eyes; eye shallowly emarginate, elytral ground vestiture scutelike; costal margin near apex descending; E Asia; 2.2-2.8 mm

\[ \text{Neopteleobiinus} \]

— Female 7-segmented; female frons flat to convex; male frons, if strongly concave, with excavation extending above eyes; eye less strongly to not emarginated

\[ \text{Hylastinus} \]

8(7). Eye entire, oval, less than 3.0 times as long as wide; protibia armed on lateral margin of apical fourth by six or more closely set, socketed teeth; body stout, declivity more gradual, abdomen distinctly ascending to meet elytral apex; elytral vestiture of uniform length, mostly of scales (except almost subglabrous in *crenatum*); almost worldwide; *Frazinus* and other Oleaceae; 1.7-4.5 mm

\[ \text{Hylesinus} \]

— Eye shallowly emarginate, somewhat elongate, at least 3.5 times as long as wide; protibia armed by 2-5 socketed teeth, body more slender; declivity shorter, more abrupt; abdomen horizontal, not rising to meet elytral apex; elytral vestiture of ground cover of short hair or scales, and interstrial rows of longer, erect bristles

\[ \text{Kissophagus} \]

Hylastinus Bedel [1888:388, Type-species: *Ips obscurus* Marsham, original designation].

Distribution: 2 in Europe, 1 in N Africa; one of these (*obscurus*) has been introduced into most temperate areas of the world. One is phloeophagous in *Cytisus*; one (*obscurus*) breeds in the roots of various clovers. Keys: Reitter (1913:45).

Kissophagus Chapuis [1869:34, Type-species: *Hylesinus hederae* Schmitt, monobasic].

Distribution: 4 in Europe and neighboring areas. All are phloeophagous and monogamous. Key: Reitter (1913:44).

Pteleobiinus Bedel [1888:392, Type-species: *Bostrichus vittatus* Fabricius, subsequent designation by Hopkins 1914:128].

Distribution: 1 in Europe, one of these is recorded from N Africa. They are phloeophagous in *Ulmus* and *Sorbus* and are monogamous. Keys: Reitter (1913:42), Balachowsky (1949:94).
Cryptocerus Schell [1907c:599, Type-species: Cryptocerus spinipennis Schell, monobasic. Synonym: Hyloperus Browne 1970:546, Type-species: Hyloperus beicornis Browne = Cryptocerus spinipennis Schell, original designation]. Distribution: 1 in Africa (Nigeria to Tanganyika). It was attracted to light and was also taken from a Piptadenia buchananii log.


Hylesinus Fabricius [1801:390, Type-species: Hylesinus crenatus Fabricius, subsequent designation by Westwood 1838:39. Synonyms: Leperinus Reitter 1913:41, Type-species: Bostrichus fraxini Panzer = Bostrichus curtus Fabricius, subsequent designation by Swaine 1918:70]. Distribution: 10 in North America, 1 in South America, 5 in Europe, 9 in Asia, 1 in Africa (Uganda). More than 20 additional nominate species occur in S Asia, Australia, and neighboring areas. All are phloeophagous and are common in Fraxinus or other Oleaceae hosts; they are monogamous. Keys: Wood (1982:110) for North America, Murayama (1963:6) for NE Asia.

Ficicis Lea [1910:147, Type-species: Ficis cariens Lea, subsequent designation by Hopkins 1914:122. Synonym: Ficiphagus Murayama 1958:930, Type-species: Ficiphagus golathooides = Hylesinus porcatus Chapuis, original designation]. Distribution: About 16 nominate species in the area from India and Japan to Australia. All are monogamous and phloeophagous in Ficus, rarely in other hosts (particularly Artocarpus).


Phloeoborus Ericson [1836:54, Type-species: Phloeoborus rudus Ericson, subsequent designation by Hopkins 1914:126. Synonym: Phloeotrupes Ericson 1836:53, Type-species: Phloeotrupes grandis Ericson, subsequent designation by Hopkins 1914:127]. Distribution: About 24 species, S Mexico to N Argentina. All are xylophagous in rather large host material and are monogamous; they are occasionally attracted to light. They have an intimate association with fungi, but are not mycetophagous. Keys: Blandford (1897:150, Eggers (1942:267), Wood (1982:122).

Tribe Tomicini

Tomicinae Thomson [1859: 145]. Type-genus: Tomicus Latreille, 1802 [23]

Hylurgini LeConte [1876: 373]. Type-genus: Hylurgus Latreille, 1807

Dendroctonini Nilsen [1913: 273]. Type-genus: Dendroctonus Erichson, 1836

Xylocchinides Nilsen [1912: 273]. Type-genus: Xylocchinus Chapuis, 1889

DESCRIPTION.—Frons very weakly to moderately sexually dimorphic; male usually impressed, female convex; eye oval to ovate, entire; antennal scape elongate, funicle 4- to 7-segmented; club symmetrical, feebly to moderately flattened; three sutures usually indicated; pronotum unarmed, except a few very small asperities sometimes present in Xylechinus and some Xylechinosus; procoxae contiguous to moderately separated, precoxal lateral costa absent; metaseutellar area separated from postnotum by a distinct suture; sutural groove on mesal surface of elytra continuing to base without a series of interlocking nodules and cavities; tibiae armed by socketed denticles.

BIOLOGY.—All species are monogamous; all are phloeophagous except for the xylophagous Pachycotes (and Hylurgus). The parental galleries are usually binarous, except in Dendroctonus, Hylurgus, and some Tomicus they are monomorous. Those of Sinophloeus, Hylurgonotus, and Pachycotes are not known to me. The eggs are placed in niches and packed in frass except that some Dendroctonus have modified the niches into elongate grooves into which numerous eggs are packed in single or double rows. The larval mines usually show on the inner surface of peeled bark and are oriented in a direction away from the parental mine. Symbiotic relationships with fungi may occur in all genera, but they are adapted toward overcoming resistance of the host and are not of a mycophagous type.

TAXONOMY.—The worldwide distribution of this diversified tribe suggests an ancient origin, although only one Tertiary fossil has been reported (Xylechinosus, Oligocene). The most conspicuous division of the group is that presented in couplet 1 of the key, except that Xylechinos should be placed with the first group of genera. The Tomicini represent the most highly evolved segment of an evolutionary trend that began in the Hylastini, continued in the Hylurini, and reached its greatest specialization in the Tomicini.

Two major clusters of genera appear within the tribe; first, the Xylechinos group of genera (Xylechinos, Chaetoptelius, Xylechinosus, Sinophloeus, Dendrotrupes, Hylurgopinus, Pseudoxylechinus, and Pseudohylesinus) and, second, the Dendroctonus group of genera (Hylurgus, Tomicus, Dendroctonus, Hylur­

drectonus, and Pachycotes). The first group appears to have radiated in a wide variety of hosts from South America and Australia since the beginning of the Tertiary. The second group appears to have been associated anci­ently with Araucaria hosts and is sparsely, uniformly represented in major geographical areas, except for Africa, in modern Araucaria and other Pinaceae.

Key to the Genera of Tomicini

1. Metepisternal setae scalidike or plumose; antennal funicle 7-segmented
   — Metepisternal setae usually hairlike (bifid in one Hylurgonotus having a 6-segmented funicle); antennal funicle 4- to 7-segmented

2(1). Anterolateral areas of pronotum distinctly separate (minute in Indian species); antennal club apparently with either two or four transverse sutures; male frons strongly impressed
   — Anterolateral areas of pronotum unarmed; antennal club with three sutures clearly marked; male frons impressed or not

3(2). Antennal club more strongly flattened, more slender, at least 2.0 times as long as wide; apparently with two sutures; frontal rectangle at least as wide as long (0.8-1.0 times); Europe and Asia to Australia and New Zealand; mostly in broadleaf hosts; 1.8-5.0 mm
   — Chaetoptelius

   — Antennal club less strongly flattened, stouter, less than 1.5 times as long as wide; apparently with four sutures; frontal rectangle longer than wide (about 1.2 times); South America; Araucaria; 1.5-3.4 mm
   — Xylechinosus

4(3). Male frons strongly impressed; median frontal carina present; pronotum either without a constriction affecting dorsal profile (Sinophloeus) or with a moderate lateral constriction on anterior third (Dendrotrupes)
   — Male frons convex or moderately flattened, median carina present or absent; pronotum with a conspicuous transverse constriction on anterior third affecting dorsal profile

5(4). Antennal club elongate, 2.0 times as long as wide, apparently with four or five sutures;
Fig. 35. Xylechinus montanus Blackman, dorsal aspect (After Bright 1976: 206).

decidual interstriae 2 impressed, 3 (sometimes 1-7) armed by rounded tubercles; pronotum conspicuously wider than long (0.7 times as long as wide); larger; South America; Notthophagus; 2.3-3.0 mm

- Antennal club more compact, less than 1.5 times as long as wide, with three sutures; declivity variable; pronotum almost as long as wide (0.9 times). New Zealand; hosts not coniferous; 1.5-2.0 mm

Dendrotupes 6(4).

Elytral vestiture hairlike, ground vestiture moderately stout; frontal carina absent; antennal club slightly flattened, segment 1 one-fourth of its length; North America; Ulmus; 2.0-2.5 mm

- Vestiture of ground, conspicuous scales (one exception with no ground scale); median frontal carina usually present; antennal club more conical

7(6). Strial punctures small, close; interstriae two or more times as wide as striae, unarmed (except coarsely tuberculate and without ground vestiture in rugatus), erect setae closer and curser; elytral ground setae more slender and apically pointed, variegated pat-terns obscure; antennal club somewhat more flattened and apex less pointed; China; broadleaf hosts; 1.8-3.0 mm. Pseudoxylechinus

- Strial punctures coarse; interstriae less than 1.3 times as wide as striae, often armed by tubercles of moderate size; elytral ground setae usually stout, apically rounded, and forming conspicuous variegated patterns; antennal club more nearly conical, segment 1 usually conspicuously longer; North America; coniferous hosts; 2.5-5.5 mm

Pseudohylechinus

8(1). Ground vestiture on elytra scalelike, metepisternal setae scalelike (Fig. 35); antennal funicle 5-segmented; median frontal carina present (except absent in a few South American species); pronoesae rather widely separated, North and South America, Europe, Asia, Africa, Australia; coniferous and broadleaf hosts; 1.5-3.5 mm

Xylechinus

- Ground vestiture on elytral disc hairlike, metepisternal setae hairlike (except some Hylurgopus), female Hylurdectorous)

9(8). Protibiae armed by five or more socketed teeth on distal and lateral margins; male frons convex except in Hylurdectorous; phloeo-phantus

- Protibiae armed by three socketed teeth (four in two Hylurgopus) on distal margin; male frons feebly to strongly, extensively excava-ted; xylephagous in Aucunaria

10(9). Antennal funicle 8-segmented, club conical

- Antennal funicle 5-segmented, club moderately flat

11(10). Procoxae contiguous; pronotum more slender, 0.85-1.1 times as long as wide, only slightly constricted on anterior third; erect interstrial setae abundant, confused; a short median carina from epistomal margin to level of antennal insertion; Europe, W Asia, Pinus; 3.1-5.3

Hylurgopus

- Procoxae moderately separated; pronotum stouter, less than 0.85 times as long as wide, strongly constricted on anterior third; erect interstrial setae in uniseriate rows (except confused in psueudus); a fine median carina from epistoma to middle of frons (absent in psueudus); Europe, Asia, N Africa; 2.5-4.5 mm

Tomicus

12(10). Antennal club with sutures somewhat pro-curved; procoxae conspicuous; male frons con-vex to weakly impressed; vestiture never scalelike in either sex; North America, Euro-pe, Asia, Pinus, Picea, Larix, Pseudotsuga; 2.5-9.0 mm

Dendroctonus

- Antennal club with sutures straight, trans-verse; procoxae moderately separated; male frons rather strongly concave; female elytra with some scales (except araucariae); Aus-tralia, New Guinea, Araucaria; 1.3-1.5 mm

Hylurdectorous
Chaetoptelius Fuchs [in Reitter 1913: 43, Type-species: Hylesinus vestitus Mulsant & Rey, automatic. Synonyms: Homarus Broun 1881: 740, Type-species: Homarus mundulus Broun, automatic, preoccupied; Acratops Broun 1882: 409, Type-species: Homarus mundulus Broun, automatic, preoccupied; Chaetopterus Fuchs 1912: 46, Type-species: Hylesinus cestitus Mulsant & Rey, monobasic, preoccupied]. Distribution: 1 species in Europe and W Asia, 1 in New Zealand, about 8 in Australia and New Guinea. All are phloeophagous and monogamous.

Xylechinomus Schell [1963a: 209, Type-species: Xylechinus taunayi Eggers, original designation]. Distribution: About 9 species in South America. All are phloeophagous in Aucmoria.


Pseudoxylechinus Wood & Huang [1986: 465, Type-species: Pseudoxylechinus uniformis Wood & Huang, original designation]. Distribution: 7 species in Asia. All are phloeophagous and monogamous in broadleaf trees.


Hylurgus Latreille [1807: 274, Type-species: Hylesinus ligniperda Fabricius, monobasic]. Distribution: 3 species in Europe, W Asia, N Africa. All are phloeophagous in coniferous hosts and monogamous.


Hydractonus Schell [1938b: 40, Type-species: Hydractonus pinarius Schell, monobasic. Synonym: Xylodactyon Schell 1972: 64, Type-species: Xylodactyon araucar-
Tribe Phrixosomini
Phrixosoma Wood [1978: 111, Type-genus: Phrixosoma Blandford, 1897]

DESCRIPTION.—Frons not sexually dimorphic, frequently with a fine, median carina; eye completely divided; antennal scape elongate, funicle 5- or 6-segmented, club strongly flattened, slightly asymmetrical, unmarked by sutures, except 1 partly septate; pronotum unarmed by asperities, procoxae contiguous; scutoscutellar suture remote from scutellar groove, postnotum separated from scutoscutellar area of metanotum by a complete suture; tibiae armed on lateral margin by socketed denticles.

BIOLOGY.—These monogamous, phloeo-phagous, tropical species are restricted to hosts of the Guttiferae. The parental galleries are usually biramous, although a third egg tunnel is not uncommon, with the galleries either longitudinal, transverse, or without definite orientation. The eggs are deposited in niches and sealed in by ii-ass. The larval mines show on the inner surface of peeled bark, but they are almost entirely in the bark and usually wander indiscriminately without respect to the grain of the wood.

TAXONOMY.—Only one genus is known (Fig. 36). It is apparently very old and represents a group that is otherwise extinct. They are unknown in the fossil record. The one genus in South America and Africa in Guttiferae has changed so little since separation of these land masses that division into species groups is not recommended. Although more closely allied to Hylesini than to other tribes, this genus is quite unique.


Tribe Hyorrhynchini

DESCRIPTION.—Frons sexually dimorphic, male slightly to strongly impressed, female convex; eye completely divided, antennal scape either long or short, funicle 5- or 6-segmented, club asperate and either unmarked by sutures or with two sutures; pronotum armed or not; procoxae moderately to widely separated, precoxal ridge obsolete; scutoscutellar suture remote from scutellar groove; scutoscutellar area separated from postnotum by a distinct suture; tibiae without socketed denticles.

BIOLOGY.—The species are myelomyce-toplagous or sylomycteophagous and form simple, monoramous tunnels in the pith or xylem of twigs or small branches. Only two larvae were seen (Suerus notissimus) and these were in the parental chamber. Males of Suerus are very rare, dwarfed, and deformed; reproduction in this genus is apparently by
arrhenotocous parthenogenesis. In *Hyorrhynchus* and *Pseudohyorrhynchus* the males are similar in shape and abundance to the females, suggesting a normal bisexual relationship.

**Taxonomy.**—A dozen species assigned to three genera are listed in the literature. All occur in the area from India and Japan to New Guinea. They form an aberrant, relict group of uncertain affinity but are considered to be among the most primitive of the Hylesininae. Although definitely members of the Hylesininae, they share more primitive characters with primitive Scolytinae and Platypodidae than with other members of their own subfamily.

**Key to the Genera of Hyorrhynchini**

1. Antennal funicle 5-segmented, club rather weakly compressed; male dwarfed, rare, flightless; male from convex, with median carina; tarsal segment 3 entire; Sri Lanka (Ceylon) and New Guinea to Japan; female 1.6-2.0 mm, male 1.0-1.3 mm. **Suesu**

2. (1). Antennal funicle 6- to 7-segmented, club strongly flattened, male subequal in size to female, shares parental gallery; male frons concave or not, with or without a carina; tarsal segment 3 emarginate to bilobed. 2

2(1). Antennal funicle 6-segmented, club with two clearly marked sutures; male from concave, without a carina; tarsal segment 3 emarginate; interstitial tubercles minute; India to Japan; 2.7-3.0 mm. **Hyorrhynchus**

2(2). Antennal funicle 7-segmented, club without sutures, tarsal segment 3 deeply bilobed; male from not impressed, with a median carina; interstitial tubercles on declivity rather coarse; Japan; 3.5-3.6 mm. **Pseudohyorrhynchus**

**Suesu Murayama** [1951: 1, Type-species: *Suesu sphacrotropeoides* Murayama = *Hyorrhynchus nisima* Eggers, original designation]. Synonym: *Neohyorrhynchus* Schell [1952c: 202, Type-species, *Hyorrhynchus nisima* Eggers, original designation]. Distribution: 2 species from Sri Lanka (Ceylon) and New Guinea to Japan. Xylomycetophagous in small branches and, apparently, at least partly parthenogenetic (only one series of males known).

**Hyorrhynchus Blandford** [1894a: 58, Type-species: *Hyorrhynchus lewisi* Blandford, monobasic]. Distribution: About 10 species from India to Japan. Habits have not been reported except host species include *Acer*, *Fagus*, and *Macaranga*; the species are xylomycetophagous and monogamous (Nobuchi, pers. comm.).

**Pseudohyorrhynchus Murayama** [1950b: 61, Type-species: *Pseudohyorrhynchus wada* Murayama, original designation]. Distribution: 1 species from Japan. Specimens of this monogamous species attack living *Cornus* twigs where they are xylomycetophagous.

**Tribe Diameerini**

Diameridae Hagedorn [1909: 734, Type-genus: Diameerus Ericson, 1936]

Strombophorini Schell [1954c: 75, Type-genus: Strombophorus Hagedorn, 1909]

*Sphaerotrypini* Murayama [1965: 5, Type-genus: *Sphaerotrypes* Blandford, 1894]

**Description.**—Frons dimorphic, feebly to very strongly impressed in male, flattened to convex in female; eye entire to completely divided; antennal scape usually elongate; funicle 6- to 7-segmented, club flattened, sutures variable, one to several (five or more, mostly pseudosutures); procoxae moderately to widely separated; scutocutellar suture remote from scutellar groove, postnotum fused to scutocutellar area of metanotum, intersegmental suture obsolete on median half.

**Biology.**—These monogamous, phloeo­phagous species are largely restricted to tropi­cal and subtropical areas of the eastern hemi­sphere. The parental galleries are mostly biramous and either longitudinal or trans­verse. The eggs are deposited in niches and sealed in by frass. The larval mines show on the inner surface of peeled bark and tend to radiate away from the parental tunnel without respect to the grain of the wood in most spe­cies; the latter parts of the tunnels in some species are parallel to the grain of wood.

**Taxonomy.**—Seven genera represented by about 123 species occur in Africa and south­eastern Asia to Australia. *Pseudodiamerus*, *Pernophorus*, and *Strombophorus* occur only in Africa. They appear to form a sister group derived from the same ancestral stock as Both­rosternini and, if this is the case, these groups have differentiated and radiated since early Tertiary. Features used to characterize this tribe vary and tend to intergrade with Phloeosinini. Although future study may re­quire combination of these two tribes, their division gives a convenient break in a large and diverse group.
Key to the Genera of Diamerini

1. Eye oval, neither strongly reduced on lower half nor completely divided; antennal club with fewer than three sutures, funicle 3-, 6-, or 7-segmented
   — Eye either strongly narrowed on lower half or entirely divided into two parts; antennal club apparently with five or more sutures marked by crossstriations and/or rows of setae; funicle 6-segmented (except 7-segmented in Pernophorus)..........2

2(1). Costal margin on basal fourth of elytra normal, not emarginate, metepisternum not expanded; median anterior area of pronotum usually finely asperate; antennal funicle 6-segmented; club elongate, sutures 1 and 2 feebly indicated (straight) to absent; Africa, NE Asia to Australia; 1.1-2.5 mm
   — Costal margin on basal fourth of elytra either normal or deeply, abruptly emarginate, when emarginate metepisternum expanded into this emargination, pronotum never asperate (flexible lateral asperities in Bothrosternoides).............3

3(2). Costal margin on basal fourth of elytra deeply emarginate (Fig. 37); suture 1 on antennal club strongly, subangulate procurred; Africa, NE Asia to Australia; 3.0-5.0 mm...........Diamerus
   — Costal margin on basal half of elytra almost normal, straight to weakly emarginate; basal margins of elytra either costate or armed by a row of coarse crossstriations; protibia with two to four curved spines, male from shallowly impressed; suture 1 on antennal club weakly indicated (straight) or absent.............4

4(3). Eye more than 3 times as long as wide; funicle 7-segmented; club with suture 1 straight, feebly; protibia with two apical and two lateral spines; costal margin not emarginate; basal margins of elytra crenulate; pronotum without lateral granules, Africa (Angola); 2.2-3.0 mm...........Pseudodiamerus
   — Eye twice as long as wide; funicle 5-segmented; club unmarked by sutures; protibia with two apical and one small posterior subapical spine and several lateral posterior granules; costal margin shallowly emarginate at base; basal margins of elytra strongly crenate; some prothoracic granules or small asperities in lateral areas, male with median epistomial tubercle; body very stout; Malaya; 2.3 mm...........Bothrosternoides

5(1). Eye completely divided, scutellum visible, longer than wide; pronotum unmarked by asperities; body very stout, subglobular; Africa, NE Asia; 1.5-5.0 mm...........Spheropteryges
   — Eye strongly constricted on lower half to about one-third width of upper half; pronotum at least partly asperate, scutellum not visible; body elongate-oval...........6

6(5). Antennal funicle 7-segmented; elytral vestiture hairlike to subshiny; Africa; 4.0 mm...........Pernophorus
   — Antennal funicle 8-segmented, elytral vestiture with ground cover scutellate; Africa; 1.5-3.5 mm...........Strombophorus

Fig. 37. Diamerus curvifer Walker, lateral aspect of female.
   — Antennal funicle 8-segmented, elytral vestiture with ground cover scutellate; Africa; 1.5-3.5 mm

Acacacis Lea [1910: 149, Type-species: Acacacis abundans Lea, monobasic. Synonyms: Trogloditeca Sampson 1922: 146, Type-species: Trogloditeca trahaz Sampson, monobasic; Pseudocacaca Schedl 1963: 477, Type-species: Acacacia borneensis Browne, original designation; Neodiamerus Schedl 1971b: 282, Type-species: Neodi­urmus granulicollis Schedl, original designation]. Distribution: 5 species in Africa, 2 in Sri Lanka, 2 in Malaya, 1 in Borneo, 1 in New Guinea, and 2 in Australia. All are phloeoephagous and monogamous.

Pseudodiamerus Eggers [1933b: 18, Type-species: Pseudodiamurus striatus Eggers, monobasic]. Distribution: 3 species in Africa. All are apparently phloeoephagous and monogamous.


Sphaerotrypes Blandford [1894a: 61, Type-species: Sphaerotrypes pila Blandford, subsequent designation by Hopkins 1914: 129. Syn-
TAXONOMY. — The tribe is restricted to the American tropics, with two species extending into the southern United States. It appears to be the New World counterpart of the closely allied Diamerini. The genera of Bothrosternini differ anatomically from one another only slightly and may be recognized with difficulty in some instances. The pectorial and antenomic structure and the costal basal margins of the elytra in at least some members suggest a very primitive position in classification. Though primitive as a group, modern representatives appear to have evolved since the beginning of the Tertiary to their present ecological and structural status, because clearly identifiable related groups are not known outside of the neotropical realm. They appear to be more nearly allied to Diamerini and Hyorrhynchini than to any American groups.

Key to the Genera of Bothrosternini

1. Lateral margins of pronotum rounded
   2
   — Lateral margins of pronotum marked by a sharply elevated, costate subcostal line
   3
2(1). Sutures of antennal club transverse, straight; rostrum distinctly wider than distance between eyes; prothoracic intercoxal ridge absent; oviposition in twigs; Central and South America; 1.6-3.6 mm
   Ctenius
   — Sutures of antennal club strongly procurred; rostrum width at tip equal to distance between eyes; from excavated in both sexes, with a median tubercle just above epistoma; body oval; seed borers; NE USA to South America, intercepted elsewhere in maize, etc.; 1.9-2.6 mm
   Pagiocerus
3(1). Sutures of antennal club strongly procurred; pith borers in twigs and woody vines; Central and South America; 2.1-3.8 mm
   — Sutures of antennal club transverse, straight...4
4(3). Pecopisternal area partly excavated, with cavity densely filled by yellow pubescence, particularly in female; prothoracic intercoxal piece with a transverse, subcarinate ridge; elytral interstriae usually not strongly carinate; ambrosia beetles in axial tunnels of woody vines; Central and South America; 1.9-3.3 mm
   Bothrosternus
   — Pecopisternal area normal, not densely pubescent; prothoracic intercoxal ridge absent; elytral interstriae narrowly curinate from posterior part of disc to apex; pith borers in branches and twigs; Central and South America; 2.2-3.6 mm
   Sternobothrus

Ctenius LeConte | 1868: 171, Type-species: Ctenius strigicollis LeConte, monobasic. Synonym: Nemophilus Chapuis 1869: 27,
Fig. 38. Bothrosternini: 1-8, Cnesinus spp., (1) cubenensis Blackman, dorsal aspect, (2) same, female head, (3) pasamensis Blackman, dorsal aspect, (4) same, male head, (5) robust Blackman, male head, (6) retulusus Blandford, female head, (7) costulatus Blandford, dorsal aspect, (8) same, female head, (12) Blackmani Scheff, dorsal aspect; 9-11, Bothrosternus foecatus Blackman, (9) dorsal aspect of female, (10) female head, (11) propodeum of female. (After Blackman 1943: pl. 15).
Type-species: *Nemophilus strigillatus* Chapuis = *Cnesius strigicolli* LeConte, subsequent designation by Hopkins 1914: 125]. Distribution: About 101 species from the USA to Argentina. All are monogamous and myeloophagous except that one is partly phloeophagous. Keys: Wood (1968b: 88, 1982: 209).

**Pagiocerus** Eichhoff [1868a: 148. Type-species: *Pagiocerus rimosus* Eichhoff = *Bostrichus frontalis* Fabricius, subsequent designation by Hopkins 1914: 126]. Distribution: About 5 species are known from the USA to Argentina, 1 is occasionally intercepted worldwide in large seeds, including maize. All are monogamous and spermophagous.


**Bothrosternus** Eichhoff [1868a: 150. Type-species: *Bothrosternus truncatus* Eichhoff, monobasic]. Distribution: About 12 species from Mexico (Veracruz) and Jamaica to Peru and Brazil. Monogamous and some species apparently with a type of parthenogenesism (involving consanguineous polygyny), and myeloophagous in woody vines. Key: Wood (1982: 247).


**Tribe: Phloeotribini**

*Phloeotribinae* Chapuis [1869: 42. Type-genus: *Phloeotribus* Latreille, 1796]  
*Phloeotribinae* Nilsen [1912b: 273. Type-genus: *Phloeotribus* Rey, 1893]

**DESCRIPTION.**—Frons sexually dimorphic, male variously impressed, female flat to convex; eye entire; funicle 5-segmented, club almost non-existent to strongly asymmetrical, deeply divided into three movable, sub-lamellate segments; procoxae contiguous; pronotum armed or not, its lateral margins rounded; metatergum fused to its postnotum.

**BIOLOGY.**—All are monogamous and phloeophagous. Parental galleries are branched and engrave the wood rather deeply. Eggs are deposited in niches packed in frass. Larval mines follow a rather definite course away from the parental tunnels and usually do not cross one another; in the latter stages they may engrave the wood rather deeply. A few species bore rather deeply into subsurface tissues of woody vines; one species breeds in the fruiting pods of its host (*Inga*).

**TAXONOMY.**—The tribe apparently originated in South America, where a majority of the species now occur. *Aricerus* and one very primitive *Phloeotribus* apparently reached Australia very early, much later a few species of *Phloeotribus* reached North America and then spread from there to northern Asia, Eu-
rope, and North Africa. The tribe apparently was derived from the same parental stock as the Phloeosini, although the relationship is not close. The distribution, freely movable antennal club segments (Fig. 39), and the tibial structure of Articus and at least one species of Philotribus suggest an origin in early Tertiary or late Cretaceous while it was still possible to spread to Australia, but not into Africa. The one Australian and a few European Philotribus (Fig. 27) have virtually no club on the antenna, suggesting the possibility that the club of Scolytidae could have been derived independently from that of other curculionoids.

**Key to the Genera of Philotribini**

1. Lateral margin of prothorax without socketed teeth, outer apical angle rather strongly produced, with few (about three) major serrations; lateral margin of pronotum acutely elevated, suberased; antennal club rather slender, almost symmetrical, ventral margins of segments not noticeably extended; phloeoaphagous, Australia to New Guinea; 3.1-4.6 mm
   - *Articus*

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**Tribe Phloeosini**

Phloeosini Ross 1912b: 273, Type-species: *Phloeosinus* Chapuis, 1869.*

**Description.**—Frons usually dimorphic, male impressed, female flat to convex; eye varying from entire to emarginate to completely divided; antennal funicle 5- to 7-segmented, club flattened, slightly to strongly asymmetrical, with or without sutures; pronotum armed or not; tarsal segment 3 compressed to broad and bilobed; scutellum visible or not; metanotum fused to postnotum.

**Biology.**—All are monogamous except for a few species of polygynous *Olonthesta* and one bigamous *Chromesia*. Most are phloeoaphagous, although *Dendrocinus* and three species of *Chromesia* are xylophagous and *Hylops* larvae become xylonyctophagous in the later stages. The parental tunnels are mostly monoramous, with a conspicuous turning niche, a few are rather primitively (unequally) biramous. Eggs are placed in niches and packed in frass. Larval mines tend to follow a definite course away from the parental tunnel and rarely cross one another.

**Taxonomy.**—This tribe appears to consist of a diverse assemblage of somewhat distantly related genera or clusters of genera that appear to be relics from a former much larger group. Their worldwide distribution, diverse structure, and possession of several primitive traits suggest an ancient origin that extends
well into the Cretaceous. Within the tribe, two clusters of genera are apparent. *Pseudochromates* and *Chromates* (America) are closely related to one another and are the most highly evolved from a structural point of view. *Cladocetus*, *Phloeosinopsoides*, *Olynthogaster*, and *Phloeosinus* (Fig. 40) form a second cluster of genera to which *Phloeocranus* (Fig. 41) and *Phloeodictica* might form a primitive base. All are Old World genera except that about half of the *Cladocetus* species occur in tropical America and a segment of *Phloeosinus* has extended into North America in comparatively late Tertiary time. The *Cladocetus* species of the Philippines (1), Africa (6), and tropical America (6) have apparently changed only slightly since attaining their present generic distribution (perhaps early Tertiary). The American *Dendrosinus* and *Carpkoterae* and the Australian *Hyleopus* are not closely related to one another or to the other known generic groups of this tribe.
5(4).  Funicle 6-segmented; elytral bases not produced; procoxal notches at sutural base of elytra not unusually deep or narrow; pronotum contiguous, smaller ... 6

6(5).  Funicle 7-segmented; procoxae contiguous; pronotum unarmed; funicle 7-segmented; scutellum visible; tarsal segment 3 broad, strongly bilobed; phloecophagous except larval xylonyctetaphagous in later stages; Australia; *Aratusia*; 2.4-4.0 mm ........................... *Hylocoptes*

Fig. 42-43. Antennae of Phloeosini: 42, above *Phloeosinus thyatir* (Perris); 43, below, *Chromenes immaculatus* LeConte.

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Color usually reddish brown, SE Asia to New Guinea; mostly in nonconiferous hosts; 1.4-5.5 mm ........................... *Olondragaster*

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Eye less than one-half divided by an emargination; tarsal segment 3 broad, emarginate to bilobed; prothorax with three or more socketed denticles on apical and subapical margin, four or more smaller teeth on lateral margin; vestiture more abundant; male frons usually shallowly impressed; female frons convex, often with a median carina, vestiture inconspicuous in both sexes; color brown to dark brown; N. Africa to N Asia, North America, Australia; mostly in coniferous hosts; 1.4-4.1 mm (*Phloeosinus Hagedorni* presumably fits near here) ........................... *Phloeosinus*

11(3).  Antennal club with sutures strongly procurred, clearly marked by rows of setae and grooves; phloecophagous; S America; 1.3-2.0 mm ........................... *Pseudochromenes*

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Antennal club without sutures; mostly phloecophagous, North and South America; 1.2-2.7 mm ........................... *Chromenes*

Phloeocerus Schell [1942: 7], Type-species: *Phloeocerus bruchoides* Schell, monobasic. Synonymy: *Diamerides* Browne 1949: 893, Type-species: *Diamerides litsea* Browne – *Phloeocerus bruchoides* Schell, original designation; Distribution: 1 species from India to Indonesia in *Litsea*. This species is monogamous and phloecophagous.

**Dendrosinus Chapuis** [1869: 28, Type-species: *Hyletis globosa* Eichhoff, monobasic]. Distribution: 10 species from USA (Florida) and Mexico (Jalisco) to Argentina. All are monogamous and xylophagous. Key: Wood (1982: 283).

**Hyleoidea Schedl** [1908b: 35, Type-species: *Hyleoidea glabrata* Schedl, monobasic]. Distribution: 1 species in Australia in *Aruncaria* branches. It is monogamous and partly xylophagous. The later larval stages penetrate the xylem and become xylomycephagous. Parental tunnels are transversely biramous and without apparent symbiotic fungi.

**Carpophorineae Wood** [1973b: 171, Type-species: *Chaetophloeus rhodopterus Egg. Bright, original designation*. Distribution: 1 species in Mexico (Oaxaca). It is monogamous and phloeo- phagous.

**Catenophorus Nunberg** [1956b: 195, Type-species: *Catenophorus congonus* Nunberg, original designation]. Distribution: 1 species in the Congo. The habits are unknown.

**Cladotracinae Strohmeyer** [1911: 17, Type-species: *Cladotracus affinis* Strohmeyer, monobasic. Synonyms: *Hopliotes* Eggers 1923: 140, Type-species: *Hopliotes banosus* Eggers, monobasic; *Hoplitotomus* Wood 1961: 2, Type-species: *Hoplitotomus banosus* Eggers, automatic; *Hoplitophthorus* Wood 1961: 2, Type-species: *Hoplitophthorus sentosus* Wood = *Hopliotes interruptus* Eggers, original designation*. Distribution: 8 species in Africa, 6 in Cuba to Brazil and Bolivia, 1 in the Philippine Islands. The two species for which habits are known are monogamous and phloeo-phagous.

**Phloeosinopoides Schedl** [1964c: 317, Type-species: *Phloeosinopsis triseriatus* Schedl, automatic. Synonyms: *Phloeosinopsis* Schedl 1964b: 297, Type-species: *Phloeosinopsis triseriatus* Schedl, original designation, preoccupied]. Distribution: About 8 species from Taiwan to New Guinea. All are monogamous and phloeo-phagous.


**Onlonthogaster Motschulsky** [1866: 401, Type-species: *Onlonthogaster nitidicollis* Motschulsky, subsequent designation by Hopkins 1914: 126]. Synonyms: *Holonthogaster* Gemminger & Harold 1872: 2676, Type-species: *Onlonthogaster nitidicollis* Motschulsky, automatic; *Helyedius* Sampson 1921: 35, Type-species: *Helyedius exasper Sampson*, monobasic; *Hylurgulus* Eggers 1927c: 392, Type-species: *Hylurgulus summatanus* Eggers, monobasic; *Phloeosinopsis* Schedl 1936a: 23, Type-species: *Phloeosinopsis armatus* Schedl = *Phloeosinopsis spinifer* Schedl, original designation]. Distribution: About 25 species from SE Asia to Australia. All are phloeo-phagous and monogamous except for 2 polygynous species from New Guinea. Hosts include *Lysia*, *Myristica*, etc.

**Phloeosinites Hagedorn** [1907: 119, Type-species: *Phloeosinites rehii* Hagedorn, subsequent designation by Hopkins 1914: 126]. Distribution: 8 fossil species in Baltic amber (Oligocene). The relationship of this genus to *Phloeosinus* was not determined.

**Pseudochromes Blackman** [1939: 87, Type-species: *Chromes acutelatus* Hagedorn, original designation]. Distribution: 11 species in South America. The habits have not been reported. Key: Blackman (1939: 86).

**Chromes LeConte** [1868: 168, Type-species: *Chromes hiscoriae* LeConte, monobasic. Synonyms: *Rhopalopelta* Chapuis 1869: 46, Type-species: *Rhopalopelta tucumanus* Chapuis, subsequent designation by Hopkins 1914: 128; *Thaumatosinus* Reitter 1913: 39, Type-species: *Dendrosinus bunairei* Reitter = *Chromes rotundatus* Chapuis, monobasic; *Prochraeuma* Wood 1956b: 254, Type-species: *Prochraeuma annectens* Wood, original designation]. Distribution: 39 species in South America, 40 in North and Central America and adjacent islands. All are monogamous, except for the bignous *C. inceptus*, and all are phloeo-phagous except
for the mycophagous *C. quadridens* and three xylophagous species. **Keys:** Blackman (1933c: 330), Wood (1982: 316).

**Tribe Hypoborini**

Hypoborinae Nolda [191I: 376, Type-genus *Hypophloeus* Erichson, 1859]

**Description.—** Frons dimorphic or not, male impressed, female convex or less strongly impressed, except in some *Liparthrum* species this feature is reversed; eye entire; funicle 3- to 6-segmented, club with up to three sutures, sometimes absent; pronotum variously armed in restricted areas; procoxae contiguous; tarsal segment 3 narrow; scutellum not visible; crenulations on elytral bases not continued laterad from interstriae 5; postnotum fused to metatergum (remnants of suture sometimes visible).

**Biology.—** All are monogamous and phloepagous. In all except *Chaetophloeus* the parental gallery is a simple, oval cave. Eggs are packed in frass in niches on the margins of the central cave (*Liparthrum*) or of the egg tunnels (*Chaetophloeus*). Larval mines radiate out from the parental chamber and rarely cross one another; they are visible on the inner surface of pecked bark.

**Taxonomy.—** This tribe is sparsely and widely distributed in the warm climates around the world. Except for *Liparthrum* (Fig. 44), which is almost worldwide in the warm areas, the remaining genera are of limited distribution. One is American, 1 Australian, 2 Madagascar, and 4 African (1 of these reaches nearby areas of Europe and Asia in cultivated fig). It appears to be a relic group that once enjoyed much greater distribution and diversity than at present.

The American genus, *Chaetophloeus*, is quite different structurally and biologically from the remaining closely related genera. Members of this tribe apparently prefer arid or semi-arid areas or habitats and tend to be rare. Since they breed in shrubs or small trees of marginal economic importance, it is suspected that a majority of the species await discovery.

**Key to the Genera of Hypoborini**

1. Funicle 6-segmented, club small, conical, with two straight sutures; Australia; Acacia; 1.3 mm
   — Funicle with 3- to 5-segments; club flattened, sutures present or absent

2.1. Prothorax strongly flattened, rather broad, lateral apical half armed by a row of 7-10 closely set, socketed teeth; proventral asperities confined to two or three paired clusters on lateral thirds, each cluster containing 1-5 denticles; funicle 5-segmented, club clearly marked by three sutures; phloepagous; North and South America; 1.1-2.5 mm
   — *Chaetophloeus*
— Prothorax slender, lateral margin armed by about four rather widely spaced, socketed teeth; pronotal apertures mostly on median third, more abundant; funicle 3- to 5-segmented.

3(2). Antennal funicle 3-segmented, club rather broad, sutures very broadly procured; prothorax slender, with one large spine on outer apical angle and four small, socketed denticles on lateral margin; crenulations on basal margins of elytra feeble; body subglabrous; Madagascar; 1.5 mm

— Prothorax not armed on outer apical angle by a major spine; antenna variable; elytra bearing setae.

4(3). Funicle 4- or 5-segmented, club with sutures obscure, club more broadly oval

— Funicle 3-segmented, club usually more slender.

5(4). Antennal funicle 4-segmented (appearing 3-segmented, but 4- or possibly 3-segmented on slide mount), club unmarked by sutures; basal margins of elytra a continuous costa, individual crenulations clearly indicated; anterior half of pronotum asperate; stric not impressed, punctures coarse, deep, wider than interstriae; Madagascar; 1.6 mm

— Prothorax 4- or 5-segmented; crenulations on basal margins of elytra well-formed; strial punctures smaller; pronotal apertures often present, but less conspicuous.

6(5). Funicle 4-segmented, club devoid of sutures; meso- and metasternum slender, about equal to prothorax; philoeophagus; S USA to N South America, S Europe and N Africa to China and Micronesia; 0.8-1.5 mm

— Liparthurus

7(6). Funicle 5-segmented, club with three obscure sutures; meso- and metasternum rather strongly flattened, much wider and more coarsely serrate than prothorax; philoeophagus; S Europe, N Africa to Asia Minor; 1.1-1.4 mm

— Hypodorus

7(6). Antennal club with three distinct sutures; meso- and metasternum tuberculate; funicle slender; prothorax; philoeophagus; Africa; 1.2-1.8 mm

— Styraeoptinus

— Antennal club long and slender, sutures not indicated; scape ornamented by a tuft of long hair; discal interstriae; 2 on basal fourth with one tubercle greatly enlarged in male, 3 with four tubercles on posterior half and upper half of declivity; philoeophagus; Africa; 1.6-2.0 mm

— Stegostoma


Cryphophillus Schell [1953c: 294, Type-species: Cryphophillus eggersi Schell, original designation]. Distribution: 1 in Sumatra (Indonesia), 1 in Madagascar.


All are apparently monogamous and phloeo\phagous.

**Dacryostactus Schauffuss** [1905: 79 (reprint p. 3), Type-species: *Dacryostactus kolbei* Schauffuss, monobasic]. Distribution: 1 species in Africa. Monogamous and phloeo\phagous.

**Tribe Polygraphini**

*Polygraphidae* Chapuis [1869: 48, Type-genus: *Polygraphus* Erichson, 1830]

*Carphobius* Nishida [1961: 370, Type-genus: *Carphobius* Eichhoff, 1864]

**DESCRIPTION.**—Frons dimorphic, male variously impressed and sparsely pubescent, female concave to convex and usually ornamented by conspicuous setae; eye emarginate to completely divided; antennal funicle 5- or 6-segmented, club slightly to strongly flattened, symmetrical to strongly asymmetrical, with or without sutures; procoxae contiguous; tarsal segment 3 slender; pronotum unarmed; scutellum not visible; crenulations on bases of elytra either individual (separate) or represented by a continuous costa (*Serrastus*), continued to humeral angle; metanotum fused to its postnotum.

**BIOLOGY.**—All are phloeo\phagous. *Carphobius* and some *Polygraphus* are monogamous; apparently *Charostatus* and *Serrastus* share this habit; *Carphoborus* (Fig. 45) and most *Polygraphus* are polygynous. Parental tunnels are monoramous or biramous in monogamous forms and radiate in polygynous forms. The nuptial chamber is unusually large in most species. Eggs are packed in frass in niches. Larval mines wander considerably and have a greater tendency to cross one another than in most other tribes.

**TAXONOMY.**—In my initial study of the tribes of Scolytidae (Wood 1978), the Polygraphini were reluctantly given tribal status only after much hesitation and the pondering of many questions. Since then, all reservations have been dismissed. Although quite specialized in several respects, representatives of two genera (*Serrastus, Polygraphus*) have the outer apical angle of the protibia produced beyond the tarsal insertion and are armed as in primitive representatives of other unspecialized tribes. The tribe generally appears to have been derived from the same ancestral stock as the Phloeosini, but the one known species of *Phloeographus* bears a remarkable superficial resemblance to certain *Tomicus* species (Hylesini). The genera form a rather compact unit without conspicuous divisions. Four small genera are exclusively African (*Serrastus, Charostatus, Phloeographus, Cardroctonus*), one is Malayan (*Bothinoderoctonus*), and one is American (*Carphobius*). The larger genus *Carphoborus* is primarily North American and probably originated there from stock derived from Asia. European and Asian species of *Carphoborus* appear to have been derived from the more primitive and diverse American fauna. The largest genus *Carphoborus* is primarily North American and probably originated there from stock derived from Asia. European and Asian species of *Carphoborus* appear to have been derived from the more primitive and diverse American fauna. The absence of this group in South America suggests either an origin since early Tertiary, if Africa were the site, or else an origin in tropical Eurasia. *Polygraphus* reached North America in comparatively recent time, *Carphoborus* and *Carphobius* much earlier. Eurasian *Car*...
phoeboerus were probably derived from a secondary radiation that ensued from North America to Asia. Carphophilus apparently represents a relict from a very early ancestral stock not now represented elsewhere.

Key to the Genera of Polygraphini

1. Basal margins of elytra armed by a continuous costa; protibia very slender, its median apical macro-horn laterad, about one lateral denticle present, posterior face asperate; female 5-segmented; club strongly flattened, moderately asymmetrical, sutures not indicated; philophagous; Africa; 1.8-2.0 mm .......................... Serratustus

   — Basal margins of elytra serrate, armed by a row of emarginations; protibia more broadly flattened, lateral margins armed by several socketed denticles

2(1). Funicle 5-segmented (5- or 6-segmented in Polygraphus, if 6-segmented then eye completely divided); male from anterior by a median pair of tubercles near upper level of eyes; ventricle of abundant scales (except glabrous in some Bathinodromus) .......................... 3

   — Funicle 6-segmented; eye never divided into two parts; male from unarmed by median tubercles; vestiture hairlike or sparse if scalylike

3(2). Eye completely divided by a deep emargination (some Asian and African species only emarginate); antennal club rather strongly flattened, asymmetrical, devoid of sutures; philophagous; North America, Asia, Europe, Africa; 1.5-5.5 mm .......................... Polygraphus

   — Eye less than half divided by an emargination; antennal club symmetrical (or nearly so), clearly marked by sutures

4(3). Sutures of antennal club prescurred; vestiture sparse or coarse, 1st pair of antennal clubs on interstitial; tropical Africa .......................... 5

   — Sutures of antennal club straight or nearly so; vestiture much more abundant, northern hemisphere

5(4). Antennal club with three weakly procurred sutures indicated, apex strongly acuminated; vestiture sparse, of minute rows on declivity, declival interstriae 2 slightly impressed, unarmed, 1 and 3 armed by small tubercles; SW Africa .......................... 6

   — Antennal club with suture 1 partly septate, 1 weakly, 2 moderately procurred; striae punctures very fine; Africa; 1.3-2.0 mm .......................... Cardroctonus

6(5). Male from shallowly impressed below upper level of eyes, female usually convex; vestiture of abundant scales; antennal club moderately large, flattened; philophagous; North America, N Asia, Europe, N Africa; 1.4-2.6 mm .......................... Carphophilus

   — Male from profusely excavated from eye to eye from epistoma to well above eyes, female similarly but less strongly excavated; antennal club small, more nearly conical; vestiture confined to a few interstitial setae on and near declivity; philophagous; India to Malay, 1.8-2.5 mm .......................... Stenostatus

3(2). Antennal club symmetrical, with three transverse sutures indicated; vestiture abundant, hairlike; philophagous; North America; 1.6-2.1 mm .......................... Carphophilus

   — Antennal club rather strongly asymmetrical, part of suture 1 indicated, strongly oblique; vestiture usually confined to declivity, scalelike; philophagous; Africa; 2.5-5.3 mm .......................... Chartrustus

Serratustus Nunberg [1909: 302, Type-species: Serratustus iceniensis Nunberg = Chortastus similis Eggers, monobasic]. Distribution: 2 species in Africa (Ghana to Zaire). They are monogamous and philophagous.


Cardroctonus Schell [1966b: 361, Type-species: Cardroctonus orientalis Schell, original designation]. Distribution: 2 species in Africa.


Carphoborus Eichhoff [1864: 27, Type-species: Hylesinus minutus Fabricius, monobasic. Synonym: Estenophorus Beitter 1913: 58, Type-species: Hylesinus perrisi Chapuis,

Bothinodroctonus Schedl [1969: 201], Type-species: Bothinodroctonus hicinclus Schedl, monobasic]. Distribution: 4 species from India to Borneo and China. One species is phloeoophagous in Odisa.


Chortastus Schultess [1905: 15], Type-species: Chortastus cameranus Schultess, monobasic. Synonym: Afrochermes Schedl 1971a: 197, Type-species: Afrochermes bugnarti Schedl, original designation]. Distribution: 7 species in Africa. Apparently all are monogamous and phloeoophagous.

Subfamily Scolytinae

Scolytini Latreille [1807: 273, Type-genus: Scolytus Geoffroy, 1762]

In previous classifications, this subfamily has been divided into two or more major divisions equivalent to subfamilies. However, it appears that this unit contains both the most primitive elements of the family that are most closely related to primitive Platypodidae and also the main evolutionary thrust of the platypod-scolytid group. This diversity makes characterization of the subfamily rather difficult.

Members of this subfamily have the bases of the elytra simple, forming a straight, transverse line across the body. A large, flat scutellum is usually visible. The elytral bases are weakly subcostate in some Scolytini, Ctenoporus, and Cryphalini. The body tends to be more elongate, with specialization directed toward cylindrical compaction and the xylomyctophagous habit. A broadly oval body outline is usually conflined to primitive, phloeoophagous genera. Armed elytral bases that suggest a relationship to the Hylesiniæ occur in Ctenophorini (Cnemognyx, allies of galeritus).

Five clusters of relationship are recognized within the subfamily. Progressing from primitive to the more specialized, these include: (1) Ctenophorini, Scolytini, and Scolytoplatypodini; (2) Micracini and Caetopini; (3) Carphodicticiini, Ipini, Dryocoetini, Crypturgini, Xylotermini, and Xyleborini; (4) Xylocryptini and Cryphalini, and (5) Corthylini. Of these, the Corthylini are by far the most distinctive from an anatomical point of view.

Tribe Scolytini

Scolytini Latreille [1807: 273, Type-genus: Scolytus Geoffroy, 1762]

Camptocerus Chapuis [1869-49, Type-genus: Camptocerus Latreille, 1829]

DESCRIPTION.—Frons usually strongly dimorphic, male variously impressed, female flat to convex, one or both often ornamented by hair; posterior face of head truncate; eye oval, entire; scape short to elongate, funicle 7-segmented, club rather large, flattened, sutures present or not; pronotum unarmed, its lateral margins costate; protibia (usually all three tibiae) unarmed on lateral margin, outer apical angle extended into a spine curving toward and exceeding inner apical angle, socketed denticles never present; metapleural suture descending subvertically to groove receiving groove on costal margin of elytra then turning abruptly and continuing parallel to groove to near metacoxal process; in two genera venter of abdomen ascends conspicuously to meet apex of weakly declivous elytra.

BIOLOGY.—All are monogamous except for a few neotropical and one European bigynous Scolytus. Camptocerus species are xylomyctophagous; those in the other three genera are phloeoophagous. Parental galleries are biramous, except for a few that are monogamous. In Camptocerus, a biramous, transverse tunnel without niches is usually made in the cambium region, then a radial egg tunnel (sometimes branched) is extended from it into the xylem. Eggs are deposited in niches in this radial tunnel. The larval mines of phloeoophagous species follow a definite course and rarely cross one another. Camptocerus larvae enlarge the egg niche into a cradle just large enough to accommodate the mature beetle, somewhat similar to some other ambrosia beetles.
TAXONOMY.—Except for the Eurasian element of *Scolytus*, members of this tribe are exclusively American. Their obvious origin is neotropical. Some members of this group resemble the primitive ancestral line that probably gave rise to the Hylesini; in fact, some *Cnemonyx* have developments on the basal margins of the elytra. They also appear closely allied to the stock from which Platypodidae diverged. The four genera assigned here form a compact group, although the *Cnemonyx* appear more primitive and, in some respects, overlap the other three.

*Scolytus* appears to have reached North America from South America by the beginning of the Tertiary, when a secondary radiation occurred. Elements of this radiation then reached Eurasia, where another radiation occurred that was based on a progressively reduced gene pool. The number of Eurasian species in this genus now may equal or exceed the American component, although the anatomical and biological diversity there is greatly reduced.

Key to the Genera of *Scolytini*

1. Scutellar area of interstriae 1 not depressed, scutellum flush (even) with elytral bases; basal margins of elytra with a fine raised line (some *Cnemonyx* with emarginations instead), outline of anterior margins form a continuous, straight, transverse line with scutellum; ventral profile of abdomen ascending gradually
   - Scutellum depressed, subtriangular, apically (posteriorly) pointed; elytral bases depressed in scutellar area, appearing emarginate in median area; ventral profile of abdomen usually ascending abruptly at segment 2

2(1). Antennal club usually with two or three sutures clearly marked by setae; scutellum small, longer than wide, often convex; apical margins of meso- and metathoracic tibiae commonly bearing tubercles on anterior edge in addition to inner and outer apical spines; usually more coarsely sculptured; *phloëophagous*, *USA* and Mexico to Argentina; 1.6-3.5 mm

3(2). Antennal club with suture 1 only, marked internally by a partial septum; scutellum flat, 1.5 or more times as wide as long; meso- and metathoracic tibiae acutely margined on apical anterior edge, without supplemental tubercles; usually very finely sculptured; *xylómycetophagous*, Central and South America, 2.6-4.5 mm

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**Scolytus Geoffroy** [1762: 309, *type-species*: *Bostrichus scolytus* Fabricius, design-

**Tribe Ctenophorini**

*Ctenophorini* (Chapuis [1869: 49, Type-genus: *Ctenophorus* Chapuis, 1869]—Scolytodes Ferrari, 1967)

*Probychilidae* Eichhoff [1878a: 34, 46, 167, 298, Type-genus: *Probychilus* Eichhoff, 1878]—*Gymnochilus* Eichhoff, 1867


**Description.**—Frons usually dimorphic, male impressed and female flat to convex in *Pychnarthrum* and *Gymnochilus*, sexual differences obscure in *Microborus*, male convex and female variously sculptured and ornamented in *Scolytodes*; posterior face of head truncate; eye usually elongate, entire to sinuate, scape elongate, funicle 6- or 7-segmented, club with or without sutures; pronotum armed or not, its lateral margins costate; procoxae widely separated; protibiae with one or more socketed denticles on lateral margin, spine on lateral apical angle usually extending beyond level of tarsal insertion; pleural suture about as in *Scolytini*.

**Biology.**—All are monogamous, except for a few polygynous *Scolytodes*. All are phloecophagous, except for the xylephagous *Scolytodes multistriatus* Wood and species that infest *Cecropia* leaf petioles. Parental galleries vary from a simple to an elongate cave to stellate in *Scolytodes*; they are hiramous in *Pychnarthrum* and *Gymnochilus* and indefinite, nondirectional, and without definite pattern in *Microborus*. The eggs may be scattered loosely in the parental chamber or placed in crude niches in *Scolytodes*; definite niches are formed in *Pychnarthrum* and *Gymnochilus*; they were not observed in *Microborus*. The larvae usually feed communally in *Scolytodes*; they form individual mines that follow a somewhat definite direction in *Pychnarthrum* and *Gymnochilus*; they are individual and without a definite direction in *Microborus*. Symbiotic relationships with fungi were not observed.

**Taxonomy.**—The tribe is restricted to the American tropics, except that *Microborus holops* Blandford was introduced into tropical Africa. *Scolytodes* and *Microborus* are closely related to one another. *Pychnarthrum* and *Gymnochilus* are remotely related to those genera and to one another. *Pychnarthrum* could easily be placed in Hylesini. This tribe occupies a position intermediate between the *Scolytini* and the more highly evolved tribes in this subfamily. In all members the outer apical angle of the protibia projects beyond the tarsal insertion, a primitive feature shared by primitive members of several other tribes. It is the Ctenophorini protibia, not the type found in *Scolytini*, that appears to resemble the ancestral type of all
scolytids. The eye shape, usually unarmed pronotum, protrusion of interstices (10), simple sculpture of the elytra, the elytral locking mechanism, and diversity of habits all suggest that, when considered as a whole unit, this is probably the most primitive of all the tribes of Scolytidae. It is clearly of neotropical origin and has spread into southern North America only recently. This phylectic line is represented in the Old World by Scolytotrychus, a group that has diverged significantly in both structure and habits.

Key to the Genera of Cryptrophorini

1. Eyes elongate, approximate above and below, coarsely faceted, shallowly emarginate; entire surface of pronotum smooth and punctured, not armed

   — Eye oval, finely faceted; pronotum asperate anteriorly or, if smooth, then anterior margin of elytra bearing a line, raised line

   2(1). Antennal club subglobular, about as long as wide, sutures not clearly indicated; pronotum longer than wide, its lateral margins straight or feebly constricted; vestiture hairlike, usually sparse; small, slender species; phloeoephagous; Central and South America, Jamaica, Africa

   — Antennal club asymmetrically flattened, pointed, at least 1.5 times as long as wide; sutures 1 and 2 clearly marked by setae; pronotum wider than long, its lateral margins arcuate; vestiture of abundant, short, bristlelike scales, larger, stout species; phloeoephagous; Florida and Texas to Brazil; 1.3-2.1 mm

   3(2). Antennal funicle 7-segmented, club large, broad, usually with procured sutures or sutures obsolete; elytral vestiture consisting of abundant, minute hair and sparse interstitial rows of long, erect, scalelike bristles; summit of pronotum on basal third, asperities on anterior area coarse; elytral base without a line, raised line; phloeoephagous; Mexico (Puebla) to Brazil and Bolivia; 1.5-2.3 mm

   — Antennal funicle 6-segmented, club small, sutures present or not; elytral vestiture sparse (usually), hairlike; pronotal asperities fine, if present; summit at middle or indefinite; basal margins of elytra marked by a fine, raised line; mostly phloeoephagous; Florida and Mexico to Argentina; 0.9-3.5 mm

   4(3). Microborus

   Blandford [1897: 175, Type-species: Microborus boops Blandford, monobasic. Synonym: Pseudocryptopus Eggers 1919: 236, Type-species: Pseudocryptopus cameranus Eggers = Microborus boops Blandford, monobasic]. Distribution: 8 species from Jamaica and Mexico to South America, 1 (boops) was introduced into tropical Africa. All are monogamous and phloeoephagous. Key: Wood (1982: 452) for Central America.


   Gymnochilus Eichhoff [1868b: 399, Type-species: Gymnochilus zonatus Eichhoff, monobasic; Synonymy: Problechulus Eichhoff 1878a: 46, 167, Type-species: Gymnochilus zonatus Eichhoff, automatic; Meringopalpus Hagedorn 1905: 547, Type-species: Meringopalpus fallax Hagedorn = Gymnochilus zonatus Eichhoff, monobasic]. Distribution: About 14 species in Mexico to Brazil and Bolivia. All are monogamous and phloeoephagous. Key: Wood (1982: 462) for North and Central America.

   Scolytodes Ferrari [1887: 77, Type-species: Scolytodes lariquinatus Ferrari, monobasic. Synonym: Hexacolus Eichhoff 1868b: 399, Type-species: Hexacolus glaber Eichhoff, monobasic; Ctenochilus Chapuis 1869: 49, Type-species: Ctenochilus lariquinatus Chapuis = Hexacolus lariquinatus Blackman, monobasic; Prionocyles Blandford 1897: 177, Type-species: Prionocyles atratus Blandford, subsequent designation by Hopkins 1914: 128; Epomadus Blandford 1897: 179, Type-species: Epomadus caelestius Blandford, monobasic; Erinephilus Hopkins 1902: 34, Type-species: Erinephilus schaezrii Hopkins, original designation; Hylocresoma Eggers 1940: 138, Type-species: Hylocresoma striatum Eggers, monobasic; Hexacolus Schell 1963a: 217, Type-species: Hexacolus minutissimus Schell = Scolytodes minutissimus Schell, original designation; Cyrilalo-
The unique genus *Scolytoplatypus* appears to be a highly specialized geographical replacement of the neotropical *Scolytidae*. It shows quite clearly how the transition from unsketched tibial spines to socketed tibial teeth (derived from setae) took place (Wood 1978). This transition occurred well after Platypodidae had diverged from the main ancestral line and after family characters for Scolytidae had been fixed.


**Tribe Micracini**

*Micracides* LeConte [1876: 346, 367, Type-genus: *Micracides* LeConte, 1868]


**Description.**—Frons usually dimorphic; either sex may be variously impressed, sculptured, or ornamented by setae, female frons often concave, male frons rarely concave (two species); dorsomedian occipital area usually extended slightly caudal; eye oval to elongate, entire; scape very short to elongate, strongly flattened to slender, ornamented or not; funicle 6-segmented (5-segmented in *Micracides* LeConte, Africa), club with or without sutures; promontum asperate on anterior half, lateral margins rounded; protibia usually with sides parallel, socketed denticles usually confined to apical margin; procoxae usually distinctly separated (contiguous in three African genera); subapical setae almost always present.

**Biology.**—All American genera are bigynous, except that *Microhymena* is monogamous; habits of African genera are largely unreported. Most species occur in broadleaf trees and shrubs in desert or semidesert areas. *Stenotolyptus, Phloeocephales*, and most *Pseudothysanidae* are phloeocephales, *Thysanea, Micracides*, and *Hyloconidens* are xylophagous; the species of *Microhymena* are myceliophagous in small twigs. Details of their life cycle are poorly known, except that the development of most species is very slow.

**Taxonomy.**—The tribe occurs in North and South America and Africa, with one species in...
N Asia (China). Almost every American genus has a closely allied counterpart in Africa; obviously the generic traits were rather well established before the faunas were separated prior to early Tertiary, but some modification continued after isolation. The Asiatic *Pseudothyasers mongolica* (Sokanovskii) was obviously derived from American stock much more recently. Because most of the species in this group breed in small twigs and branches of trees and shrubs having little or no economic importance, they are regarded by forest biologists as scientific curiosities and, consequently, are poorly known.

As seen in Table 2, three clusters of genera in this tribe are represented in both America and Africa. The first species in each cluster is a specialized representative of the ancestral stock that produced its counterpart in the other continent, and it is considered to have given rise to the other genera within its own continent. *Micracini* appears to be an unrepresented in America and is thought to have been derived very early from a specialized representative of the ancestral stock. The allies of this genus or its ancestor could possibly have given rise to the other genera within its own continent. *Micracini* appears to be a specialized representative of the ancestral stock that produced its counterpart in the other continent, and it is considered to have given rise to the other genera within its own continent. *Micracini* appears to be a specialized representative of the ancestral stock that produced its counterpart in the other continent, and it is considered to have given rise to the other genera within its own continent. *Micracini* appears to be a specialized representative of the ancestral stock that produced its counterpart in the other continent, and it is considered to have given rise to the other genera within its own continent.

### Key to the Genera of *Micracini*

1. Elytra broadly rounded behind (except subgenus *Pseudothyasa*), protibia usually much more slender, less strongly flattened (except *Thysanocerus*); lateral margins of antennal club constricted at sutures 1 and (usually) 2, except when sutures absent (American species) or sutures procurred (African species) .......................... 2

2. Elytral apices acuminate (partly lost in some *Micracini*), usually macroconic, protibia more strongly flattened, at least apically (except in African species); antennal club without constrictions at sutures, sutures always indicated on anterior face in American species, absent in some African species .......................... 7

3(1). Promontum longer than wide, its summit less strongly developed; protibia rather broadly flattened, sides parallel, subtruncate apically, phloeo phagous; USA to Costa Rica, 1.2-2.1 mm .......................... 4

4(3). Antennal club with sutures present, marked by setae; female mandibular and declivital spines absent; female frons concave to convex; phloeo phagous; Madagascar and Africa; 1.1-2.7 mm .......................... 5

5(4). Antennal funicle 6-segmented, mandible bearing one or more very long, slender spines directed dorsal; female declivity armed on inner side of club; antennal scape elongate, 1.3-2.5 mm .......................... 7

6(3). Elytral declivity in both sexes variously sculptured but never sulcate; antennal scape long or short, club with or without sutures, mostly phloeo phagous; *Aphonocleptus*, a few xylophagous; North and South America, 1 in China, 0.7-2.0 mm .......................... 8

### Table 2: A comparison of American and African genera of *Micracini* arranged in order of structural complexity, with the first member in each cluster being the most primitive

<table>
<thead>
<tr>
<th>American genera</th>
<th>African genera</th>
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<tbody>
<tr>
<td><em>Pseudothyasers</em></td>
<td><em>Lanarius</em></td>
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<tr>
<td><em>Stenoclytus</em></td>
<td><em>Teudobius</em></td>
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<td><em>Thysanocerus</em></td>
<td><em>Sedoscirtes</em></td>
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<td><em>Phloeoceropus</em></td>
<td><em>Pseudothyasa</em></td>
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<td><em>Hylocerus</em></td>
<td><em>Phloeocerus</em></td>
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<td><em>Micracini</em></td>
<td><em>Pseudomicracini</em></td>
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| 1. | Elytra broadly rounded behind (except subgenus *Pseudothyasa*) | Protibia usually much more slender, less strongly flattened (except *Thysanocerus*); lateral margins of antennal club constricted at sutures 1 and (usually) 2, except when sutures absent (American species) or sutures procurred (African species) .......................... 2 |
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(7). Eye short, oval, not more than 1.5 times as long as wide; sutures straight to weakly procured or bisinuate; (South American) Hylocerus with strongly procured sutures and with posterior face of proboscis tuberculatc; proboscis rather slender, wider apically ........................................... 1

(8). Antennal club with sutures moderately to profoundly procured, clearly visible in lateral view; proboscis more strongly flattened, all 5 teeth on apical margin; scape usually very strongly expanded; antennal club rather broad, sutures more broadly procured, monogonous, mykyphagous. North America to Colombia; 1.3-2.5 mm ........... Micraciella

— Eye entire, always widely separated below; proboscis more strongly flattened, all 5 teeth on apical margin; scape usually less strongly expanded; antennal club rather broad, sutures more broadly procured, monogonous, mykyphagous. North America to Colombia; 1.3-2.5 mm ........... Micraciella

(9). Sutures 1 and 2 on antennal club bisinuate to profoundy procured, then posterior face of proboscis armed by tubercles; American species ........... 12

(10). Antennal club unmarked by sutures, uniformly finely pubescent, elongate, more than twice as long as wide; female declivity simple, male declivity impressed medially, elevated laterally and armed by large spines; Madagascar, Africa; 1.6-2.8 mm ........... Saurouctos

(11). Sutures 1 and 2 on antennal club straight, indicated by rows of setae; Philocerus, Mexico; 1.0-1.8 mm ........... Phloeoceptrus

(12). Eye elongate, 2.0 or more times as long as wide, coarsely faceted; antennal club rather large, sutures very strongly procured; proboscis rather strongly flattened (posterior face never tuberculatc); American species ........... 12

(13). Antennal club smooth, sutures marked by rows of setae. .......... 9

(14). Antennal club with sutures straight, or if bisinuate or procured, then posterior face of proboscis armed by tubercles; American species ....... 10

(15). Antennal club with sutures moderately to profoundly procured, proboscis slender, never armed by tubercles on posterior face; African species ........... 11

109). Sutures 1 and 2 on antennal club straight, visible only at margins, obsolete in central area, club small (Fig. 47); philocephagous; Mexico; 1.0-1.8 mm ........... Phloeoceptrus

— Sutures 1 and 2 on antennal club bisinuate to weakly or strongly procured, clearly visible in central area of anterior face, club larger; proboscis armed on posterior face by many tubercles or rugae; xylophagous; North and South America; 1.3-3.2 mm ........... Hylocerus

110). Eye larger, more elongate, 2.5-3.0 times as long as wide; sutures of antennal club moderately procured; proboscis slender, with denticles on apical margin; female from convex; declivity armed by moderately coarse tubercles in both sexes; philocephagous; Africa; 2.5-3.0 mm ........... Philocerus

— Eye usually smaller, oval, about twice as long as wide; sutures of antennal club moderately to profoundly procured, proboscis slender, with 1 or more denticles on lateral margin; female from convex to concave; declivity unarmed; Madagascar, Africa; 1.1-1.8 mm ........... Pseudolimnicaris

127). Eye shallowly emarginate, often approximate below; proboscis less strongly flattened, at least 1/2 of 5 apical teeth on outer (lateral) margin; scapes usually less strongly expanded; antennal club rather broad, sutures more broadly procured, monogonous, mykyphagous. North America to Colombia; 1.3-2.5 mm ........... Micraciella

— Eye entire, always widely separated below; proboscis more strongly flattened, all 5 teeth on apical margin; scapes usually very strongly expanded; antennal club more elongate, sutures usually much more strongly, narrowly acumen; bisinuate, xylophagous; North and South America; 1.6-3.4 mm ........... Micraciella


Traglostus Schell [1938d: 454, Type-species: Traglostus exornatus Schell, monobasic. This genus is doubtfully distinct from Lanurgus. Distribution: 4 species from Kenya to South Africa.


Pseudohylocerus Blackman [1920: 46, Type-species: Pseudohylocerus drakens Blackman — Cryptoches rigidus LeConte, original designation. Synonyms: Cryptoleptes Blackman 1920: 51, Type-species: Cryptoleptes dislocatus Blackman, original designation, preoccupied; Chalcohyus Blackman 1943b: 363, Type-species: Chalcohyus secundigerus Blackman, original designation; Bostrichips Schell 1951a: 21, Type-species: Bostrichips spinatus Schell, monobasic; Gretschkinia Sokanovskii 1959: 276, Type-species: Gretschkinia mongolica Sokanovskii, monobasic; Aphanoleptes Wood 1960b: 63, Type-species: Aphanoleptus coniferum Wood, original designation; Cryptoleptes Wood 1962: 76, Type-species: Cryptoleptes dislocatus Blackman, automatic; Neoglostatus Schell 1978.
300. Type-species: Neoglottatus squamosus Schell, monobasic. Distribution: 61 species in North and Central America, 8 in the Antilles Islands and South America, 1 in China. All are bigynous; most are phloeo-phagous, a few (about 6) are xylophagous, a few bore in leaves, etc. Key: Wood (1982: 511) for North and Central America.


Micracis LeConte [1868: 164, Type-species: Micracis nigeratus LeConte, subsequent designation by Hopkins 1914: 125]. Distribution: 11) species in North and Central America, 1 in Cuba, 2 in South America (Venezuela): several others have been named from South America but most, if not all of these, have been or should be transferred to other genera. All are bigynous and xylophagous. Key: Wood (1982: 579).

Tribe Cactopini

Cactopinae: Chamberlin [1939: 243, Type-genus: Cactopus]...

DESCRIPTION.—Frons dimorphic, male strongly impressed or excavated, with the epistomal margin armed by a pair of (usually...
confluent) hornlike spines of large to enormous size (Fig. 48), female convex or modestly impressed, epistoma unarmed by spines; posterodorsal area of head modestly produced caudad; eye small, oval, entire; antennal scape rather short, funicle 5-segmented, club almost conical to strongly flattened, sutures straight to procured, marked by rows of setae; promontum asperate on anterior slope, summit at or near posterior margin, sometimes projecting caudad beyond basal margin; procoxae contiguous; elytral sculpture unique, rather conservative, with transverse sutures, to moderately large and slightly asymmetrical, with slightly oblique sutures, surfaces marked by grooves and rows of setae, apparently not septate; pronotum elongate, sides conspicuously constricted on middle half, pronotum unarmed; posterior face of head truncate, dorsomedian area not extended caudad; procoxae narrowly to rather widely separated; protibia slender to very stout and short, armed by socketed denticles on lateral margin; scutellum visible; basal margin of elytra rounded in two genera, elevated and carinate in one genus.

Biology.—All arc monogamous and either phloeophagous or in cactus (CerctIs and allied genera). Those in cactus breed in dry, dead (yellowing) tissue immediately below the epidermis, or in scar tissue in deep wounds (hubbardi). One species breeds in Yucca leaves (depressus). The parental galleries form an irregular cave, with egg niches. Eggs are deposited individually in niches in two species; some species in cactus deposit them in clusters. Larval mines may be individual or lost in a criss-crossing maze. Successive generations have been bred in the same piece of dry cactus for four years. Symbiotic relationships with fungi have not been reported.

Taxonomy.—This unique tribe is restricted to the Mexican plateau region. Its nearest affinity to other groups appears to be with the Micracilli, although the relationship is remote. They are exceedingly rare.


Tribe Carphodicticini

Carphodicticus Wood [1971: 19, Type-genus: Carphodicticus Wood, 1971]

Description.—Frons weakly to moderately dimorphic, male strongly convex, female slightly to moderately flattened and sometimes abundantly pubescent; eye short, broadly oval and entire to very elongate and sinuate to shallowly emarginate; scape short and rather stout to elongate and rather slender, funicle 5-segmented, club flattened, small, and symmetrical, with transverse sutures, to moderately large and slightly asymmetrical, with slightly oblique sutures, surfaces marked by grooves and rows of setae, apparently not septate; pronotum elongate, sides conspicuously constricted on middle half, pronotum unarmed; posterior face of head truncate, dorsomedian area not extended caudad; procoxae narrowly to rather widely separated; protibia slender to very stout and short, armed by socketed denticles on lateral margin; scutellum visible; basal margin of elytra rounded in two genera, elevated and carinate in one genus.

Biology.—Carphodicticus is monogamous and phloeophagous. Numerous pairs of parent adults appeared to use the same entrance tunnel. Each pair followed a previously made tunnel for a short distance, then formed their own branch gallery for oviposition, such that the entire system consisted of branching and rebranching galleries. Eggs were deposited individually in niches at the cambium. Larval mines were exposed on peeled bark and were rather short. The host had been felled for several months before this species attacked; a Phleotrichus had largely abandoned the unusually hot, dry tissues, but this species was thriving.

Taxonomy.—The head and pronotal structure suggest that this group is very primitive. It was probably derived from the same ancestral stock as the Dryocoetini, Ipini, Crypturgini, Xyletorini and Xyleborini, but at a much earlier date. The disjunct distribution and rarity suggest that it is a relict group that had reached its maximum potential prior to the Tertiary. This tribe represents a first step toward one of the three most highly evolved tribes (Xyleborini) of Scolytidae.

Key to the Genera of Carphodicticiini

1. Eye entire, broadly oval, short, about 1.3 times as long as wide; scape rather short, about three times as long as pedicel; antennal club rather small, sutures transverse; elytral apex strongly mucronate; ventrolateral margin of declivity armed by a row of rather strongly elevated stria-
armed by a row of rather strongly elevated serrations; apparently xylophagous. India and Sri Lanka (Ceylon); 1.3-2.3 mm. **Craniodicticus**

Eye sinuate to emarginate, elongate, more than twice as long as wide (not visible on type of **Dendrodicticus**), elytral apex rounded, not mucronate; lateral margin of declivity uniformly elevated, not armed by serrations. **2.0 mm**

**2(1).** Basal margins of elytra rather large, not elevated; antennal club rather large, distinctly asymmetrical, sutures slightly oblique; procoxae more narrowly separated, prothorax short (only slightly longer than antennal club), stout (almost half as wide as long); phloeophagous; South America (Venezuela); 2.0-2.4 mm. **Craniodicticus**

Basal margins of elytra rather strongly, acutely elevated along a continuous costa; antennal club rather small, symmetrical, sutures transverse; procoxae more widely separated, prothorax longer, much more slender; habits unknown; South America (Argentina); 2.0 mm

**Craniodicticus** Blandford [1895: 317, Type-species: **Craniodicticus mucronatus** Blandford, monobasic]. Distribution: 1 species in S India, 1 in Sri Lanka (Ceylon). They apparently are xylophagous, since one sample was "removed from wood" and the other from a creeper called "jungle rope."

**Carphodicticus** Wood [1971: 19, Type-species: **Carphodicticus cristatus** Wood, original designation]. Distribution: 1 species in South America (Venezuela). It is monogamous and phloeophagous; utilizes the entrance tunnels of a host, and tibiae are also shared by these characters. The general body habitus, shape of the eye, basic type of antennal club (trend toward being obliquely truncate), and tibiae are also shared by these tribes. The **Ips** occupy a position between Carphodicticiini and Dryocoetini in which these characters were being formed. In **Dendrodicticus** are so poorly expressed that they are detected only with difficulty. However, that genus does exhibit a stage in transition to the circumtropical **Acanthotomicus**

**Acanthotomicus** Blandford [1895: 317, Type-species: **Acanthotomicus mimicus** Blandford, monobasic]. Distribution: 1 species in South America (Argentina).

Tribe *Ips*

*Ips* Bedel [1888, 386, Type-genus: **Ips** DeGeer, 1775]

**DESCRIPTION.**—Frons usually dimorphic, male convex, female variously excavated, prothorax, or ornamented by setae; eye sinuate, lower half usually much narrower than above; antennal scape slender, elongate, funicle 5-segmented, club either obliquely truncate or sutures on posterior face strongly displaced toward apex; pronotum rather strongly declivous on anterior half, rather closely, coarsely asperate, procoxae contiguous, intercoxal piece deeply notched or absent; prothorax armed by three or four socketed teeth; scutellum visible; elytral declivity moderately sculptate to strongly excavated, lateral margins usually armed by tubercles or spines; vestiture hairlike.

**BIOLOGY.**—All are phloeophagous. Most are heterosanguineously polygamous, although some some **Acanthotomicus** are monogamous. Hosts include members of the Pinaceae, except **Acanthotomicus** breeds primarily in various angiosperm trees. Eggs are deposited in niches. Larval mines are individual and rarely cross one another; they are exposed on the surface of peeled bark. The life cycle is comparatively short, with two or more generations per year apparently the normal habit.

**TAXONOMY.**—In most tribes of Scolytidae the sexes are easily distinguished by a difference in the number of abdominal terga. The female tergum 8 is reduced in size and is telescoped beneath tergum 7 such that it is ordinarily hidden from view. A visible tergum 8 is present in the male. However, in Carphodicticiini, **Ips**, Dryocoetini, Crypturgini, Xyloterini, and Xyleborini a small tergum 8 is visible in both sexes. The general body habitus, shape of the eye, basic type of antennal club (trend toward being obliquely truncate), and tibiae are also shared by these tribes. The **Ips** occupy a position between Carphodicticiini and Dryocoetini in which these characters were being formed. In **Dendrodicticus** they are so poorly expressed that they are detected only with difficulty. However, that genus does exhibit a stage in transition to the circumtropical **Acanthotomicus**

**Acanthotomicus** appears to have an ancient origin (prior to the Tertiary) and to have given rise, directly or indirectly, to **Pityogenes**, **Pityokteines**, **Orthotomicus**, and **Ips**. **Pityogenes** appears to have arisen in Europe and northern Asia from African **Acanthotomicus**-like stock and to have reached North America rather recently. Something resembling the neotropical **Acanthotomicus mimicus** species group probably gave rise in North America in early Tertiary to a stock that then evolved into **Pityokteines** and **Ips** in North America and to **Orthotomicus** in Europe and Asia. At a later date, a few representatives of **Pityokteines** and **Ips** then migrated into Europe and Asia and one species of **Orthotomicus** reached North America. The reasoning on which the above is
based is (1) on the continent of origin of several species groups found today, only a fractional number of those species groups now occur in the invaded territory and (2) no species group is found in the invaded territory that is not presently also found in the area of origin. Fossils that might document this supposition are unknown. *Dendrochilus* and *Acanthotomicus* breed in a variety of non-coniferous hosts; *Pityogenes*, *Pityokeites*, *Orthotomicus*, and *Ips* occur exclusively in Pinaceae.

Key to the Genera of *Ips*

1. Eye short, oval, entire, not sinuate on anterior margin; antennal club rather small, flattened, unmarked by sutures; declivity convex to slightly, broadly flattened, without granules or tubercles; elytral ventricle not abundant, in rows, intersticial setae hairlike to scalelike; prothorax dender, armed by 3 orocketed denticles on apical half of lateral margin; Africa; 1.0-2.0 mm

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*Dendrochilus*

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Eye more elongate, sinuate on anterior margin; antennal club usually larger, marked by sutures (except absent in many *Acanthotomicus*); declivity usually excavated and variously armed by tubercles or spines

2(1). Elytral declivity rather narrowly bisinuate, lateral margins rather broadly elevated, rounded, and armed by not more than 3 pairs of denticles; lower margin of elytral declivity rounded; usually smaller than 3 mm

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*Dendrochilus*

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Elytral declivity broadly, rather deeply excavated, margins acutely elevated and armed by 3 or more pairs of denticles (1 to 6 pairs in tropical *Acanthotomicus*); lower margin of declivity with an acutely elevated, transverse ridge separating declival excavation from apical margin (Fig. 49); usually larger than 3 mm

3(2).

Prosternal intercalar piece short, obtuse; female frons sometimes deeply, rather narrowly excavated; male declivity with 2 or 3 pairs of enlarged denticles; antennal club compressed, 2 sutures visible on apical third of posterior face; North America, Europe, Asia, N Africa; Pinaceae; 1.8-3.7 mm

---

*Pityogenes*

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Prosternal intercalar piece long and acutely tapered; female frons convex, never excavated; male declivity more narrowly impressed; female frons and anterior pronotum with dense, long vestiture (2 American exceptions); North America, Asia, Europe; Abies; 1.6-3.0 mm

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*Pityokeites*

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Antennal club obliquely truncate, sutures recurved; third (lowest) major denticle not on lateral margin of elytral declivity, displaced mesal from margin; eye of normal size; North America, Asia, Europe; Pinaceae; 2.2-4.3 mm

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*Orthotomicus*

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Antennal club flattened, sutures either procurred or medially to strongly bisinuate; lateral margins of elytral declivity armed by 1 to 6 pairs of major denticles, third pair (if present) or incorporated into crest of lateral margin; eye usually either abnormally large or else very small

5/4. Sutures of antennal club (when present) moderately to very strongly procurred; eye large, very coarsely faceted; its width about equal to length of scape; its length more than twice length of scape; Mexico to South America, S Asia to Australia, Africa; angiosperm hosts (some Asian exceptions); 1.4-2.7 mm

---

*Pityogenes*

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Sutures of antennal club moderately to strongly bisinuate (procurred in concisus, maritimus, orientalis); eye small, finely faceted; its width equal to much less than length of scape; its length equal to much less than twice length of scape; North America to N Nicaragua, Asia, Europe, N Africa; Pinaceae; 2.1-6.9 mm

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Fig. 49. *Ips* spp.: 1, *pterribilis* (Eichhoff), male; 2, same, male head; 3, same, male declivital spines; 4, same, female declivital spines; 5, *hunteri* Swaine, male; 6, *woodi* Thatcher, male declivity; 7, same, female head; 8, same, female declivity; 9, *pulifrons* utahensis Wood, male; 10, same, female head; 11, *woodi*, female. (After Hopping 1965: 536)
designation by Hopkins 1914: 126, original spelling Onthotomicus Ferrari (1867: 44), a lapsus calami that was corrected by Ferrari (1869: 256). Synonym: Neotomicus Fuchs 1911: 33, Type-species: Bostrichus laricis Fabricius, subsequent designation by Hopkins 1914: 125. Distribution: 1 species in North America, about 10 in Asia, Europe, and N Africa. All are heterosanguineously polygynous and philoepagous. Keys: Reitter (1915: 108) for Europe, Balachowsky (1949: 255) for France, Stark (1932: 407) for the USSR. Acanthotomicus Blandford [1894a: 89, Type-species: Acanthotomicus spinosus Blandford, monobasic. Synonym: Minips Eggers 1932: 33, Type-species: Ips pilosus Eggers, original designation; Isophthalus Schell 1933c: 173, Type-species: Isophthalus quadrituberculatus Schell, designated by Wood 1980: 80]. Distribution: 10 species in Central and South America, more than 20 in Africa and about 14 in China and Japan to Australia and the Philippines. All are philoepagous; of 13 species studied in nature by me, 1 was monogamous and 12 heterosanguineously polygynous. Key: Wood (1982: 664) for Central America. Ips DeGeer [1775: 190, Type-species: Tomicus typographus = Dermentes typographus Linnaeus, subsequent designation by Bergroth 1854: 230. Synonyms: Cumatotomicus Ferrari 1867: 44, Type-species: Bostrichus stenographus Duftschmidt = Dermentes sexdenatus Boerner, subsequent designation by Hopkins 1914: 119; Cyrtotomicus Ferrari 1867: 44, Type-species: Bostrichus acuminatus Gyllenhal, subsequent designation by Hopkins 1914: 120]. Distribution: 25 species in North and Central America, about 18 in Asia, Europe, and N Africa; at least 1 has been introduced to Australia and the Philippine Islands. All are heterosanguineously polygynous and philoepagous. Numerous species belonging to other genera have erroneously been assigned to this genus at one time or another. Keys: Schell (1950b: 69) for Europe and Asia, Hopping (1965-1966) and Wood (1982: 660) for North and Central America. Tribe Dryocoetini Dryocoetidae Lindemann [1876: 165, Type-genus: Dryocoetes Eichhoff, 1864]. Thamnurginae Nüsslin [1911: 377, Type-genus: Thamnurgus Eichhoff, 1864].

Taphrophyschus Reitter [1913: 29, Type-genus: Taphrophyschus Eichhoff, 1878].

DESCRIPTION.—Frons usually sexually dimorphic, male convex to variously impressed, female convex to flattened or with elevations, variously ornamented by setae in many species; eye distinctly emarginate to divided; antennal scape slender, elongate, funicle 4- to 6-segmented, club obliquely truncate to strongly flattened, if flattened then sutures variously procured to obsolete, and, on posterior face, strongly displaced toward apex; pronotum arched from base or not, if anteriorly declivous then declivity usually involving more than anterior half, armed or not, if armed then asperities small, usually abundant; procoxae contiguous to narrowly separated, protibia with lateral margin armed by four to several socketed teeth (Chlosterion and a few Coccytodes have three); scutellum visible; elytral declivity usually convex, sometimes shallowly sulcate or variously flattened, sometimes armed by small granules, vestiture hairlike.

BIOLOGY.—Apparently all are polygynous, with heterosanguineous polygyny occurring in all except the consanguineous Dryo­coetini, Coccytodes (Fig. 50), and Ozopem­men. Most are philoepagous, Dactylotrypes and some Coccytodes are spermophagous, and at least one species (Dryocoetius coffeae) is myelophagous. Most eggs are placed in individual niches. Most larvae form independent mines, but some feed in congress. TAXONOMY.—This is a large, rapidly evolving group; consequently, generic boundaries are not always clear. Three major groups of genera are apparent: (1) Dryocoetius, Coccytodes, and Ozopemen, (2) Dactylotrypes, and some Coccytodes are spermophagous, and at least one species (Dryocoetius coffeae) is myelophagous. Most eggs are placed in individual niches. Most larvae form independent mines, but some feed in congress. Although structural diversity may not warrant it, these three species groups will be discussed separately. In group 1, reproduction in all species involves arrhenotocous parthenogenesis. Males, if known, are dwarfed, deformed, flightless, and haploid. With about two possible American exceptions in Coccytodes, all species originally occurred in the Ethiopian, Oriental, or Australian realms. Many spermophagous Coc­cytodes have been transported through
commerce far beyond their original geographical distributions. Of the dozen or so American species, all but two are known to have reached America through commerce, and it is presumed that in time these two will be found to have foreign origins.

Group 2 is one of the few scolytid groups to invade herbaceous plants (mostly Cucurbitaceae and Euphorbiaceae). A thorough study of Thamnurgus, Xyloleptes, and Taphronurga will probably find that intergradation between them is complete and, consequently, that they must be combined into one genus. Group 2 undoubtedly is the most ancient of this tribe. If Dendrocranium (American) was separated from the almost indistinguishable Xyloleptes (African) by early Tertiary, then the origin of their common ancestor and of the tribe must be pushed back into the Cretaceous. Early members of this group probably gave rise to groups 1 and 3.

Group 3 appears to have originated in the Old World, with Dryocosmus and Lymantar reaching northern North America rather recently. Schell repeatedly called attention to the similarity between some of the small, slender Cyrtogenius and Pityophthorus; however, the antennae, elytral locking mechanism, and other characters are so totally different that there is no possibility of a close relationship between these groups.

Key to the Genera of Dryocosmin

1. Protibia armed on lateral margin by 5 or more socketed teeth (rarely 1 or 2 reduced, if so, then sutures on anterior face of antennal club preserved, except only 2 teeth present in Dohargoeleptes); posterior face of antennal club with only one suture indicated (except 2 in some Taphronurga); sutures on anterior face either preserved or club obliquely truncate, suture 1 more commonly on apical half; male of normal size, joins female in new parental gallery

2. Protibia armed on lateral margin by 2 to 4 socketed teeth; posterior face of antennal club marked by 2 sutures, suture 1 on anterior face usually on basal third, both sutures either straight or recurved; lateral margins of pronotum usually acutely or subacutely elevated at least near base (some exceptions); male dwarfed, of abnormal shape, flightless, never joins female in new parental gallery (except unknown in Chiloxylon)

3. Antennal funicle 4- or 6-segmented; pronotum unarmed, feebly if at all declivous on less than anterior fourth; eye deeply emarginate to divided; male from moderately to strongly impressed

4. Antennal funicle 2- to 5-segmented; anterior half of pronotum declivous and armed by apices (except feebly declivous and unarmed in Thamnurgus)
3(i). Antennal funicle 6-segmented; pronotum conspicuously longer than wide; feebly declivous on less than anterior half; sutures on antennal club procured; pronotae narrowly separated; Africa; Euphorbiaceae; 1.4-5.5 mm

Antennal funicle 4-segmented, sutures of club straight or slightly recurved (when present); pronotum feebly to moderately declivous on more than anterior third; processae conspicuous

4(3). Eye divided; prothorax rather broad, margin with only 2 socketed teeth; antennal club membranaceous and pubescent, with 1 stylet indicated at middle on front and back; pronotum smooth, shining throughout, very feebly declivous on anterior half; striae not impressed, punctures small, in rows, scarcely larger than those of interstriae; Madagascar; 1.9 mm

Doragoeleptes

5(2). Prothorax more broadly flattened on at least apical half, lateral margin arched by 7 or more socketed teeth; male from variously impressed, female flat to convex and ornamented or not; sutures on antennal club modified to profusely procurred, except recurved in some Thamnargus; scutellum very small, not flat, in stelae of Cacturbiaceae or Euphorbiaceae

Prothorax less strongly flattened on apical third, lateral margin arched by 5 socketed teeth (rarely 3 to 6); male from convex (rarely feebly impressed); female variously modified and frequently ornamented by hair; sutures on antennal club recurved, straight, procurred, or obsolete; scutellum rather large, flat, in phloem or xylem of trees and shrubs

6(5). Groove on posterior face of metafemur for reception of tarsus poorly developed, short, occupying less than apical third; Europe and Asia to Africa

Metafemoral groove conspicuous, occupying more than apical three-fourths on posterior face; America and Canary Islands

7(6). Pronotum less distinctly declivous on anterior third, punctured to anterior margin, margins of some punctures feebly to finely asperate; antennal club rather small, sutures straight to recurved; male from feebly impressed, Europe and SW Asia to N Africa; mostly in Euphorbiaceae; 2.0-3.0 mm

Thamnargus

Anterior third of pronotum finely asperate; punctures obsolete in apical area

8(7). Antennal club shorter than scape, 1.3 times as long as wide; sutures weakly procurred, male from rather strongly impressed, SE Europe; Clematis; 1.8-2.0 mm

Taphronargus

Antennal club distinctly longer than scape, more broadly rounded, sutures rather weakly to very strongly procurred; male from indistinctly impressed, S Europe; Cryptocladus, etc.; 2.0-2.7 mm

Xyloplectus

9(8). Sutures of antennal club obscure, strongly procurred, basal area of club not concave, body more slender, pronotum with asperities usually restricted to anterior half; America; Cacturbiaceae; 1.2-2.7 mm

Dendrocranulus

10(5). Antennal funicle 4-segmented, sutures of club very strongly procurred; male from shallowly to moderately impressed, female from less distinctly impressed; slender species with punctures on epical disc confused; partly xylophagous; North America, N Asia, Europe; 1.6-2.0 mm

Lymantor

Antennal funicle 5-segmented (rarely 2-3, or 4-segmented in New Guinea and Indonesia species), sutures on club procurred or not; male from usually convex, female from frequently pubescent

11(10). Pronotum with summit distinctly elevated near middle, often a moderate, transverse impression behind summit; antennal club strongly flattened, basal area slightly concave, summit 1 distinct, straight to strongly bisinuate, its lateral extremities reaching basal fourth; median portion never exceeding middle of club, 2 sutures on posterior face; mico- and metalithine more slender, hair on pronotum and elytra fine, usually long; Europe and Asia; broadleaf hosts; 1.8-3.2 mm

Taphrocephus

Pronotum with doral profile evenly arched, summit inconspicuous or else on basal fourth; basal area of antennal club less strongly flattened, more strongly concave or if not concave then sutures obsolete and pubescence extending to base; micro- and metalithine usually more broadly flattened; pronotal and elytral setae of more normal length

12(11). Antennal funicle 2-segmented, procurred cornaceous area of club occupying more than three-fourths of basal area; pronotae conspicuous; New Guinea to New Britain Island; 1.2-1.4 mm

Dendrographus

Antennal club 3-, 4-, or 5-segmented, usually much larger

13(12). Body very stout, 2.0-2.1 times as long as wide, pronotum rather coarsely asperate to base, summit on basal fourth; antennal club either devoid of sutures or with 1 on basal fourth, almost straight except recurved at margins; processae narrowly separated; declivity strongly arched, convex, apical fourth exceeding vertical and slightly undercutting central
14(1:). Antennal club with suture 1 weakly to pro-

foundly procured, rarely with sutures absent

and pubescent to base; funicle of small species

with as few as 3 segments (most 4- or 5-seg-

mented); procoxae narrowly separated, rarely

interrupted piece longitudinally emarginate;

commonly with ventrolateral margin of de-

civity slightly elevated or armed; Micronesia

to Africa; mostly non-coniferous hosts, 1.3-3.0

mm

Cyclogenus

— Antennal club with suture 1 resolved, always

present, never pubescent to base; procoxae

contiguous, intercoxal piece always longitudi-

nally emarginate or absent; ventrolateral mar-

gins of decivity never acutely elevated or spe-

cally armed; North America, Asia, Europe, N

Africa; mostly coniferous hosts; 1.5-5.1 mm

Drupoecetes

15(1). Prothorax rather broad apically, lateral apical

angle abrupt (almost 90 degrees). 1 denticle

on this angle; another on apical margin, and a

third on lateral margin one-fourth thibia length

from apical angle; funicle 4-segmented, club

constructed at partly septate suture 1 (not ac-

tuately obliquely truncate), sutures 2 indicated

by setae; habitus resembling Drupoecetes,

uniseriate interstitial setae almost scalelike in

decivity, decivity very steep; striae puncta-

ces coarse, deep; Brazil; 1.7 mm . Chilodesylon

— Prothorax narrowed near apex, outer apical an-

gle not abrupt; funicle 4-segmented, club

never septate, obliquely truncate or nearly so

Procoxae

16(13). Procoxae narrowly to moderately separated,

anteri or margin of pronotum usually armed

with serrations (absent in some forms); pronot-

um usually more coarsely asperate in ante-

rior areas, its summit more definite and near

middle; India and Sri Lanka (Ceylon) to

Philippines; broadleaf hosts; 1.3-3.5 mm

Drepanoccia

— Procoxae contiguous, intercoxal piece either

longitudinally notch ed or absent; anterior

margin of pronotum unarm ed, procoxae usu-

ally more finely asperate to unarm ed anteri-

orly, its summit less definite and usually well

behind middle...

Drepanoccia

17(16). Lateral margins of pronotum obscurely to

subacutely elevated only near base; fronts

never convergently aculate; anterior half of

pronotum always strongly declivous and as-

perate;elytral declivity either moderately im-

pressed on central half and with interstital

tubercles or discal punctures strongly con-

fused; mesocoxae subcontiguous, separated by
distance equal to width of antennal pedicel; phloeo phagus; Indonesia and

Malaya to Fiji; broadleaf hosts; 3.3-3.5 mm

Ossopeum

— Lateral margins of pronotum subacutely elevat-

ed on more than basal half, fronts com-

monly convergently aculate; anterior half of

pronotum declivous or not; elytral declivity

usually convex, rarely impressed, granules

absent or inconspicuous; mesocoxae rather

widely separated by distance two or more

times greater than width of pedicel; punctu-

tures on elytral disc almost always in rows

(some exceptions); phloeo phagus or sper-

mophagus; introduced almost worldwide;

apparently no endemic American species;

broadleaf hosts and palm fruits; 1.3-3.7 mm

Cocotrypaes

Tyrophorus Schreiner [1882:246, Type-

species: Tyrophorus elongatus Schreiner,

monobasic. Synonyms: Hypaspistes Hage-

dorn 1908: 374, Type-species: Hypaspis-

tus cameranus Hagedorn, monobasic, preoccu-

pied; Orthaspistes Hagedorn 1909b: 733,

Type-species: Hypaspistes cameranus Hag-

dorn, automatic: Pseudothamnurgus Eggers

1912a: 115, Type-species: Thamnurgus scu-

tator Pandelé, subsequent designation by

Schedl 1961: 738. Distribution: 13 species in

Africa and S Europe.

Dolurgoeleptes Schedl [1965a: 61, Type-

despecies: Dolurgoeleptes malagassicus Schell,

monobasic. Distribution: 1 species in Mad-

gascar.

Triotemnus Wollaston [1864: 264, Type-

species: Triotemnus subretusus Wollaston,

monobasic. Synonym: Cladocto proctus

Schell 1975: 454, Type-species: Cladocto-

proctus scraft Schell, original designation].

Distribution: 9 species in N Africa and the

Canary Islands, 2 in India. Most species breed

in the stems of Euphorbia, Delphinium,

Aconitum, Teucrum, and Bupherum. Key:

Peverimhoff [1949].

Thamnurgus Eichhoff [1864: 40, Type-

species: Bonriusus euphorbiac Kiefer, sub-

sequent designation by Hopkins 1914: 130].

Distribution: About 40 species in Asia, Eu-

rope, and Africa. A thorough review of the

species of this and the next two genera would

probably result in combining them into one

genus. Keys: Reitter [1913: 85] for Europe,


Taphronurgarus Reitter [1913: 84, 90, Type-

species: Taphronurgarus exul Reitter, monoba-

sic. Distribution: 1 species in SE Europe to

SW Asia. In Clematis. It is probable that this
genus will eventually be combined with Thamnoma.


Dactylotreps Eggers [1927a: 37, Type-species: Dactylotreps nuppenboogaarti Eggers = Xyloterus longicollis Wallaston, monobasic]. Distribution: 1 species in the Canary Islands in fruits of Phoenix canariensis and Dracaena draco; it may have been introduced into France (Balachowsky 1949: 180). The male apparently joins the female in the parental gallery.


Cyrtogenus Strohmeyer [1910c: 127, Type-species: Cyrtogenus bicolor Strohmeyer, monobasic. Cyrtogenus Strohmeyer (1911: 16) a valid emendation of Cyrtogenus. Synonyms: Carpininus Hopkins 1915a: 9, 47, Type-species: Carpinosinus pini Hopkins, original designation: Orosiotes Niissima 1917: 1, Type-species: Orosiotes kunatoensis Niisima, monobasic; Metahylastes Eggers 1922: 165, Type-species: Metahylastes africanaus Eggers, monobasic; Pelcercus Eggers 1923: 216, Type-species: Lepicurus nitis Hagedorn, original designation; Euleptips Schell 1939b: 344, Type-species: Euleptips glaber Schell, original designation; Osdendornt Schell 1957a: 13 and duplicate description by Schell 1964a: 243, Type-species: Pelcercus grandis Bescn, monobasic; Minidendrurus Schell 1965a: 68, Type-species: Minidendrurus maculatus Schell, monobasic, the species designated by Schell (1961: 732) was not an original species and is an invalid designation; Carpophloeus Schell 1959b: 143, Type-species: Carpophloeus rugipennis Schell, monobasic; Taphrobrotorus Nonberg 1961: 617, Type-species: Taphrobrotorus auctae Nonberg, original designation; Arteptophytococcus Schell 1969: 157, Type-species: Arteptophytococcus aries Schell, monobasic; Taphrotopenus Nonberg 1961: 617, Type-species: Taphrotopenus tenuis Schell, nomen nudum, for Taphrotopenus tenuis Schell, nomen nudum]. Distribution: About 16 species in Africa, more than 40 in the area from India and Japan to Australia and Micronesia. They are phloeophagous and heterosanguineously polygynous.

Drycoetes Eichhoff [1864: 38, Type-species: Bostrichus autographus Ratzeburg, subsequent designation by Hopkins 1914:...
Type-species: Anodius Motschulsky 1860: 135, Type-species: Bostrichus autographus Ratzeburg, subsequent designation by Wood 1974: 232, suppressed by International Commission on Zoological Nomenclature 1979: 149; Dryocoetus Balachowsky 1949: 180, Type-species: Bostrichus villosus Fabricius, original designation. Distribution: 7 species in North America, about 50 in Asia, Europe, and Africa have been assigned to this genus, but more than half of them have been transferred to other genera. All are heterosan-
guineously polygynous and phloeophagous. Keys: Reitter (1913: 75) for Europe, Mu-

Chiloxylon Schiedl [1959a: 550, Type-species: Chiloxylon rufulus Schiedl, monobasic]. Further study of this genus is needed; it may be allied to Dendroterus of the Corthylini (Pityophthorina), rather than to Dryocoetes. Distribution: 1 species in Brazil (Matto Grosso).

Dryocoetiops Schiedl [1957a: 13, Type-species: Oszopon laevis Strohmeyer, original designation]. Distribution: About 15 species in SE Asia, Sri Lanka (Ceylon), Indonesia, and New Guinea. One species observed in nature appeared to be consanguineously polygynous (or some form of parthenogenesis) and was myelophagous.

Oszopon Hagedorn [1908: 382, Type-species: Oszopon regius Hagedorn, monobasic]. Distribution: About 27 species in SE Asia and Indonesia to Fiji. All are consanguineously polygynous and phloeophagous.

Coccytropes Eichhoff [1878a: 306, Type-species: Bostrichus dactyliperda Fabricius, subsequent designation by Hopkins 1914: 118. Synonyms: Poecilips sannio Schaufluss, monobasic; Cryptolyides Formenek 1908: 91, Type-species: Cryptolyides don-ishtorpei Formenek = Bostrichus carpopha-
gus Hornung, monobasic; Thamnurgides Hopkins 1915a: 45, Type-species: Thamnurgides persicae Hopkins = Coccytropes advena Blandford, original designation; Spermatoplex Hopkins 1915a: 45, Type-species: Spermatoplex rhizophorae Hopkins, original designation; Dendrurgus Eggers 1923: 144, Type-species: Dendrurgus rhizophorae Eg-
gers = Spermatoplex rhizophorae Hopkins, subsequent designation by Wood 1982: 731, Hyphaene Hagedorn 1913: 254, nomen nudum, Type-species: Hyphaene guineensis Hagedorn, nomen nudum = Bostrichus car-
pophas Hornung, no status. Distribution: More than 100 species have been assigned to this genus, mostly from Africa, S Asia, and adjacent areas. Species in most other areas have been introduced through commerce. All are consanguineously polygynous and phloeophagous or spermophagous; a few species may assume both feeding habits. This exceedingly difficult genus is in a state of taxonomic chaos.


Tribe Crypturgini

Crypturini LaCointe [1876: 374, 387, Type-genus: Crypturis Eichhoff, 1836]

Description.—Frons usually not dimorphic, male sometimes slightly impressed, fe-

name convex; eye deeply emarginate, except sinuate in Deroporia; antennal scape moder-
ately long, slender, funicle 2- to 3-segmented, club comparatively small, two sutures on api-
cal half, 1 sometimes septate, both frequently absent; pronotum usually unarmed; procoxae
armed by several socketed denticles; scutel-
lum visible; elytral punctures in rows or con-
fused, setae hairlike; anterior surfaces and (frequently) elytra uniformly reticulate.

Biology.—They are monogamous and

philophagous except that those species asso-
ciated with Euphorbia bore throughout subepidermal tissues of recently killed stems, apparently with little regard to the cambium. Crypturis usually utilizes the entrance tun-
nel of another insect. Larval mines are inde-
pendent. Details of the habits have not been

studied.

Taxonomy.—This tribe apparently was
derived from the same ancestral stock that
gave rise to the Dryocoetini, although the
true affinities have not been worked out. It
appears to have arisen well into the Tertiary in
the Ethiopian realm where at least some
members of five of the six known genera occur
today. Crypturis appears to have reached
North America from Asia rather recently.

Doburgus (North America) appears to be a
primitive relict of an earlier radiation that is
now extinct except for this species.
Key to the Genera of Crypturgini

1. Antennal funicle 3-segmented, club with sutures 1 and 2 present, club distinctly constricted at middle; pronotum longer than wide, unarmed, a distinct constriction on anterior third; elytra rather coarsely striate, strial setae larger than suture, interstrial setae short; W North America; Dolurgus .......................... 2

2(1). Antennal club not constricted at middle; suture indicated or if present then club at sepuncture 1 .......... 2

2(2). Antennal club rather strongly constricted at middle; suture 1; elytral punctures confused or striae, if indicated, not impressed; elytral sutures little larger than those of interstriae .......... 3

3(1). Antennal club not constricted at middle, suture 1 indistinct or indicated only by a partial, interstrial seta .......................... 4

3(2). Elytral declivity strongly flattened to concavely impressed, pronotum wider than long, weakly if at all declivous on anterior half, never armed by granules, anterior margin unarmed, N Africa; Euphorbia; 1.6-2.6 mm .......... Coleobothrus

4(2). Antennal club unmarked by sutures; anterior half of pronotum declivous and armed by coarse asperities, anterior margin serrate; eye entire to finely asperate; Canary Islands, host unknown; 1.5-2.0 mm .......... Deropria

5(4). Benicants of sutures 1 and 2 usually present in antennal club; elytral striae more strongly impressed, punctures rather coarse, always in rows, elytral vestiture on disc short, longest setae shorter than distance between interstrial rows; North America, Asia, Europe, N Africa; Pinaceae; 0.9-1.5 mm .......... Crypturgus

5(5). Benicants of sutures 1 and 2 usually absent in antennal club; elytral veins more strongly impressed, punctures rather coarse, always in rows, elytral vestiture on disc short, longest setae distinctly longer than distance between interstrial rows; Canary Islands, S Europe, N Africa; Euphorbia; 1.1-1.7 mm .......... Cusurgus

**Dolurgus Eichhoff** [1868a: 147, Type-species: *Hylastes pusillus* Mannerheim, monobasic]. Distribution: 1 species in W North America (Alaska to N California). It is monogamous and phloeoaphagous.

**Coleobothrus** Enderlein [1929: 144, Type-species: *Coleobothrus jandiacus* Enderlein, original designation]. Distribution: 2 species in the Canary Islands and 2 in Africa. Key: Menier (1973: 208).


**Deropria** Enderlein [1929: 143, Type-species: *Aphanarthrum elongatum* Eggers, original designation]. Distribution: 1 species in the Canary Islands.


**Tribe Xyloterini**

Xyloteriniæ Lindemann [1876: 165, Type-genus: *Xyloterus* Ericson, 1836 = *Trypodendron* Stephens, 1800]

**Trypodendron** Treidl [1907: 18, Type-species: *Trypodendron stephensii* Stephens, 1830]

Description.—Frons dimorphic, male weakly to very strongly impressed, female convex; eye completely divided; antennal scape long, funiculus 4-segmented (Fig. 51); club without sutures, basal area sometimes corneous, derived from obliquely truncate type; procoxae contiguous, proepimeron of female with mycetangium; pronotum asperate on anterior slope; prostibia flat in male; inflated and armed by small unsokedentate denticles on posterior face in female; scutellum visible; elytra conservatively sculptured.

**Biology.**—All species are monogamous and xylomycetophagous. The male joins the female in parental galleries. The eggs are deposited in niches above and below in the egg tunnels. The larvae enlarge the niches into...
cradles just enough to accommodate the newly transformed adult beetle. The brood emerges through the parent entrance tunnel. Temperate species overwinter in litter on the forest floor.

**Taxonomy.**—This is a small group consisting of three small genera. They appear to have been derived from the same parental stock that gave rise to the Xyleborini. They apparently originated in Asia, with *Trypodendron* extending westward into Europe and eastward in late Tertiary to northern North America. *Xyloterinus* (North America) and *Indocryphalus* (Asia) were derived from the same parental stock, with *Xyloterinus* apparently reaching North America in the warm period that preceded the last ice age.

Key to the Genera of Xyloterini
(Modified from Wood 1957b: 344)

1. Basal area of antennal club distinctly subcuneous, its apical margin strongly, rather narrowly proconvex on anterior face; protibia thickened, posterior face tuberculate in female; flattened and usually finely tuberculate in male; male from broadly, deeply excavated from epistome to vertex, convex in female; male pronotum subquadrate, anterior margin straight to slightly recurved and unarmed, female anterior margin proconvex and armed by several teeth; long axis of proepimeral excavation of female longitudinal and very narrow; North America, N Asia, Europe; coniferous and broadleaf trees; 2.7-4.6 mm

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**Indocryphalus Eggers** [1939: 5, Type-species: *Indocryphalus malaisei* Eggers Xy-

Xyloterinus Swaine [1918: 44, 83, Type-species: Bostrichus politus Say, original designation]. Distribution: 1 species in E North America. It is monogamous and xylomycetophagous.

Tribe Xyleborini

Xyleborus LeConte [1876: 346, 358, Type-genus: Xyleborus Eichhoff. 1864]
Webbiae Hopkins [1915: 224, Type-genus: Webbia Hopkins. 1915]

DESCRIPTION.—Body dimorphic, male dwarfed, deformed, flightless, eye reduced in size, often aberrant in shape (Fig. 52); frons convex, unadorned; eye emarginate to divided in a few oriental forms; antennal scape elongate, funicle 5-segmented except 3- or 4-segmented in a few oriental forms, club obliquely truncate except basal corneous area reduced or absent in some genera; pronotum asperate on anterior slope (a few exceptions, especially in male), procoxae varying from contiguous to widely separated; scutellum varying from large and flat to modified to absent; elytra variable, conservatively to elaborately sculptured; meso- and metatibiae flat, broad, tapered on distal third, lateral margin armed by a row of numerous, small, closely set socketed teeth, these usually alternating with marginal or submarginal setae in more highly evolved forms; meso- and metatarsi retractible into tibial grooves.

BIOLOGY.—Consanguineous polygyny is universal, apparently all males are haploid, deformed, and flightless. All are xylomycetophagous. Eggs are deposited in clusters in the parental tunnels. The larvae usually extend the parental galleries or feed exclusively on the fungal mycelium in the parental tunnels. The brood emerges through the parental entrance tunnel. Temporare species may overwinter either in the brood host or in litter on the forest floor. At least one species (Xyleborus dispar) passes through a definite diapause in the adult stage during the winter months.

TAXONOMY.—The worldwide circumtropical distribution of this tribe, with a few species occurring in temperate areas, suggests that it is at least moderately old. The occurrence of the same species groups of Ambrosiodmus in Africa and South America indicates that the basic characters of groups within that genus had been fixed by early Tertiary. However, the distributions of other groups and the large number of species in the tribe indicate that very rapid, recent evolution is in progress. In this tribe, armenotocous parthenogenesis is universal. This suggests a possible relationship to the higher Dryocoetini; however, a relationship to the Xyloterini is more likely. Because of the recent, active evolution affecting this group, generic limits are not clearly defined. Common and particularly confusing features of this tribe are size races within what otherwise appears to be a single species, in some cases these behave as entirely different species and in others, involving those same forms, there is total intergradation of the two sizes. This is probably a product of this type of mating system that will be more fully understood when details of their habits are known.

The generic classification of this tribe presented below is tentative and flawed; however, it is presented as a first attempt to organize a very large and difficult group even though a third of the species in the tribe were not studied. It is hoped that it might give at least limited direction to those who will concentrate more particularly on this group.

Key to the Genera of Xyleborini
(Females only)

1. Basal segment of labial palpus cylindrical, only slightly wider than segment 2 or 3, none of segments ornamented by a special tuft of setae; propodeum and adjacent surfaces flush with general contour of ventral surface of head; antennal club rather strongly flattened, without visible sutures; corneous area reduced, usually holocentrous to base; lateral margins of pronotum acutely elevated, pleural area con- cave (in transverse axis); anterior margin of pronotum unarmed; prothorax inflated; armed on its posterior face by minute tubercles; African, 2 species introduced into America; 1.4-4.7 mm. Premnobius

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— Basal segment of labial palpus enlarged, conspicuously wider than segment 2 or 3, its posterior face usually flat, one or more segments ornamented by specialized setae; pregnal and adjacent areas usually conspicuously impressed below general contour of head.

Antennal club with sutures 1 and 2 rather strongly procurred, both segments 1 and 2 coriaceous and usually glabrous except at sutures; prothorax slender, almost cylindrical; posterior face armed by tubercles; lateral margins of pronotum generally elevated, plesural area transversely concave; body very slender, anterior margin of pronotum armed by 2 or more very coarse serrations; domicile parasites of other ambrosia beetles; Mexico to Brazil; 2.7–6.0 mm; *Samosponus*.

Antennal club oblivioulsy truncate or nearly so, sutures (when visible) on or very near margin of corneous area, recurved (except pulvnescent to base in some oriental forms); prothorax usually strongly expanded on apical half; lateral margin of pronotum rounded (except *Cussonia, Webbia*); "parasitic" habit unknown.

— Scutellum, moderately large, its surface flush with adjacent surface of elytra; ventral margin of metafemur either rounded or rather obtusely angulate, on its posterior face groove for reception of tibia usually clearly indicated on distal half.

— Scutellum either not visible or (Xyleborus) base of elytra at suture notched thereby exposing cone-shaped acrostich that appears displaced cephalad, or (coelep 20) scutellum visible on anterior face of declivital slope of elytral bases; scutellar area usually with abundant setae associated with mycetangium; base of elytra more strongly flattened, its (longitudinal) ventral margin attenuately, very acutely angulate (except *Schedilia*), for reception of tibia usually only near apical joint.

— Posterior face of antennal club marked by 2 sutures on apical third (suture 2 poorly represented in some *Coptoborus*), anterior face with apical portion convex (or concave only distal from segment 2), segment 2 comparatively large, sclerotized, prothorax armed by 6 or 7 socketed teeth on lateral margin, metathorax with 6 to 9 socketed teeth, anterior coxal part almost contiguous.

— Posterior face of antennal club with no more than 1 suture visible at or very near apex (usually none); apical portion of anterior face usually flat to concave, segment 2 (if visible) not corneous; number of metathoracic teeth variable; anterior coxal part contiguous or separated.

— Prothorax with posterior face inflated and armed by numerous fine tubercles; metathorax usually with 8 or 9 socketed teeth; segment 2 on antennal club usually forming a complete, oblique annulus, on anterior face its apical margin usually acutely crenate as on segment 1; Mexico to South America; 1 species introduced into Africa; 2.1–3.3 mm; *Dryocoetidae*.

— Prothorax with posterior face flat, unarmed, metathorax almost never with more than 7 socketed teeth.

65(5). Dechiy commencing at or anterior to middle of elytra, its lower half transversely, broadly impressed and either flat or shallowly concave; discal interstrial punctures unisectate then declivital surface covered by dense, conflated, small scales, if declivital setae hair-like then discal interstrial punctures rather dense, confused. India to Philippines and New Guinea; 2.5–5.0 mm; *Leptoglebiana*.

— Elytral dechility usually convex, commencing either posterior to middle or strongly tapered on posterior half, never with a strong transverse impression, elytra never ornamented by scales.

76(7). Posterior fourth of elytra comparatively broad, rather broadly rounded behind, suture never emarginate, declivital interstria 1 to 3 similar, tubercules minute, if present; body comparatively stout, less then 2.6 mm as long as wide; Mexico to South America, introduced to Africa; 1.7–3.0 mm; *Theoborus*.

— Posterior third of elytra attenuate or acuminate, narrowly rounded behind, suture often emarginate; 1 or more declivital interstriae sometimes armed by small denticles; body slender, at least 2.6 mm as long as wide; Mexico and South America, Africa to SE Asia; 1.5–5.0 mm; *Coptoborus*.

— Prothorax with posterior face inflated and armed by numerous fine tubercles; posterior face of antennal club either with or without a suture; elytral dechility and at least part of disc with interstrial carinate (carinat some times reduced to rows of tubercles), stria scale between carinat usually granular or dull, with punctures usually obsolete; SE Asia to Australia; 1.3–3.1 mm; *Arixyleborus*.

— Prothorax with posterior face almost flat, smooth, elytra with different sculpturing.

98(9). Antennal club with segment 2 at anterior face usually conspicuous, sometimes rather large, apical margin of segment 1 on both faces rounded, often inconspicuous or absent on anterior face, almost always visible on subapical area of posterior face; procoxae always contiguous, intercostral piece long, longitudinally emarginate, posterior element of intercostral piece never inflated or armed, mesocoxa usually more widely separated by distance greater than thickness of scape.

— Segment 1 of antennal club conspicuous, its distal margin very acutely elevated into a continuous costa (forming a complete circle) extending from anterior face to apex, suture almost never visible on posterior face; process varying from contiguous to widely separated, if
2(12). Pronotum almost never quadrate, its anterior margin usually procured and armed by a definite transversal suture; lateral margins of declivity rounded; lateral punctures often confused; ventrite usually much more abundant; SE Asia to Africa; 2.4-4.6 mm............ Eucallaeta

2(11). Pronotum commonly subquadrate, its anterior margin almost always unarmed, posterolateral marginal declivity subacutely elevated from notal apex to interstriae 7; strial and interstitial punctures usually in rows, elytral ventitie comparatively sparse, confined to strial and interstitial rows; Asia and Australia to Africa; 2.4-4.6 mm............ Eucallaeta

2(10). Pronotum almost never quadrate, its anterior margin usually procurred and armed by a definite transversal suture; lateral margins of declivity rounded; elytral punctures often confused; ventrite usually much more abundant; SE Asia to Australia; 2.8-4.0 mm............ Eucallaeta

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21(19). Protibia inflated and densely asperate on posterior face; anterior face of antennal club unmarked by asperities; smooth; basal corneous area of antennal club occupying less than basal half in central area, its apical margin recurved .

22(21). Strial punctures in definite rows (except concolor margin of corneous area usually forming a complete ring; scutellum usually visible on anterior declivous slope of elytral margins; body stout [less than 1.5 times as long as wide], usually black in color; punctures on elytral disc dense, confused.

23(17). Elytra moderately acuminate at natural apex; declivous margin abrupt, usually armed; SE Asia to New Guinea and Philippines; 1.5-3.0 mm .

Webbia

20(19). Posterior face of antennal club with at least 1 sutural visible, apical margin of corneous area never costate; scutellum not visible on anterior slope at bases of elytra; body more slender (at least 2.0 times as long as wide), color usually yellowish to reddish brown .

21(18). Posterior face of antennal club unmarked by asperities; smooth; basal corneous area usually forming a complete ring; scutellum usually visible on anterior declivous slope of elytral margins; body stout [less than 1.5 times as long as wide], usually black in color; punctures on elytral disc dense, confused.

22(21). Strial punctures in definite rows (except concolor margin of corneous area usually forming a complete ring; scutellum usually visible on anterior declivous slope of elytral margins; body stout [less than 1.5 times as long as wide], usually black in color; punctures on elytral disc dense, confused.

23(17). Elytra moderately acuminate at natural apex; declivous margin abrupt, usually armed; SE Asia to New Guinea and Philippines; 1.5-3.0 mm .

Webbia

Prenobius Eichhoff [1878a: 65, 404, Type-species: Prenobius cavipes Eichhoff, monobasic. Synonym: Prenobius Eichhoff Browne 1962a: 79, Type-species: Xyleborus joveri Schedel, original designation]. Distribution: 24 species in Africa, 2 of them were introduced into America. All are consanguineously polygynous and xylomycetophagous. Key: Wood [1982: 756].


Dryocoetoides Hopkins [1915a: 10, 52, Type-species: Dryocoetoides guatemalensis Hopkins = Xyleborus capucinus Eichhoff, original designation]. Distribution: 2 species in Central America, about 22 in South America, 1 of which was introduced into Africa. All are consanguineously polygynous and xylomycetophagous. Key: Wood [1982: 762] for Central America.

Leptoxyleborus Wood [1980: 94, Type-species: Phloeotrupes sordidula Motschulsky, original designation]. Distribution: 4 species in SE Asia. All are consanguineously polygynous and xylomycetophagous.


Coptotoborus Hopkins [1915a: 10, 53, Type-species: Coptotoborus enarginitus Hopkins = Xyleborus esvaporatus Schedel, original designation. Synonym: Streptocranus Schedel 1983a: 52, Type-species: Streptocranus mirabilis Schedel, monobasic]. Distribution: 5 species in Central America, about 10 in South America, and about 6 in SE Asia and adjacent islands. All are consanguineously polygynous


**Anasus Lea** [1894: 322, Type-species: *Anasus thoracicus Lea, monobasic. Synonyms: Pseudoxyleborus Eggers 1930: 906, Type-species: Pseudoxyleborus beesi Lea, monobasic; Anaxyleborus Wood 1980: 90, Type-species: Tomius truncatus Erichson, original designation*. Distribution: About 35 species in India and Malaya to Australia. All are consanguineously polygynous and xylomycetophagous.

**Eucalacineae Hopkins** [1915a: 10, 54, Type-species: *Xyleborus wallacei Blandford, original designation*. Distribution: About 50 or more species in Africa to SE Asia and Australia. All are consanguineously polygynous and xylomycetophagous.

**Terminalinus Hopkins** [1915a: 10, 57, Type-species: *Terminalinus terminalis Hopkins, original designation. Synonyms: Kelantopus Nunberg 1961: 621, Type-species: Xyleborus punctatipilosus Schell, original designation*. Distribution: About 30 or more species in Africa to SE Asia and Australia. All are consanguineously polygynous and xylomycetophagous.
49, Type-species: *Tosaxyleborus pallidipennis* Murayama = *Cnemus murayamai* Schedl, original designation. Distribution: About 17 species in SE Asia to Indonesia, the Philippines, and Japan. All are consanguineously polygynous and xylomycetophagous. Key: Nunberg (1972: 476).

*Xyleborus Reitter* [1913: 79, 83, Type-species: *Bostrichus saxeseni* Ratzeburg, subsequent designation by Swaine 1918: 50]. Distribution: 8 species in North and Central America, at least 4 in South America, at least 20 in SE Asia to Africa. All are consanguineously polygynous and xylomycetophagous. Key: Wood (1982: 542) for North and Central America.

*Xenoclytus Browne* [1904: 125, Type-species: *Xenoclytus inurbanae* Browne, monobasic]. Distribution: 1 species in New Zealand. It is consanguineously polygynous and xylomycetophagous.

*Hydrodemus Wood* [1980: 94, Type-species: *Xyleborus globus* Blandford, original designation]. Distribution: About 6 species in SE Asia to Indonesia and the Philippines. All are consanguineously polygynous and xylomycetophagous.


*Xyloclytus Browne* [1950: 641, Type-species: *Xyleborus sumatranus* Hagedorn, original designation]. Distribution: 5 species in SE Asia to Indonesia and New Guinea. All are consanguineously polygynous and xylomycetophagous. Key: Browne (1960: 642).

*Coptodryas Hopkins* [1915a: 10, 54, Type-species: *Coptodryas confusa* Hopkins, original designation. Synonyms: *Microperus* Wood 1980: 94, Type-species: *Xyleborus these* Eggers, original designation; *Adrycoetes* Eggers, nomen nudum, in Schedl (1952: 371), Type-species: *Adrycoetes nitidus*, nomen nudum, = *Xyleborus pullus* Schedl, no status]. Distribution: About 20 species in SE Asia to Australia and adjacent islands. All are consanguineously polygynous and xylomycetophagous.

*Webbia Hopkins* [1915b: 222, Type-species: *Webbia dipterocarpi* Hopkins, original designation. Synonyms: *Xelyborus* Schedl 1939b, nomen nudum (Browne 1963a: 57); *Pseudowebbia* Browne 1961: 308, Type-species: *Xyleborus trepanicauda* Eggers, original designation; *Prowebbia* Browne 1962b: 208, Type-species: *Prowebbia subacuta* Browne, original designation]. Distribution: About 12 species in Malaya. All are consanguineously polygynous and xylomycetophagous. Key: Browne (1962b: 210) to the *palo* group of species.

Tribe Xyloclytini

*Xyletoxoidae* Eichlolf [1873a: 171, Type-genus: *Xyletoxus* Eichhoff, 1872]

**DESCRIPTION.**—Frons apparently not di-morphic, usually unadorned; eye emarginate to divided; antennal scape elongate, funicle 6- or 7-segmented, club strongly flattened, sutures procurred, present or obsolete, 1 partly septate or not; pronotum asperate on anterior slope, anterior margin usually armed; propodeum contiguous; scutellum large, flat; tarsi retractable into tibial grooves; venter of abdomen moderately to very strongly ascending to meet elytra.

**BIOLoGY.**—All are apparently monogamous and philopatrous. The egg galleries are monomorous in *Ctenoxylon* and biramous in *Scytoxylon*. The eggs are deposited individually in niches and sealed in by frass. The larval mines radiate out from the parental gallery and may be rather long.

**TAXONOMY.**—This is a small group of pre-dominantly African genera that are poorly known. It appears to be a primitive branch of the same phylectic line that gave rise to the
Cryphalini. Together these two tribes appear to occupy a position intermediate between primitive Micracini and Corthylini. A principal distinguishing character of Xyloctonini is their ability to totally withdraw the meso- and metatibiae into tibial grooves. This character is shared by a small group of genera in the Cryphalini that are allied to Scolytogenses; thus, tribal placement for them is dependent on the number of segments in the antennal funicle. The limited distribution of this tribe, accompanied by conspicuous anatomical diversity, makes comments on its antiquity difficult.

Key to the Genera of Xyloctonini

1. Eye entire to feebly emarginate; sutures 1 of antennal club septate; almost straight; funicle 7-segmented; elytra declivous behind, abdomen raised only slightly to meet them; interstriae costate; Africa; 1.5-2.1 mm
   - Cryphalominus
   - Eye moderately emarginate to divided; sutures of antennal club weakly to strongly procured... 2

2(1). Eye moderately emarginate, about one-third divided by an emargination; basal (usually) and lateral margins of pronotum rounded; funicle 6-segmented, sutures of antennal club feebly to moderately procured, 1 not septate; elytral declivity steep, abdomen ascending very slightly; Africa; 1.9-2.6 mm
   - Glostatus

   - Eye more than half divided by an emargination to completely divided; basal and lateral margins of pronotum with a fine, raised line (either continuous or beaded); sutures of antennal club strongly procured. 1 partly to entirely septate (when sutures reduced septum remains); abdomen moderately to very strongly ascending to meet moderately to feebly declivous elytra... 3

3(2). Antennal funicle 7-segmented, club moderately flattened, asymmetrical, comparatively small, about equal in length to scape, suture 1 with posterior half septate, elytral declivity rather steep, abdomen ascending moderately to meet apex; eye always divided; Africa; 1.8-2.6 mm
   - Xyloctonus

   - Antennal funicle 6-segmented, club strongly flattened, symmetrical, large, comparatively longer than scape, suture 1 partly septate or not, elytral declivity short, very gradual, abdomen very strongly ascending to meet apex; eye divided or not... 4

4(3). Antennal club devoid of sutures except for strongly procured septum in posterior half of suture 1; scutellum large, flat, subtriangular, its surface rough with that of elytra, India to Philippines and Fiji; 1.0-2.4 mm... Scorilomimus

   - Antennal club with 2 or 3 very strongly procured sutures, some of them septate; scutellum averaging smaller, subquadrate, adjacent basal area on interstriae 1 and 2 impressed thereby causing scutellum to project slightly dorsad; Africa; 1.3-2.8 mm

**Xyloctonus**

*Cryphalominus* Eggers [1927b: 174, Type-species: *Cryphalominus striatus* Eggers, monobasic]. Distribution: 3 species in Africa (Congo to East Africa).

**Glostatus** Schell [1939d: 386, Type-species: *Glostatus declivecompressus* Schell, monobasic. Synonyms: *Ctonocryphus* Schell 1941: 398, Type-species: *Ctonocryphus xyloc­tonus* Schell, monobasic; *Apogo­latus* Schell 1957a: 155, Type-species: *Apogo­latus acacius* Schell, monobasic; *Para­glostatus* Schell 1964c: 304, Type-species: *Ctonocryphus nigricrassus* Schell, original designation; *Rhopalocryphus* Numberg 1967: 320, Type-species: *Rhopalocryphus seydlici* Numberg]. Distribution: 16 species in Africa. Apparently all are monogamous and phloeo­phagous.

**Ctonoxylon Hagedorn** [1910c: 4, Type-species: *Ctonoxylon auratum* Hagedorn, subsequent designation by Hopkins 1914: 119, Schell's (1961: 426) designation is invalid]. Distribution: About 32 species in Africa. Apparently all are monogamous and phloeo­phagous.

**Scorilomimus Blandford** [1895-319, Type-species: *Scorilomimus dilatus* Blandford, monobasic. Synonyms: *Neoxyloctonus* Eggers 1923: 143, Type-species; *Neoxyloctonus philippinensis* Eggers, monobasic; *Scolyo­crites* Schell 1962f: 490, Type-species: *Scyrilomimus maculatus* Beesen, original designation]. Distribution: About 15 species from India and Sri Lanka (Ceylon) to Samoa. All are monogamous and phloeo­phagous.


**Tribe Cryphalini**

*Cryphalidea* Lindemann [1876: 165, Type-genus: *Cryphalidea* Eichhoff, 1839].

**Tryphoploctinae** Nusslin [1911: 373, Type-genus: *Try­phoploctina* Fairmaire, 1868].

**Eumorphinae** Nüsslin [1911: 375, Type-genus: *Eumor­phus* Thomson, 1869].

**Euploctinae** Miyazawa [1954: 200, Type-genus: *Euo­plctus* Eichhoff, 1875, amended from *Euploctus* by Wood 1978: 114].
Fig. 53. Cryptophalinae, tribal and generic characters: 1-2, Hypothoneurom (Stephanoderes) distalis (Zimmermann), outline of female; 3-4, same, male; 5, Pseudocryptophalinae pulcherrima (LeConte) (Coryphlus), showing concealed metepisternum and horizontal abdomen; 6, Procryptophalinae utahensis Hopkins, anterior aspect of antennal club; 7, same, posterior aspect; 8, Tritypophalinus (Cryptophalus) pepsilis Hopkins, anterior aspect of antennal club; 9, same, posterior aspect; 10, Neoptygomerus (Cryptophalinae) knabi (Hopkins), anterior aspect of antennal club; 11, same, posterior aspect.
and structural diversity of this tribe suggest a pre-Tertiary origin. However, the proliferation of large numbers of species, particularly in Cryptophalus, indicates that recent, very rapid evolution is in progress. Trypophloeus, Procryptophalus, Ephractopus, and Cryptophalus appear to have reached North America from Asia rather recently. Hypothenemus, Cryptocarenus, Trischidius, and Scolytogenes in North America were recent derivatives from the neotropical realm. The South American element of Cryphalus and intercalary piece longitudes very ancient, endemic elements (Acorthylus, Neocryptus, Stegomerus, Cryptocarenus) and more recent arrivals (Hypothenemus, Scolytogenes). The more recent elements are largely confined to the tropics and are shared with Africa; similarity of species groups suggest a connection of faunas as late as early Tertiary. The main center of distribution for the tribe appears to be in the Oriental and Australian realms. This is also the area where rapid evolution has produced a great abundance of very closely related species. In this area, generic limits are often obscure, whereas in other parts of the world they are quite distinct. This is probably the most poorly known tribe in the world and it is likely to remain so until much more material is available for study.

**Key to the Genera of Cryptophalus**

1. Basal and lateral margins of pronotum rounded, procoxae usually narrowly separated, intercalary piece continuous (except contiguous and intercalary piece longitudinally emarginate in *Trypophloeus, Stegomerus, Acorthylus*).

2. Basal and usually basal third of lateral margins of pronotum marked by a finely raised line; procoxae either contiguous or narrowly separated, eye entire or narrowly emarginate.

3. Eye shorter, less than twice as long as wide, entire (rarely with a few facets absent suggesting a weak, narrow emargination).

4. Antennal funicle 3- to 5-segmented, club slender (1.8 or more times as long as wide), 2 sutures clearly marked, its apex subacutely pointed (Fig. 52); elytral interstriae 10 continuing to apex; North America, N Asia, Europe; *Salix, Populus, Alnus*, 1.4-2.1 mm. **Trypophloeus**

Antennal funicle 3- to 5-segmented, club broad (less than 1.3 times as long as wide), its apex rather broadly rounded, suture 1 usually marked, 2 obsolete or nearly so, interstriae 10 obsolete before attaining level of base of abdominal sternum.

5. Eye entire; antennal club broader, basal area more strongly flattened, suture 1 straight, septate, 2 obsolete; funicle 4-segmented; female frons not conspicuously pubescent,
North America to NE Asia. Populus, Salix, Fraxinus; 1.3-2.2 mm

- Eye entire to weakly sinuate; antennal club with sutures procurred or absent, 1 not separate when present

5(4). Antennal funicle 4-segmented, club with procurred sutures indicated by rows of setae; E North America, N Asia, Europe; Fraxinus, Fagus, Corylus; 1.3-1.7 mm

- Antennal funicle 3-segmented, club devoid of sutures. NE Asia; Euonymus; 1.4 mm

6(2). Antennal funicle 5-segmented, club large, subcircular, about as wide as long; sutures conspicuously procurred; discal striate not impressed, poorly defined (punctures often confused); Mexico to South America; vines (bina); 1.1-1.9 mm

- Antennal funicle 3-segmented, club elongate, at least 1.5 times as long as wide; sutures almost straight

7(6). Antennal funicle shorter than scape, segments 2 and 3 small, subequal in size; elytral striae impressed, punctures rather coarse; S South America; host unknown; 1.4-1.5 mm

- Antennal funicle with segment 2 greatly enlarged, as long as scape; elytral striae not impressed, strial rows usually not distinguishable (at least one exception); South America; Pteros, etc.; 1.2-1.8 mm

8(1). Basal margin of pronotum marked by a fine, raised line, lateral margin rounded; sutures on antennal club procurred, usually distinct

- Both basal and lateral margins of pronotum marked by a fine, raised line; sutures on antennal club present or absent

9(8). Eye enarginate; pronotal asperities confused; antennal grooves or sutures moderately procurred

- Eye entire; pronotal asperities arranged in concentric rows; antennal sutures rather strongly to profoundly procurred or obsolete

10(9). Antennal funicle 3-segmented, club with sutures 1 and 2 marked by moderately procurred grooves and rows of setae; pronotal asperities coarse, confused; eye conspicuously enarginate; Africa; hosts unknown; 2.0-2.3 mm

- Antennal funicle 4-segmented, club with subter 1 septate and angulate; eye rather small, shallowly enarginate; SE Asia; 1.2-1.6 mm

11(10). Antennal funicle 4-segmented; vestiture of abundant, confused scales; sutures on antennal club very strongly procurred or obsolete; Europe, Asia, Tibet, Fagus, etc.; 1.1-1.5 mm

- Antennal funicle 3-segmented; vestiture of uniseriate rows of scales on discal interstriae, a few supplemental scales on declivity, sutures on antennal club rather weakly procurred, sometimes obscure; SE Asia; broadleaf trees; 1.1-1.5 mm

12(8). Posterior edge of metatibia (usually also mesotibia) with a groove for reception of tarsus on lateral half from apex at least two-thirds of distance toward base, grooved area glabrous, usually with a row of setae along its mesal margin, tibia usually more broadly flattened, gradually tapered on its distal third, with socketed teeth more numerous and distributed over at least apical third (possible confusion with Xylotomini, except eye entire in these Cryptophalini); male subequal in size to female, capable of flight

- Metatibia either without groove for reception of tarsus or groove restricted to less than distal one-fifth of tibial length, setae randomly distributed on its lateral half, tibia usually subtruncated apically, socketed teeth usually restricted to apical one-fifth; male either normal or deformed

13(12). Antennal club with suture 1 partly septate, suture either straight or strongly procurred, if straight then funicle 3-segmented; body usually stouter, pubescence moderately abundant; groove forming lateral line on pronotum rather poorly defined

- Antennal club with suture 1 aseptate (or obwoundly septate, if suture present then funicle 4-segmented; body rather slender, elytral vestiture sparse, largely confined to declivity, groove forming lateral and basal raised line on pronotum rather strongly impressed

14(10). Antennal funicle 3-segmented, club with sutures 1 and 2 weakly procurred, clearly marked by setae, 1 also grooved and partly septate; venter of abdomen horizontal; India to Sri Lanka (Ceylon), Euphorbia; 1.0-1.3 mm

- Antennal funicle 4-segmented, club with sutures strongly to profoundly procurred, 1 marked on mesal half by a septum, remaining sutures marked by setae or obsolete (septum complete in several small New Guinea species); venter of abdomen weakly to very strongly ascending to meet apex of elytra, apex of elytra usually ascending also; pantropical; hosts usually lianas; 1.0-2.5 mm

15(13). Antennal club with sutures 1 and 2 weakly procurred and clearly marked by rows of setae, 1 also grooved; basal half of pronotum reticulate or minutely rugose, punctures usual to obsolete; Micronesia; hosts unknown; 1.1-1.4 mm

- Antennal club with sutures entirely obsolete; basal half of pronotum smooth, shining, with a few coarse punctures; India and E C-S to Japan; Phellodendron; 1.2-1.3 mm

- Antennal club with sutures entirely obsolete; basal half of pronotum smooth, shining, with a few coarse punctures; India and E C-S to Japan; Phellodendron; 1.2-1.3 mm
16(12). Tarsal segment 3 rather broad, bilobed; proceoxae narrowly separated, interponal piece not longitudinally emarginate; antennal club with asperate sutures clearly marked by grooves and setae ........ 17

— Tarsal segment 3 narrow, often laterally compressed, not bilobed; proceoxae contiguous, interponal piece longitudinally emarginate or partly absent .... 18

17(16). Antennal funicle 5-segmented, sutures on club weakly to rather strongly procurred; philoepagous in broadleaf and coniferous hosts; E. Hemisphère, North America (1 dubious record from South America); 1.0-2.3 mm

— Antennal funicle 4-segmented, sutures on club recurved (occasionally weakly procurred); philoepagous in broadleaf and coniferous hosts; E. Hemisphère, North America (1 dubious record from South America); 1.0-2.3 mm

18(16). Antennal funicle 3-segmented, club with or without sutures, never with a septum; male normal, not dwarfed or flightless .......... 19

— Antennal funicle 3- to 5-segmented, sutures always indicated on club, 1 frequently partly sepatate; male dwarfed, flightless .......... 21

19(18). Antennal club with moderately preserved sutures clearly marked by grooves and rows of setae; eye emarginate; stric obsolete, punctures on disc confused; SE Asia to Philippines; 0.8-1.3 mm

— Antennal club without indications of grooves or rows of setae; eye entire; strial punctures in recognizable rows .... 20

20(19). Anterior margin of pronotum armed by 0-6 serrations; aspersities on anterior half of pronotum less numerous; body stout, 1.2-2.0 times as long as wide; frons conveys to flattened in both sexes; SE Asia to Hawaii; 0.6-1.8 mm

— Antennal margin of pronotum armed by 10-16 serrations; aspersities smaller, much more numerous, often extending to base; body more slender, 2.5-2.6 times as long as wide; female frons rather narrowly impressed; SE Asia and Indonesia to Micronesia; 1.3-1.5 mm

21(19). Antennal funicle 3- to 5-segmented, club with or without sutures, when funicle 3-segmented then club always with suture partly sepatate .......... 22

— Antennal funicle 3-segmented, club never sepatate, sutures sometimes marked by rows of setae; body rather stout, 2.0-2.3 times as long as wide; very small .... 23

22(21). Anterior margin of pronotum armed by 10-16 serrations; antennal funicle 3-segmented; club never sepatate, sutures marked by rows of setae; mature body color yellowish to reddish brown; vestiture usually very sparse (rare exception); myloepagous; tropical America (1 introduced to Africa); 1.4-3.3 mm

— Anterior margin of pronotum usually armed by 1-8 serrations; antennal funicle 3- to 5-segmented, when 5-segmented then suture 1 of club partly sepatate; antennal club clearly marked by sutures; mature color usually darker, vestiture usually more abundant; philoepagous, myloepagous, spermophagous, 1 mycetophagous, worldwide in tropical and warm temperate areas; 0.6-3.8 mm

23(21). Antennal club with sutures clearly marked by rows of setae; eye entire; philoepagous in trees and shrubs; E. North America to Mexico and Hawaii; 0.6-1.1 mm

— Antennal club without indications of sutures; eye emarginate; myloepagous in viner

Asia; 0.8-1.1 mm

21. Hypothesenus


Allernoporus Kurentzov [1941: 159, Type-species: Allernoporus euonymi Kurentzov, monobasic]. Distribution: 1 species in NE Asia (in Euonymus). It apparently is monogamous and philoepagous.

Neocryphalus Nunberg [1956a: 139, Type-species: Neocryphalus argentinensis Nunberg, original designation]. Distribution: 2 species in South America (Argentina).

Acorthylus Bréthes 1922a: 304, Type-species: Acorthylus asperatus Bréthes, monobasic; Synonym: Phaurothrips Schell 1935a: 24, Type-species: Phaurothrips bacqui Schell, monobasic). Distribution: About 5 species in South America. All are monogamous and phloeoophagous.


Coriacophilus Schell [1939b: 339, Type-species: Stephanopus coriaceus Eggars, original designation]. Distribution: About 4 species in SE Asia to Philippines.

Ernothorides Thomson [1859: 147, Type-species: Bostrichus tiliae Panzer, original designation. Synonyms: Cryphaloximus Beiritter 1889: 94, Type-species: Cryphaloximus lederi Reitter = Bostrichus tiliae Panzer, monobasic; Stephanorhopalus Hopkins 1915a: 35, Type-species: Stephanorhopalus melodori Hopkins, original designation (specific name of type-species validly amended by Schell 1966a: 19); Euphalarus Schell 1940b: 589, Type-species: Ernothorides kahui Hopkins, original designation]. Distribution: At least 13 and perhaps 20 species in Europe and S Asia to the Philippines. All are monogamous and phloeoophagous.

Ernocladlus Wood [1980: 93, Type-species: Cryphalogenes corpulentus Sampson, original designation]. Distribution: About 4 species in S Asia to Sri Lanka (Ceylon).

Cryphalogenes Wood [1980: 91, Type-species: Cryphalogenes euphorbiar Wood, original designation]. Distribution: 4 species in India to Sri Lanka (Ceylon) in Euphorbia. All are monogamous and excavate dying tissue immediately under the epidermis.


Hypocryphalus Hopkins [1915a: 8, 41, Type-species: Hypocryphalus rotundus Hopkins, original designation. Synonym: Daecryphalus Hopkins 1915a: 8, 42, Type-species:
Dacryphalus obesus Hopkins, original designation. Distribution: About 47 species in Africa, S Asia to Australia and Samoa, 1 introduced into Mangifera indica. All apparently are monogamous and phloemophagous.

Cryptarthrum Ericson [1836: 61, Type-species: Bostrichus asperatus Gyllenhal, subsequent designation by Thomson 1859: 147, lectotype for type-species designated by Wood 1972: 41. Synonyms: Pseudeucryphalus Ferrari 1869: 252, Type-species: Bostrichus sileyanus Nordlinger, monobasic; Taenioglyptes Bedel 1888: 398, Type-species: Bostrichus abietus Ratzelburg = Bostrichus asperatus Gyllenhal, original designation; Cryptarthrum Blandford 1896b: 200, Type-species: Cryptarthrum walkerii Blandford, monobasic; Allarthrum Hagedorn 1912: 355, Type-species: Allarthrum kolbei Hagedorn, monobasic; Ericryphalus Hopkins 1915a: 8, 39, Type-species: Ericryphalus hensschi Hopkins = Hypothenemus sylecica Perkins, original designation; Pterius Hopkins 1915a: 8, 39, Type-species: Pterius pini Hopkins = Hypothenemus sylecica Perkins, original designation; Eriocryphalus Murayama 1935: 934, Type-species: Eriocryphalus birosistantissimus Murayama, original designation; Acryphalus Tsai & Li 1963: 604, 622, Type-species: Acryphalus lipingenis Tsai & Li, designated by Wood 1984: 224; Hynerocryphalus Tsai & Li 1963: 602, 622, Type-species: Cryptaphalus piecus Eggers, designated by Wood 1984: 224]. Distribution: 3 species in North America, 1 dubious record from South America, about 7 in Europe, more than 200 nominate species have been reported from Asia to Australia and adjacent islands. All are monogamous and phloemophagous. Keys: Reitter (1913: 66) for Europe, Balachowsky (1949: 206) for France, Stark (1952: 254) for USSR, Wood (1954b: 1092, 1982: 867) for North America and (1960a: 23) for Micronesia.

Margadillius Hopkins [1915a: 8, 37, Type-species: Margadillius margadalonia Hopkins, original designation]. Distribution: About 9 species in SE Asia, Philippines, New Guinea, and Indonesia. The true status and extent of this genus have not been established. Keys: Hopkins (1915a: 37).

Ptilopodus Hopkins [1915a: 7, 11, Type-species: Ptilopodus stephensii Hopkins, original designation]. Distribution: 15 species in Africa, SE Asia, and adjacent islands have been assigned to this genus, some erroneously. Key: Wood (1960a: 18) for Micronesia.

Cosmoderes Eichhoff [1878a: 495, Type-species: Cosmoderes monilicollis Eichhoff, monobasic. Synonyms: Eriocryphalus Schell 1938b: 42, Type-species: Cryptocarenus diadematus Lea, subsequent designation by Wood 1960a: 21; Dendropriocryptocarenus Blackman 1938b: 42, Type-species: Cryptocarenus diadematus Blackman = Cryptocarenus diadematus Eggers, original designation]. Distribution: About 22 species in Africa to SE Asia and Australia. At least 5 species were taken from lianas.

Cryptocarenus Eggers [1937: 79, Type-species: Cryptocarenus diadematus Eggers, original designation. Synonyms: Tachyderes Blackman 1943a: 35, Type-species: Tachyderes florinensis Blackman = Cryptocarenus diadematus Eggers, original designation]. Distribution: 5 species in North and Central America, more than 7 in South America, 1 introduced into tropical Africa. All are consanguineously polygynous and primarily myelophagous. Key: Wood (1982: 912).

Gnathyllus Schedl 1941: 392, Type-species: *Archeophalus natalensis* Schedl, monobasic; *Pachynoderes* Schedl, 1941: 393, Type-species: *Pachynoderes deprecator* Schedl, monobasic; *Lepiceroides* Schedl 1957a: 59, Type-species: *Lepiceroides aterrimus* Schedl, monobasic; *Ernophloeus* Nunberg 1958: 484, Type-species: *Ernophloeus costalimai* Nunberg = *Stephanoderes sunaensis* Eggers, original designation, *Epsips* Beeson 1941: 287, nomen nudum, Type-species: *Epsips ylorum*, nomen nudum, no status]. Distribution: 39 species in North and Central America; several hundred nominate species from other tropical and subtropical areas have been assigned to this genus, but a majority of them are now in synonymy. All are consanguineously polygynous and myelophagous,


**Periocryphalus Wood** [1971: 33, Type-species: *Periocryphalus pullus* Wood, original designation]. Distribution: 2 species in South America. Both are consanguineously polygynous and myelophagous in minute lianas.

**Tribe Corthylini**

*Corthylus* LeConte [1876: 346, 347, Type-genus: *Corthylus* LeConte, 1876].

*Pityophthorus* Eichhoff [1878a: 173, Type-genus: *Pityophthorus* Eichhoff, 1864].

*Araptus* Eichhoff [1878a: 303, Type-genus: *Araptus* Eichhoff, 1872].

*Amphicranus* Eichhoff [1878a: 460, Type-genus: *Amphicranus* Eichhoff].

**DESCRIPTION.**—Frons usually dimorphic, either or both sexes feebly to strongly modified in sculpture and ornamentation; eye emarginate; scape usually elongate, strongly flattened in some *Corthylus* (Fig. 54), etc., funicle 1- to 5-segmented, club strongly flattened, sutures present or obsolete, frequently 1 and/or 2 septate; when present, sutures on posterior face little if any displaced toward apex; anterior slope of pronotum asperate (one exception in female *Corthylus cecropii*), anterior margin frequently armed, lateral and basal margins frequently marked by a fine, raised line; procoxae contiguous, tibiae rather slender, their lateral margins rarely armed by more than four socketed teeth; metepisternal spine obsolete, replaced by small, transverse groove (Fig. 32), thus making it possible for elytra in locked position to cover at least posterior two-thirds of metepisternum (Figs. 53-54); vestiture usually hairlike, scales rarely present.

**BIOLOGY.**—Monogamy and heterosanguineous polygyny are common throughout the tribe; a few species of *Araptus* practice consanguineous polygyny. Phloophagy predominates in temperate areas, xylomyce- tophytory in tropical areas, although myelophagy and spermophagy are common. Parental galleries may be monoramous, bimoramous, or variously multiramous. The eggs are deposited in niches or, in *Corthylus*, in fully formed larval cradles. The larvae form individual mines or cradles depending on the food habit. The domicile parasitic habit is known in *Corthylocerus*, *Tricolus*, and *Amphicranus*.

**TAXONOMY.**—Except for two small endemic genera in Madagascar (*Pityophthoridion*, *Sauroptilius*) and one in Africa (*Mimiocerus*), a few primitive *Pityophthoridion* species in Africa, and several modern *Pityophthoridion* species in Eurasia, obviously derived from North America, this large, unique tribe is entirely American. The occurrence of primitive elements of ancient origin in Africa and Madagascar suggests that basic tribal characters formed prior to or early in the Tertiary. The elytral locking mechanism and antennal club are unique in the family, with the Cryptaphilini possibly forming an intermediate step between Corthylini and the primitive tribes of Scolytinae.

On a biological basis, the tribe is readily divisible into the phloophagous *Pityophthorus* and the xylomyce- tophytory *Corthylini*, although anatomical characters to support that division are less definite. The tribe obviously originated in South America and was affected by two radiations. The first occurred prior to the Tertiary and carried a few species into Madagascar and Africa, while those land masses were either connected or close enough for island hopping, and took several species over the land bridge to North America, where a minor secondary radiation occurred. The second major radiation occurred in South America during the Tertiary and produced the *Corthylini*. *Gnathotrichus* might have reached Central America or southern Mexico over the pre-Tertiary land bridge just prior to or during the early stages of its closure. A few genera and species have reached North America over the present post-Tertiary land bridge or by island hopping in recent time. The occurrence of *Gnathotrichus*, a member of the *Corthylini*, in China is more difficult to explain.

The South American element of this tribe is one of the more poorly known segments of the Scolytidae. Much remains to be learned about this remarkable group. *Chilocloph Schell* (see Dryocoetini) could belong to this tribe.
Key to the Genera of Corthylini

(Modified from Wood 1912)

1. Phloeophagus, myleophagus, or spermosophagus; antenal funicle 3- or 4-segmented (except 3- or 4-segmented in Dendroterus, Dacneophorus, and some Pityophorus costatus), club usually smaller, symmetrical; prosternal intercosomal piece acutely pointed (except obsolete in Dacneophorus); pseudececence usually more abundant, usually in rows on elytra; elytral declivity mostly convex to bisulcate, armature conservative (subtribe Pityophorina)

2. Xylocyncephagous; antenal funicle 1- to 5-segmented, club usually much larger, commonly asymmetrical; prosternal intercosomal piece absent (except obtuse in Gnaethrichus, Gnaethtripes); pseudececence usually greatly reduced to obsolete or minute; and strongly confused (not in rows); elytral declivity convex to truncate to deeply excavated (weekly bisulcate in some Gnaethrichus), commonly with spine-like processes (subtribe Corthylina) ................................................... 17

(2.1) Basal and lateral margins of pronotum rounded, devoid of a fine, raised line; elytra rather coarsely punctured (American genera), or very finely punctured (African genera), unarmed declivity steep, in American genera usually subvertical and somewhat flattened on lower half, almost never bisulcate; discal vestiture abundant .................................................. 11

2. Basal and usually lateral margins of pronotum marked by a finely raised line; elytral declivity usually more gradual, convex to bisulcate, often ornamented by granules or small denticles .................................................. 6

(3.2) Antenal club pubescent to base, unmarked by sutures, funicle 5-segmented; female funicle ornamented by a brush of long hair, male usually with a median tubercle or longitudinal carina at upper level of eyes; elytral declivity conservatively sculptured, usually convex; Africa to India and China, 1.2-2.8 mm .......................... 3

Minicorythus

— Antenal club with sutures clearly indicated; American genera .............................................. 4

(4.3) Antenal funicle 3- or 4-segmented, club with sutures at least slightly recurved, asceptate; elytral vestiture hair-like; female epistoma not emarginate, mandible never with projecting spines; strong, transverse frontal carina at upper level of eyes, when present, a female character; phillophagus, SW USA to Panama; Bursera, 1 species in Jatropha; 1.3-2.9 mm .......................... 9

Dendroterus

— Antenal funicle 5-segmented, secondary sexual characters different .................................................. 5

(5.4) Antenal funicle with asceptate sutures strongly procured; interstrial setae scalelike; male funicle strongly, transversely carinate at upper level of eyes, female epistoma deeply emarginate to accommodate a pair of mandibular spines; phillophagus: Costa Rica to Bolivia and Brazil; Astronium; Spoussia; 1.3-1.6 mm .......................... 9

— Sutures of antenal club straight or recurved; female epistoma entire, male funicle without a transverse carina; mandibular spines never present; elytral declivity convex, intersite imbricated by tubercles or spines; female funicle shallowly concave, bearing a brush of hair, armed on median fourth above eyes by an acute, transverse carina and by a pair of coarse tubercles in lateral areas at level of antenal insertion; male funicle convex, simple; Mexico; Bursera; 1.6-1.8 mm .......................... 8

Phileoterus

— Sutures of antenal club moderately to very strongly procured, only suture 1 septate, or if all external sutures obsolete then mesal half of suture 1 marked internally by a strongly procured septum at least on 1 side; phillophagus, myleophagus, spermosophagus; 8 USA to Argentina, 1.1-3.3 mm .......................... 12

(6.2) Sutures 1 and 2 clearly, equally marked by rows of setae and grooves, straight to moderately procured, if procured then both sutures at least partly septate (sutures always straight when both almost obsolete) .................................................. 7

(7.6) Lateral margins of pronotum rounded, without a fine, raised line .............................................. 8

— Lateral margins of pronotum subacute, marked by a fine, raised line (rather obscure in Spermosophorus and some Pityophorus having pronodal aspecies in subconcentric rows) .................................................. 12

(8.7) Sutures 1 and 2 of antenal club asceptate and clearly marked by rows of setae and grooves; pronomal aspecies continuing in lateral areas to base; larger species; spermosophagus in genera of Pinius, at least 2 species sometimes myleophagus; North America; 2.2-4.1 mm .......................... 3

Conophthorus

— Sutures 1 and 2 both partly to completely septate or, if asceptate, then antenal club largely glabrous or body size much smaller; pronomal aspecies not extending to basal margin; smaller species, not found in cones of conifers .................................................. 9

(9.8) Antenal club rather large, at least 2.5 times as long as funicle; monogamous species .......................... 10

— Antenal club comparatively small, less than 1.5 times as long as funicle; polygamous species .......................... 11

(10.9) Body stout, 2.5-2.8 times as long as wide; elytral declivity convex; antenal club usually with 2 sutures; phillophagus; larval mines resembling cradles (of ambrosia beetles); 5 USA to Honduras; Pinus; 1.5-3.2 mm .......................... 7

— Body very slender, 3.7-3.8 times as long as wide; elytral declivity strongly impressed; fe-
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11(9). Female proclive very greatly enlarged and bearing a rather dense, conspicuous tuft of very long hair, male proclive only slightly enlarged, usually without tuft of hair; phloeophagous, USA (Arizona, New Mexico), Pionus, 1.3-1.5 mm

--- Female oral region abnormally broad and, usually, with mandibles greatly enlarged; proclive normal; phloeophagous; Central and South America, Dacronous, Cedrela, Protium; 1.3-1.8 mm

12(7). Pronotum weakly declivous on anterior fourth, asperities small, numerous, gradually decreasing in size toward base, head unusually wide, mandibles large and stout in both sexes; eye large, coarsely faceted, one-third divided by a broad emargination; Madagascar; 3.2-3.4 mm

--- Pronotum more strongly declivous in front, asperities usually not present behind summit; local and mandibles normal

13(12). Pronotum without a transverse impression behind summit, transition between asperate and smooth areas more gradual, asperities always confluent; interstrial bristles usually stout to scalelike, 1 exception, also, almost glabrous in Sauroptilus, tropical species

--- Pronotum almost always with a distinct, transverse impression behind summit, if doublet then asperities almost always arranged in concentric rows; interstrial setae hairlike (if stout then proclival asperities concentric)

14(13). Anterior margin of pronotum unarmed, declivity very broadly excavated (as wide as body), its lateral crests profoundly elevated and separate, but abruptly ending before subapical apex; Madagascar; 3.2 mm

--- Anterior margin of pronotum armed by serrations or a continuous costa; declivity convex to moderately sulcate, impression rarely equal to more than half width of body; neotropical species

15(14). Strial punctures rather coarse, usually in rows, declivity moderately to rather strongly impressed, lateral margins armed or not; froms never arched; episternal margin with a small, median, premandibular lobe; polycygniopus; phloeophagous; axes of tubular maxillary chamelle perpendicular to caulidium, longest axis parallel to grain of wood; Colombia, Venecuala, broadleaf trees; 1.3-3.1 mm

--- Strial punctures either very small or confluent; declivity not as steep, convex to shallowly impressed, lateral margins never armed; male froms armed; spermophagous, Central and South America, Caesalpinus, etc.; 1.3-1.5 mm

16(13). Sutures of antenial club moderately procurred, segment 1 shorter than 2 or 3, greater frontal pubescence a male character; eylral punctures very fine, usually confluent, short pubescence abundant, often scalelike; striae usually obsolete; phloeophagous, monogamous; North America to Colombia, China, Quercus, rarely other hosts; 1.2-2.6 mm

--- Sutures of antenial club straight to moderately procurred, segments 1 and 2 subequal in length; pubescence usually much less abundant, never scalelike, strial punctures in rows or, if confused, then rather coarse; phloeophagous, monogamous or heterosanguineously polyphagous; America, Europe, Asia, Africa, consious and broadleaf hosts; 0.9-3.9 mm

17(1). Antennal funicle 5-segmented, club always symmetrical, with 2 or 3 clearly marked sutures; pennisula widest near its apex, its poste­ rior face usually flat, unarmed (a few minute granules in some Gnathotreps); eylral de­ cUity conservatively sculptured (except in some Gnathotreps)

--- Antennal funicle 1- to 4-segmented, club commonly asymmetrical, often greatly enlarged, sutures often reduced or absent; striae variously sculptured

18(17). Sutures of antenial club straight to moderately procurred, segment 1 not noticeably reduced in size; eylral declivity convex to narrowly, rather shallowly sulcate, subapical margin near apex acutely elevated, sutural apex entire, rather narrowly rounded behind; monogamous; North and Central America; coniferous and broadleaf hosts; 2.0-4.3 mm

--- Antennal sutures very small or confluent; declivity not as steep, convex to shallowly impressed, lateral margins never armed; male froms armed; spermophagous, some hosts; 1.3-2 mm

19(17). Antennal funicle 2- to 4-segmented, club with 2 sutures clearly marked; eylral apex divaricate (except Methacurthius, Chlorochneurus), commonly explainable, declivity often elabo­ rately excavated and armed by spines; protibia always slender, with posterior face iso­ flattened and tuberculatet body usually slender

--- Antennal funicle 1-segmented, club with 1, 2, or no sutures; eylral apex even (except Brachypappus, Cortiana emarginata), de­ cUity convex to rather weakly excavated; never explainable; posterior margin of probo-
23(22). Elytral apex divaricate, often also explanate; antennal club oval to broadly triangular; lateral margins of pronotum usually with a fine, raised line (a few exceptions); body moderately to very slender; mostly polygamous; North and South America; 1.4-4.8 mm

- *Monarchthrum*

- Elytral apex entire, never explanate; lateral margins of pronotum rounded; antennal club more than twice as long as wide (except 1.6 times in male *Metacorthylus*), its apex narrowly rounded; body comparatively stout...

24(23). Antennal funicle 3-segmented; female frons excavated and elaborately ornamented by long hair; antennal club not sexually dimorphic; elytral disc glabrous; monogamous; Mexico to Guatemala; 3.0-3.8 mm

- *Glochinocerus*

- Antennal funicle 2-segmented; frons convex and subglabrous in both sexes; antennal club asymmetrically very elongate in female, elongate-oval in male; pronotum and elytra minutely, closely pubescent; monogamous; Costa Rica to Colombia; 1.9-2.7 mm

- *Metacorthylus*

25(19). Lateral margins of pronotum rounded, elytral disc usually impunctate, declivity short, very steep, narrowly truncate on basal third, triangularly impressed below, costal margins near apex ascending slightly; antennal club subcircular, symmetrical, with 2 aseptate sutures marked by rows of setae; female frons convex, pubescence inconspicuous; monogamous; Mexico to South America; 1.2-2.4 mm

- *Microcorthylus*

- Lateral margins of pronotum marked by a fine, raised line (except some *Corthycyclon*), elytral disc usually with clearly marked, confused punctures, declivity convex, truncate, or variously sculptured (but not as above); female frons usually moderately to strongly concave, often ornamented by hair; antennal club symmetrical to strongly asymmetrical, suture present or not...

26(25). Antennal club aseptate, without sutures (some species with weak, transverse grooves, without rows of setae), usually very elongate; lateral margins of pronotum either with or without a fine, raised line, posterior face of pronotum inflated and tuberculate; female frons broadly, evenly concave and ornamented by fine hair, monogamous; Mexico to South America; 1.3-2.4 mm

- *Corthycyclon*

- Antennal club with 1 or 2 sutures, its outline subcircular to strongly asymmetrical (if sutures absent then posterior face of pronotum flat, smooth); female frons variable...

27(26). Antennal club aseptate, without sutures (some species with weak, transverse grooves, without rows of setae), usually very elongate; lateral margins of pronotum either with or without a fine, raised line, posterior face of pronotum inflated and tuberculate; female frons broadly, evenly concave and ornamented by fine hair, monogamous; Mexico to South America; 1.3-2.4 mm

- *Corthycyclon*

- Antennal club with 1 or 2 sutures, its outline subcircular to strongly asymmetrical (if sutures absent then posterior face of pronotum flat, smooth); female frons variable...

28(27). Antennal club aseptate, without sutures (some species with weak, transverse grooves, without rows of setae), usually very elongate; lateral margins of pronotum either with or without a fine, raised line, posterior face of pronotum inflated and tuberculate; female frons broadly, evenly concave and ornamented by fine hair, monogamous; Mexico to South America; 1.3-2.4 mm

- *Corthycyclon*

- Antennal club with 1 or 2 sutures, its outline subcircular to strongly asymmetrical (if sutures absent then posterior face of pronotum flat, smooth); female frons variable...

27(26). Antennal club aseptate, without sutures (some species with weak, transverse grooves, without rows of setae), usually very elongate; lateral margins of pronotum either with or without a fine, raised line, posterior face of pronotum inflated and tuberculate; female frons broadly, evenly concave and ornamented by fine hair, monogamous; Mexico to South America; 1.3-2.4 mm

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- Antennal club with 1 or 2 sutures, its outline subcircular to strongly asymmetrical (if sutures absent then posterior face of pronotum flat, smooth); female frons variable...
Elytral apex strongly, obtusely divaricate; female antennal club with 1 or 2 pairs of pointed spines; antennal scape elongate, club shaped; female frons variously impressed, with a pair of median carinae narrowly separated by a sulcus over part or all of median line; color pale yellow to yellowish brown, antennal club symmetrical, broadly oval, with 2 finely marked sutures; female protibia inflated, posterior face tuberculate, monogamous; North and South America, 1.5-2.8 mm. 

Corthylini: Pityophthorina


Araptus Eichhoff [1872: 136, Type-species: Araptus rajonpallatus Eichhoff, monobasic. Synonyms: Neodryocoetes Eggers 1933a: 9, Type-species: Neodryocoetes hymenaeus Eg­gers, monobasic; Thamnophthorus Schell 1938c: 174, Type-species: Thamnophthorus colastos Schell, subsequent designation by Blackman 1942b: 178; Neopityophthorus Schell 1938c: 180, Type-species: Pityophtho­rus laeviscus Eggers, designated by Wood 1982: 928; Sphenocerus Schell 1939e: 565, Type-species: Sphenocerus limax Schell, monobasic; Hypertensus Hagedorn, nomen nudum (in Schell 1950d: 164), Type-species: Hypertensus reitteri, nomen nudum = Spheno­cerus limax Schell, no status; Brachydendrulus Schell 1951b: 114, Type-species: Brachydendrulus eggersi Schell, monobasic; Gnathocerus Schell 1958: 116, Type-species: Gnathocerus nosatetonicus Schell, monobasic; Gnathoboratus Schell 1970a: 93, Type-species: Breviophthorus argentiniae Schell, original designation]. Distribution: 53 species in North and Central America, about 50 in South America and adjacent is­lands. Some are monogamous, some are heterosanguineously polygynous, and at least 3 are consanguineously polygynous (laeviscus, costarensis, etc.); most are phloeo­phagous, a few are spermophagous, and some are mycelophagous in vines (iliana). Key: Wood 1982: 928) for North and Central America.


Species: 98 Cm: H. Basi' Natural Aust

Type-species: Original designation


Pitophillus Blackman [1943a: 34, Type-species: Pitophillus mandibularis Blackman = Pitophillus shannoni Blackman, original designation], Distribution: 4 species in Central and N South America. All are heterosanguineously polygynous and phlo­ephagous, mostly in Protium. The status of this genus should be reviewed. Key: Wood (1982: 1142).


Sauroptilus Browne [1970: 558, Type-species: Xyleborus sauropterus Schell, original designation]. Distribution: 1 species in Madagas­car.

Phellotarus Wood [1971: 46, Type-species: Phellotarus tersus Wood, original designation]. Distribution: 3 species in South Amer­ica (Colombia to Venezuela). All are heterosanguineously polygynous and phlo­ephagous.


Pseudopitophillus Swaine [1918: 93, Type-species: Cryptopterus minutissimus Zimmermann, original designation]. Distribution: 23 species in North and Central Amer­ica, 1 in South America (Colombia), 1 in China. All are bigynous and phlo­ephagous, mostly in Quercus. Keys: Blackman (1931a: 225), Wood (1982: 966).

Pitophillus Eichhoff [1864: 39, Type-species: Bostrichus lichtensteinii Ratzeburg, subsequent designation by Hopkins 1914: 127. Synonym: Trigonogenus Hagedorn 1912: 354, Type-species: Trigonogenus fallax Hagedorn, monobasic; Hagedornia Luys 1920: 683, Type-species: Trigonogenus fallax Hagedorn, automatic; Myeloborus Blackman 1928a: 15, Type-species: Pitophillus ramipennis Swaine, original designation; Gnathophorus Schell 1935: 342, Type-species: Gnathophorus sparselialis Schell, monobasic, preoccupied; Conophthorinus Schell 1935: 343, Type-species: Conophthorinus blackmani Schell, monobasic; Brexiophorus Schell 1935c: 176, Type-species: Brexiophorus brasiliensis Schell, monobasic; Pitophthoroides Blackman 1942b: 199, Type-species: Pitophthoroides padius Blackman, original designation; Cladoborus Sawamoto 1942: 165, Type-species: Cladoborus erakii Sawamoto, monobasic; Neomips Schell 1954a: 37, Type-species: Neomips brasiliensis Schell = Pitophthus dimorphus Schell, monobasic; Cladophthus Schell 1955b: 25, Type-species: Cladophthus glabratulus Schell, monobasic; Gnathophthus Wood 1962: 76, Type-species: Gnathophthus sparselialis Schell, automatic; Hypopitophthus Bright 1981a: 14, Type-species: Pitophthus impius Wood, original designation]. Distribution: 225 species in North and Central America, about 100 in South America and adjacent islands, about 15 in Asia, 22 in Europe, 22 in Africa. Most are heterosanguineously polygynous, a few are monoga­nous; most are phlo­ephagous, a few are myelophagous. Keys: Pfeffer (1976: 334) for Europe, Blackman (1929a), Bright (1981a), and Wood (1982: 901) for North and Central America.

Corylini: Corylinia

Gnathotrichus Eichhoff [1869: 275, Type-species: Gnathotrichus cornellii Eichhoff = Tomius attenuatus Fitch, monobasic. Synonym: Gnathotrichoides Blackman 1911b: 267, Type-species: Cryptophthus sulcatius LeConte, subsequent designation by Wood 1952: 1155, Ancyloderes Blackman 1938b: 205, Type-species: Cryptophthus pilosus LeConte, original designation; Parasphleborus Hoff-
Wood: Genera of Scolytidae

1986

Gnathotrupes Schell [1951b: 125]. Type-species: *Gnathotrupes bolicicus* Schell, monobasic. Synonym: *Gnathotrupes thoracicus* Eichhoff 1938: 1678. Type-species: *Gnathotrupes terebratus* Wood, original designation; *Gnathocrus thoracicus* Schell, original designation; *Gnathocrinus thoracicus* Schell, original designation; *Gnathocrinus thoracicus* Schell 1975a: 11, Type-species: *Gnathocrinus thoracicus* Schell, original designation; *Gnathocrinus thoracicus* Schell 1975a: 12, Type-species: *Gnathocrinus thoracicus* Schell, original designation; *Gnathocrinus thoracicus* Schell 1975a: 16, Type-species: *Gnathocrinus thoracicus* Schell, original designation; *Gnathocrinus thoracicus* Schell 1975a: 101, Type-species: *Pteroclytopsis octotentatus* Schell, monobasic. Distribution: 24 species in North and Central America, about 78 in South America and adjacent islands. Most species are heterosanguineously polygamous; a few small species are monogamous; all are xylomycetophagous. Key: Wood (1982: 1170) for North and Central America.


*Amphicranus* Erichson [1835: 63]. Type-species: *Amphicranus thoracicus* Erichson, monobasic. Synonym: *Picearhopalus Guerin-Meneville 1835: 107, Type-species: *Picearhopalus nitidulus* Guerin-Meneville = *Amphicranus thoracicus* Erichson, monobasic; *Steganocrus Eichhoff 1878a: 460, Type-species: *Steganocrus dohrni* Eichhoff, monobasic. Distribution: 20 species in North and Central America, about 25 in South America. All are monogamous and xylomycetophagous; apparently some appropriate the tunnel of another species of Scolytidae or Platypodidae by driving out or killing the original occupants (domicile parasitism). Key: Wood (1982: 1186) for North and Central America.


*Microcorynus* Ferrari [1867: 58]. Type-species: *Microcorynus paradoxa* Ferrari, monobasic. Distribution: 13 species in Mexico and Central America. 19 in South America. All are monogamous and xylomycetophagous.

*Teracorynus* Ferrari [1867: 48]. Type-species: *Teracorynus nigropennis* Ferrari, monobasic. Distribution: 1 species in South America (Colombia). All are monogamous and xylomycetophagous.

*Anchonocerus* Ferrari [1859: 63]. Type-species: *Anchonocerus thoracicus* Ferrari, monobasic. Distribution: 1 species in South America (Bolivia). All are monogamous and xylomycetophagous.

**Corthycyclon Schell** [1915: 128, Type-species: Corthycyclon ustum Schell, monobasic]. Distribution: 6 species in Mexico and Central America, about 10 in South America. All are monogamous and xylocytophagous. Key: Wood (1982: 1250) for North and Central America.


**Corthycydus Wood** [1966: 18, Type-species: Brachyspartus berthauti Blandford, original designation]. Distribution: 6 species in Mexico and Central America, about 5 in South America. All are monogamous and xylocytophagous. Key: Wood (1982: 1265) for Mexico and Central America.


**Corythia** was first described by Ferrari (1867: 33-34), subsequent monotypy (Wood 1947: 202. Synonyms: Thylacos Schell 1938e: 567, Type-species: Brachyspartus moritzi Ferrari, subsequent monotypy (Wood 1982: 1298). Distribution: 1 species in South America (Venezuela).


**Corthycydus Wood** [1966: 18, Type-species: Brachyspartus berthauti Blandford, original designation]. Distribution: 6 species in Mexico and Central America, about 5 in South America. All are monogamous and xylocytophagous. Key: Wood (1982: 1265) for Mexico and Central America.


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**LITERATURE CITED**


Bergon, C. F. C. 1941. The ecology and control of the forest insects of India and the neighboring countries. Author, Dehra Dun. (5+2) ii + 1007 p.


WOOD: GENERA OF SCOLYTIDAE


GODFREY, E. L. 1. 1762. Histoire abrégée des insectes qui se trouvent aux environs de Paris dans quelle ces animaux sont rangés suivant au ordre méthodique (Scolytidae, l. 309–310, pl. v, fig. 5).


HINTON, H. E. 1956. Lepiceridae—a new name for the 
Cynthoceridae. Lepicerites—a new name for the 
scolytid genus Lepicerus Eichhoff (Coleoptera). 
Annals and Magazine of Natural History 17(10): 
472–473.

HOFFMANN, A. 1942. Description d’un genre nouveau et 
observations diverses sur plusieurs especes de 
Scolytidae (Col.). de la faune francaise. Société 

HOPKINS, A. D. 1962. A new genus of scolytidae from Flor-
rida. Enseiespaldia gen. nov. Entomological Society 

1960. Contributions toward a monograph of the 
scolytid beetles. 1. The genus Dendroctonus. U. S. 
Department of Agriculture, Bureau of Entomology, 

1914. List of generic names and their type-species 
in the coleopterous superfamily Scolytidae. U. S. 

1915a. Classification of the Cycphalinae with de-
scriptions of new genera and species. U. S. De-

1915b. Contributions toward a monograph of the 
scolytid beetles, Part II. Preliminary classification 
of the superfamily Scolytidae. U. S. Department 
of Agriculture, Bureau of Entomology, Technical 

1915c. A new genus of scolytid beetles. Washing-

HOPPING, G. R. 1963a. The natural groups of species in the 
genus Ips DeGeer (Coleoptera: Scolytidae) in 
North America. Canadian Entomologist 95: 500– 
516.

1963b. The North American species in group I of 
Ips DeGeer (Coleoptera: Scolytidae). Canadian 
Entomologist 95: 1061–1096.

1965c. The North American species in groups II 
and III of Ips DeGeer (Coleoptera: Scolytidae). 
Canadian Entomologist 97: 1202–1210.

1964. The North American species in groups IV 
and V of Ips DeGeer (Coleoptera: Scolytidae). 
Canadian Entomologist 96: 970–978.

1965a. The North American species in group VI of 
Ips DeGeer (Coleoptera: Scolytidae). Canadian 
Entomologist 97: 533–541.

1965b. The North American species in group VII 
of Ips DeGeer (Coleoptera: Scolytidae). Canadian 

1965c. The North American species in group VIII 
of Ips DeGeer (Coleoptera: Scolytidae). Canadian 
Entomologist 97: 159–172.

1965d. The North American species in group IX of 
Ips DeGeer (Coleoptera: Scolytidae). Canadian 

1965c. The North American species in group X of 
Ips DeGeer (Coleoptera: Scolytidae). Canadian 
Entomologist 97: 902–909.

LIEBERMANN, J. W. 1907. Versuche zur Aufnahme im Fabri-
cischen Systeme fehlender Käfergattungen. 
Magazin für Insektenkunde 6: 315–349.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLU-
(Insecta, Coleoptera); validation under the Ple-
nary Powers. Bulletin of Zoological Nomenclature 

clature 31: 230–238.

1979a. Opinion 1144. Phloeostichus (Coleoptera: 
Scolytidae) ruled to be a justified nomenclature 
change of Phloeosticenus Latreille, 1796. Bulletin of Zoological 

Nomenclature 36: 149–150.

1981a. Opinion 1166. Lepidactylus Wollaston, 
1854 (Coleoptera, Scolytidae) conserved. Bulletin of 

(Coleoptera, Scolytidae) conserved. Bulletin of 

KIERTY, W. 1837. Part 4. Insects: Coleoptera. Family 
Scolytidae. Pages 191–195 in Richardson, Fauza 
Borrelli-Americana; or the zoology of the northern 
parts of British America. J. Murray, London. 249 
p.


KHIYUTSYAVA, G. O. 1955. Korodoxiostus Sakhaliana 
(Bark beetles of Sakhalian Island). Akademia Nauk 

KURENOV, A. I. 1941. Korody dal’nego vostoka SSSR 
(Bark beetles of the Far East, USSR). Izdatel’svo 

KUSCHEL, G. 1966. A cosomine genus with bark-bettle 
habits, with remarks on relationships and biogeog-
raphy (Coleoptera, Curculionidae). New Zealand 

Genera des Coleopteres, vol. 7, contenant les 
faunales Curculionidae, Scolytidae, Brentidae, 
Anthribidae, Bruchidae: De Roret, Paris. Vol. 7, 
620 p.

LATURELLE, F. A. 1796. Précis des caractères génériques 
des insectes disposés dans un ordre naturel. 

1802/3. Histoire naturelle générale et particu-
lière des Crustaces et des Insectes. Ouvrage faisant suite 
à L’Histoire Naturelle générale et particulière, 
composée par Leclere de Buffon, et rédigée par C. 
S. Sonini. membre de plusieurs Sociétés savantes. 
Vol. 3. Familles naturelles des genres. Dufart, 

1894. Familien, Gattungen und Horden der 
Käfer. Coleoptera. Magazin für Insektenkunde 3: 
1–126.

1967. Genera crustaceorum et insectorum secun-
dum ordinem naturalum in familias disposita, in-

1928. Les crustaces, les arachnides et les insectes, 
distribuées en familles naturelles, ouvrage format 
des tomes 4 et 5 de celui de M. de Baron Cuvier 
sur le Règne animal (deuxième édition). Deter-

LEA, A. M. 1863. Descriptions of new species of Broutheli-
dae. Linnean Society of New South Wales, Proce-
sdings 5: 317–323.

1910. On Australian and Tasmanian Coleoptera, 
with descriptions of new species. Part I. Royal 
Society of Victoria, Proceedings, n. s., 22: 
113–152, pl. 30.


1954. Scolytidae fauna of the northern half of Honshu with a distribution table of all the scolytid species described from Japan. Yamaguti University, Faculty of Agriculture, Bulletin 5: 149–212.


1970b. Bark beetles and pin-hole borers (Scolytidae and Platypodidae) intercepted from imported logs in Japanese Port, IV. 274 Contributi... Kon... 38: 323–370.


1956 WOOD GENERA OF SCOLYTIDAE

WESTWOOD. J. O. 1836. Description of a minute coleopterous insect, forming the type of a new subgenus allied to Tomius, with some observations upon the affinities of the Xylophaga. Entomological Society of London, Transactions 1(1): 34–36, pl. VII, figs. 1a–1b.


1916. Fossil Coleoptera from the Florissant Beds. State University of Iowa, Laboratories of Natural History 7(3): 16–19.


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