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FAMILIAL AND SUBFAMILIAL CLASSIFICATION OF THE
TENEBRIONOIDEA (COLEOPTERA) AND A REVISED
GENERIC CLASSIFICATION OF THE CONIONTINI (TENTYRIIDAE)

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The presence of visible membranes between the terminal abdominal sternites of Tenebrionidae and related families is correlated with the presence of defensive glands which empty posterad of sternite 7. Species which lack defensive glands consistently have the aedeagus inverted from the typical position in most Coleoptera. These complex, correlated characters indicate a fundamental division among the Tenebrionoidea and several changes in the classification of these beetles are proposed accordingly.

Morphological comparisons of several tribes, principally the Coniontini, Praocini and Zophosini are summarized. The results indicate that the Zophosini are closely related to other African tribes such as the Adesmiini. The Praocini show close affinities to the South American Nycteliini and Physogasterini. The North American Coniontini and Coelini likewise share great affinity. While the taxa from these geographic regions are superficially similar, they differ in major structural features and are not closely related.

Finally, taxonomic changes intended to simplify the classification of the Coniontini and Coelini are proposed, with a revised generic checklist and key.

La présence de membranes visibles entre les sternites abdominales terminales des Tenebrionidae et des familles apparentées est en rapport avec la présence de glandes défensives qui s'ouvrent derrière le sternite 7. Les espèces dépourvues régulièrement de glandes défensives ont l'aedeage renversé par rapport à la position normale chez l'ensemble des coléoptères. La correspondance de ces caractères complexes indique une division fondamentale parmi les Tenebrionoidea et nous proposons en conséquence plusieurs modifications dans la classification de ces coléoptères.

Nous résumons les comparaisons morphologiques entre plusieurs tribus surtout celles des Coniontini, des Praocini et des Zophosini. Les résultats indiquent que les Zophosini sont en rapport étroit avec d'autres tribus africaines telles que les Adesmiini. Il y a des affinités étroites entre les Praocini et les Nycteliini et les Physogasterini sud-américains. Ces rapports étroits se retrouvent également chez les Coniontini et les Coelini nord-américains. Tandis que les groupes de ces régions géographiques n'accusent que des ressemblances superficielles, ils diffèrent par leurs caractéristiques structurales fondamentales et ne sont pas apparentés de façon étroite.

En fin de compte, nous proposons des modifications taxonomiques qui ont pour but de simplifier la classification des Coniontini et des Coelini et fournissons à l'appui une liste générique modifiée ainsi qu'une clef.

SUBFAMILY CLASSIFICATION OF THE TENEBRIONIDAE

Watt (1966) reviewed and summarized the various classifications which have been proposed for the Tenebrionidae. Consequently, only the most important works will be mentioned here. Tenebrionidae is used in the restricted sense of Crowson (1955) and Watt

(1966, 1967). Based on the structure of the procoxae, mesocoxae and aedeagus they exclude such genera as *Boros*, *Dacoderus*, *Tretothorax*, *Perimylops* and *Zopherus* et al. Watt (1967) also cites evidence indicating a close relationship of the Alleculidae, Lagriidae and Nilionidae to the Tenebrionidae. These families, together with the Zopheridae and Monomidae, are referred to here as Tenebrionoidea. In his analysis of the taxonomic position of *Petria* (Alleculidae: Omophtinae) Lawrence (1971) also mentions several characters which are important in the classification of the Tenebrionoidea.

The most recent classification of the Tenebrionidae treating the world fauna is that of Lacordaire (1859). This century-old work emphasizes external differences, especially in mesocoxal structure and mouthparts. In a broad sense, Lacordaire's primary divisions into Sections and Cohortes correspond to the subfamilies of more recent classifications. However, the Cohortes of his Section II are based on the vestiture of the tarsi. As noted by Watt (1966), this feature is probably related to the substrate on which the beetles walk, and is not a reliable taxonomic character. Consequently, Lacordaire's Section II, Cohorte I contains an assortment of unrelated tribes now assigned to different subfamilies. It should be mentioned that nearly all Lacordaire's tribes and subtribes are recognized as tribes today. Many of the numerous tribes proposed by subsequent workers, especially Casey (1907, 1908) and Reitter (1917) contain very few genera. These small tribes have served mainly to occlude the interrelationships within the family.

LeConte (1862), LeConte and Horn (1883) and Horn (1870), considering primarily the North American fauna, recognized three subfamilies. Their most important contribution was an appreciation of the taxonomic importance of the intersegmental membranes between the terminal abdominal sternites. They delimited the Tenebrioninae by the presence of external intersegmental membranes. The remainder of the family, with internal membranes, they divided between the Tentyriinae (mesocoxal cavities enclosed by the sterna; mesotrochantin concealed) and the Asidinae (mesocoxal cavities open laterally; mesotrochantin visible).

Most recent classifications (Gebien, 1910-11, 1937, 1938-44; Arnett, 1960) combine features of the arrangements of LeConte and Lacordaire, and differ from one another in minor ways. An exception is the proposal by Koch (1955) to divide the Tenebrionidae into only two subfamilies, depending on the condition of the membranes between the terminal abdominal sternites. On this basis, Koch combined the Asidinae with the Tentyriinae, also pointing out that the mesocoxal structure of the African Asidini does not conform to LeConte and Horn's criterion of the presence of a distinct trochantin. Brown (1971) has shown that the condition of the trochantin is also variable in the North American Asidini. Koch's classification is supported by the evidence presented below, and the name Tentyriinae will be used in the sense he advocated.

MORPHOLOGICAL AND ECOLOGICAL CHARACTERISTICS OF THE TENEBRIONOIDEA

Adults

Although most recent workers agree that the presence of external abdominal membranes is important as a diagnostic character, the high correlation with the presence of abdominal glands and reservoirs has not been noticed. The reservoirs are paired, cuticular invaginations surrounded by diffuse glandular tissue. They empty through ducts which open posterad of sternite 7 (visible sternite 5). Morphological studies by Blumberg (1961), Eisner, McHenry, and Salpeter (1964) and Kendall (1968) show that the glands and reservoirs are apparently homologous throughout the Tenebrionidae, Alleculidae and Lagriidae. Dissections made by the author reveal that similar glands are also present in the Nilionidae. The secretions

produced by these glands are probably defensive since they consist largely of quinones and other irritants (*see reviews by* Eisner and Meinwald, 1966; Schildknecht et al., 1964). The structural details of the glands and reservoirs are the subject of a comprehensive comparative study (Tschinkel, *in progress*) which may clarify the relationships among those Tenebrionidae which possess glands.

A survey by the author of over 45 tribes of Tenebrionidae, as well as members of the other families mentioned above, has revealed a nearly perfect correlation between the presence of glands and external membranes between abdominal sternites 5, 6, and 7. The single exception is the Pimeliini, where membranes are visible, as noted by Watt (1966), but reservoirs and glands are absent.

A further correlation exists between the occurrence of glands and the orientation of the aedeagus in the retracted position. As first noted by Sharp and Muir (1912) and elaborated by Blaisdell (1939), the aedeagus is rotated 180° in some Tenebrionidae, so that the primitively ventral surface is dorsal. This rotation, which also occurs in the Dacoderidae (Watt, 1967), some Salpingidae (Spilman, 1952) and the Monommidae (Sharp and Muir, 1912) is rather inappropriately termed inversion by coleopterists. With one known exception, Tenebrionidae with the aedeagus inverted lack defensive glands, while species with the aedeagus in the normal position possess them. The exception is the Cossyphini, a small Palearctic-African tribe whose members are specialized for living beneath bark. In these beetles the aedeagus is oriented with the tegmen dorsad, but defensive glands are absent and the terminal abdominal membranes are internal. This tribe is highly modified morphologically, particularly in thoracic structure, and more detailed studies will be required to clarify its relationships. Possibly the defensive glands have been lost secondarily.

The very high correlations among these highly complex structures is a fundamental difference separating the Tenebrionoidea into two distinct groups. The tenebrionid subfamily Tenebrioninae, together with the Alleculidae, Lagriidae and Nilionidae possess defensive glands and external abdominal membranes and have the aedeagus in the normal position. The subfamily Tentyriinae (*sensu* Koch) and the Monommidae lack defensive glands, have the terminal abdominal membranes internalized, and have the aedeagus inverted. In addition, these two groups seem to have evolved in different ecological situations. The Tenebrioninae, etc., are predominant in woodland habitats in tropical or subtropical climates, and many species are adapted to feeding on fungi or in rotting wood. Most of the species of this group which occur in temperate regions occupy relatively mesic, woodland habitats. Contrastingly, the Tentyriinae occur primarily in arid or subarid habitats in temperate climates, with highly distinct faunas in the deserts of southern Africa, Eurasia, South America, and southwestern North America. Nearly all of the species in this group are soil dwellers. There are exceptions to these generalizations, such as the Eleodini (Nearctic) and the Blaptini (Palearctic), which contain many species adapted to aridity, but clearly belong to the Tenebrioninae. Conversely, the Epitragini (Tentyriinae) are widespread in tropical regions, especially in the western hemisphere. These exceptions, coupled with the fact that the more generalized members of both subfamilies are winged, clearly show that loss of defensive glands and flight are not simply associated with adaptation to arid environments. Indeed, the diverse array of components in the defensive secretions (Tschinkel, *in progress*), and the variability of the associated delivery systems, especially in those Tenebrioninae inhabiting arid environments, suggests that the secretions have been very important in the evolution of these beetles. For instance, some species of *Blaps*, *Eleodes* and *Centronopus* are capable of spraying fine jets of secretion up to 30 cm. The elytra of other species, such as *Cibdelis blaschkei* Mannerheim are impressed with fine canals along which the secretions flow, rapidly coating the posterior portion of the body.

Larvae

The great majority of tenebrionid larvae which have been associated with adults are in the subfamily Tenebrioninae (see Korschevsky, 1943; Van Emden, 1947; Hayashi, 1966, 1968). Recently, larvae of several tentyriine tribes have been adequately characterized, including Erodiini, Akidini, Epitragini, Tentyriini, and Asidini, chiefly by Russian workers (Keleynokova, 1963, 1971; Skopin, 1960, 1962, 1964). Schulze (1962, 1964) and Marcuzzi and Rampazzo (1960) have described larvae from some additional tribes (Lepidochorini, Adesmiini, Coniointini, Coelini). Skopin (1964) and Keleynokova (1963) have attempted to use their results to produce larval classifications. Skopin's primary division splits the Tenebrionoidea into two groups, based on the structure of the legs. His Pedobionta includes all soil inhabiting larvae, in which the anterior legs are enlarged and modified for digging. The Pedobionta correspond to the Tentyriinae, with the addition of the Blaptini, Opatrini and Platyscelini of the Tenebrioninae. The Eleodini and Scaurini would also belong to the Pedobionta on the basis of leg structure. Skopin's Heterobionta incorporates the remainder of the Tenebrioninae as well as the families Alleculidae, Lagriidae and Nilionidae.

Clearly, Skopin's primary division is based on a highly adaptive feature. Keleynokova (1963) points out that soil inhabiting larvae are characterized by the absence of urogomphi as well as enlarged forelegs. Urogomphi are commonly present in the Tenebrioninae, and are apparently used in moving backward through the tunnels these larvae excavate in ligneous substrates. In Tenebrioninae which inhabit soil the urogomphi are reduced or absent (e.g., Blaptini, Eleodini, Pedinini). *Tenebrio* (Tenebrionini) is exemplary in this regard. Species of this genus infest stored grain products, which are probably similar to soil in physical properties. The anterior legs of *Tenebrio* are enlarged and the urogomphi are much reduced. For these reasons, Skopin's placement of the Blaptini, Opatrini, etc., in the Pedobionta is judged in error. The same conclusion was reached by Keleynokova (1963), who placed these tribes in a separate subfamily within the "tenebrionid line." In most respects, however, Keleynokova's classification into six subfamilies does not correspond to relationships indicated by adults. As noted by Watt (1966), her subfamilies are not clearly defined, and it is impossible to evaluate them at present.

One larval characteristic which is not stressed by Skopin or Keleynokova is the configuration of the mandibles. In the Tentyriinae the larval mandibles bear a dorsolateral prominence which is densely set with coarse setae. Setae on the mandibles of the Tenebrioninae, Alleculidae, etc., are never restricted to an elevated, dorsolateral region. The distribution of these character states is very highly correlated with the presence of defensive glands and the orientation of the aedeagus, and further supports a primary division of the Tenebrionoidea into two taxa.

Another character which may be of taxonomic importance is egg size. In the few tribes which have been investigated, the eggs are relatively large in the Tentyriinae (Asidini, Coniointini, Nyctoporini, Cryptoglossini) and small in the Tenebrioninae (Tenebrionini, Coelometopini, Ulomini) (Doyen, *unpublished*).

Skopin's (1964) subdivisions of his Heterobionta suggest several interesting relationships which reinforce the conclusions here derived from adult characteristics. His "Ulomimorpha" includes the Alleculidae as well as the Ulomini, and he flatly states that these should be placed in the same family on the basis of larval features. His "Pycnocerimorpha" includes the Goniaderini, Heterotarsini and Pycnocerini, tribes which have always been placed in the Tenebrioninae. On the basis of larval features, however, they are very similar to the Lagriidae. Hayashi (1968) also reached this conclusion from his studies of Japanese members of these taxa.

Evidence concerning the Nilionidae is not clear-cut. The adults greatly resemble members of the Leiochrini (Tenebrioninae), and Böving and Craighead's larval characterization is based on *Leiochrodes* sp. The characters listed by Skopin (1964) for the Nilionidae fit known larvae of the Leiochrini. However, he does not specify the taxa on which his concept is based, and the larva of *Nilio* appears to be unknown.

RECLASSIFICATION OF THE TENEBRIONOIDEA

The major morphological and ecological differences described above, and the extreme diversity in body form in both subfamilies, suggest that they have been evolving separately for a long time, and that the Tenebrionidae as now constituted are probably polyphyletic. Biogeographic evidence also lends tentative support to this conclusion. The Tenebrioninae, Alleculidae and Lagriidae enjoy a world-wide distribution, especially in the tropics. Contrastingly, the Tentyriinae, although widely distributed in temperate regions, are almost entirely absent from Australia and New Zealand, where a few tribes of the Tenebrioninae have radiated extensively into arid habitats. The few Australian genera previously included in the Tentyriinae have mostly been removed to other families (e.g., *Tretothorax*, *Zopherosis*: see Böving and Craighead, 1931; Crowson, 1955; Watt, 1966, 1967). These distributions suggest that the evolutionary line producing the Tenebrioninae arose before the separation of the Australian land mass. The Tentyriinae apparently differentiated after the separation of Australia, probably in southern Africa, which unquestionably supports the most diverse and distinct fauna now known (Koch, 1955).

If the correlated differences described above are to be reflected in the classification of the Tenebrionoidea, the Tenebrioninae, Alleculidae, Lagriidae and Nilionidae should be treated as a single taxon, coordinate with the Tentyriinae. I feel that these relationships are best reflected by recognizing a family Tentyriidae and placing the Alleculidae, Lagriidae, Nilionidae and Tenebrioninae as subfamilies of the Tenebrionidae. The Monommidae, which share most of the characters of the Tentyriidae are differentiated by having all the abdominal sternites flexibly connected by internal membranes and the front coxal cavities open, and should clearly be recognized at the family level. The proposed arrangement is compared with previous classifications in Table 1.

In addition, a number of tribes are incorrectly placed in the Tenebrioninae in recent classifications (Gebien, 1938-44; Arnett, 1960). According to the criteria described above, the Coniointini, Coelini, Branchini, Physogasterini, Praocini and Pimeliini are members of the Tentyriidae. Interestingly, all the early American workers agreed that these tribes belonged to the Tentyriinae (Blaisdell, 1939; Casey, 1908; Horn, 1870; LeConte and Horn, 1883). In addition the genera *Eupsophulus* Cockerell and *Alaephus* Horn, currently placed in the Tenebrioninae (Tenebrionini), clearly belong to the Tentyriidae, although their exact affinities are uncertain. Horn (1870) realized that these genera exhibited characteristics of both subfamilies and judged their classification as tentative.

It must be emphasized that the infrafamilial classification of these beetles remains in a confused state. The numerous tribes of the Tentyriidae are frequently very distinct and without intermediates (e.g., Stenosini, Triorophini, Nyctoporini). Conversely, while some of the tribes assigned to the Tenebrioninae are disjunct (e.g., Diaperini, Scaurini, Cossyphini), many are founded on superficial characters which have arisen independently many times (e.g., Coelometopini, which are distinguished from the Tenebrionini by being apterous).

Table 1. Comparison of classifications of the Tenebrionoidea.*

	Lacordaire, 1859	LeConte and Horn, 1883	Gebien 1937-44	Koch, 1955
Tentyriidae	Tenebrionides (Section I; Section II, Cohorte I, in part)	Tentyriinae, Asidinae	Tentyriinae, Asidinae & Coniontini, Praocini, Pimeliini, etc.	Tentyriinae
Tenebrionidae Tenebrioninae	Tenebrionides (Section II, Cohorte I, in part; Cohorte II)	Tenebrioninae	Tenebrioninae	Tenebrioninae
Alleculinae	Cistelides (=Alleculidae)	Cistelidae (=Alleculidae)	[Alleculidae]	[Alleculidae]
Lagriinae	Lagriides	Lagriidae	[Lagriidae]	[Lagriidae]
Nilioninae	Nilionides	[Nilionidae]	Leiochrini & [Nilionidae]	[Leiochrini & Nilionidae]

* The arrangement proposed here is listed on the left. The characters on which this classification is based are described fully in the text. The Monommidae, considered a distinct family by all workers, is not included. Names in brackets are not specifically mentioned in the works cited because these taxa were outside the geographic or taxonomic scope of the respective classifications.

AFFINITIES OF THE CONIONTINI, COELINI AND BRANCHINI

Say (1824) in his original description of *Eusattus reticulatus*, assigned it to *Zophosis* (Zophosini), an old world genus that is superficially similar. Subsequently, Casey (1908) speculated that the Branchini, Coniontini, Zophosini, Praocini and Nycteliinae comprise a closely related group which he designated the Coniontinae. LeConte and Horn (1883) and Champion (1884) also noticed the superficial similarity of the Branchini to *Praocis* and *Nyctelia*, and suggested a relationship to these South American tribes. In the present study, mouthparts, male and female genitalia, and internal thoracic structures were compared among the following taxa in order to reassess their interrelationships.

Coniontini

Coniontides latus LeConte

Coniontis viatica Eschscholtz

- Coniontellus inflatus* Casey
Coelotaxis punctulata Horn
Coelosattus fortineri Blaisdell
Eusattus robustus LeConte
 erosus Horn
 dubius LeConte
 reticulatus (Say)
 muricatus LeConte
- Coelini
- Coelus globosus* LeConte
 ciliatus Eschscholtz
 remotus Casey
Coelomorpha maritima Casey
- Zophosini
- Zophosis plana* Fabricius
- Praocini
- Praocis chiliensis* (Gray) (Det. L. E. Peña)
 penai Kulzer (Det. L. E. Peña)
 pilula Laporte (Det. L. E. Peña)
- Nycteliini
- Nyctelia varipes* Fairmaire (Det. L. E. Peña)
Gyriosomus modestus Kulzer (Det. L. E. Peña)
- Physogasterini
- Entomochilus varius laevis* Kulzer (Det. L. E. Peña)
- Branchini
- Branchus floridanus* LeConte
Branchus woodii LeConte
Oxinthas praocioides Champion

MOUTHPARTS

The mentum is typically large in most Tentyriidae, concealing the maxillae and ligula, which is usually membranous. In the Coniontini and Coelini the mentum is relatively small exposing the maxillae and ligula, which is always ventrally sclerotized and articulated with the mentum by a narrow membrane (Fig. 1). The labial palp hinges with a sclerotized palpifer which is embedded dorsally in the membrane above the ligular articulation. The only appreciable variation in these structures involves the size and pattern of the setae on the dorsal surface of the ligula. The coarse bristles shown in Fig. 1 are characteristic of several fossorial species of *Eusattus* as well as *Coelus*. In more generalized species of *Eusattus* and in *Coniontis* the ligular setae are much finer, more numerous and brush-like, as in *Branchus* (Fig. 2). In general shape and morphology the labial structure of *Branchus* shows no important differences from the Coniontini.

The mentum of the Physogasterini and Praocini is relatively smaller, compared to the ligula, which is articulated by a broad membranous band (Fig. 3). Portions of the ventral surface of the ligula are usually membranous, especially in the Praocini. The greatest divergence from the Coniontini involves the insertion of the labial palps. Whereas these are attached dorsally to sclerotized palpifers in the Coniontini they are articulated with the ventral (external) surface of the ligula in the Praocini and Physogasterini, and the palpifer is absent. The labial structure is very similar in the Nycteliini, but in *Nyctelia* the ligula

is relatively small and retracted beneath the mentum. In *Gyriosomus* the ligula is large and protuberant, as in the Praocini.

The mouthparts of *Zophosis* (Fig. 4) are distinctly tentyrioid in structure. The mentum is large, concealing the ligula and the maxillae. The membranous ligula is relatively small, with the labial palps articulated dorsally. The palpifer is absent. A similar structural arrangement occurs in many other tribes of Tentyriidae, including the Tentyriini, Adesmiini, and Triorophini. *Zophosis* also differs from the other taxa considered here in the structure of the maxilla. In these other tribes, the lacinia is bidentate, and the galea brush-like. In *Zophosis*, both lacinia and galea are densely setate and brush-like.

GENITALIA

The aedeagus and penis of most Tentyriidae are simple fusiform tubes (Koch, 1955). This structure is exemplified by the Coniontini and Coelini. In these tribes the tegmen consists of lateral struts, connected proximally. The sclerotized parts of the penis are narrow, lateral rods (Fig. 5, 6). In *Branchus floridanus* (Fig. 7, 8) the tegmen is a sclerotic tube, with only a small ventral membrane (the homologous membrane is dorsal in the Tenebrionidae). The paramere is strongly ridged proximally, and is apically truncate, with sharp lateral spurs. The penis is exceptionally elongate and distally curved and enlarged. The functional significance of these remarkably modified structures is unknown. In *Branchus woodii* and *Oxinthas* the male genitalia are essentially similar to those of the Coniontini. The Praocini, Nycteliini and Physogasterini are very similar to the Coniontini in respect to male genitalia, with minor differences in the degree of sclerotization and shape and proportions of the aedeagus and penis. It may be significant that the aedeagus bears lateral, subterminal patches of setae in all four tribes. The aedeagus and penis of *Zophosis* (not illustrated) are relatively much shorter and thicker and lack the subterminal setae.

Female genitalia in these beetles consist of an elongate 1st valvifer and short, distally spatulate and strongly sclerotized 2nd valvifer (Fig. 9-11). The 2nd valvifer is distally modified as a sclerotized process in many Tentyriidae (e.g., Adesmiini, Asidini, Cryptoglossini), probably for penetrating the oviposition substrate, and frequently the ovipositor tube is very elongate as compared to that of the Tenebrionidae. In the Coniontini, Coelini and Branchini the 1st valvifer is a weakly sclerotized plate with a marginal baculus (Fig. 9). The second valvifer is continuously sclerotized, with the distal process oriented horizontally. A subterminal membranous area marks the position of the gonostylus, which is recognizable as a group of elongate setae. This configuration is nearly constant throughout these tribes, the only significant variation involving size and slight differences in shape. The ovipositor is similar in the Praocini, Physogasterini and *Nyctelia* (Fig. 10) with the following differences. The ovipositor tube is usually more elongate and the baculus of the 1st valvifer is submarginal. The 2nd valvifer is oriented obliquely or nearly vertically and bears a sulcus about two-thirds of the distance to the base. Two features shared with the Coniontini are the setal clothing of the 2nd valvifer and the median, ventral sclerite situated in the membrane between the 2nd valvifers. In *Gyriosomus* (Nycteliini) the entire ovipositor is densely setate, the sulcus on the 2nd valvifer is very strong, and the median ventral sclerite is absent.

The ovipositor of *Zophosis* (Fig. 11) is relatively short and thick. Both valvifers are densely setate and the 2nd valvifer consists of a basal sclerotized plate and baculus with a narrow, lateral sclerotization articulating with the strongly sclerotized, terminal process. There are no suggestions of the gonostylus or the median, dorsal sclerite.

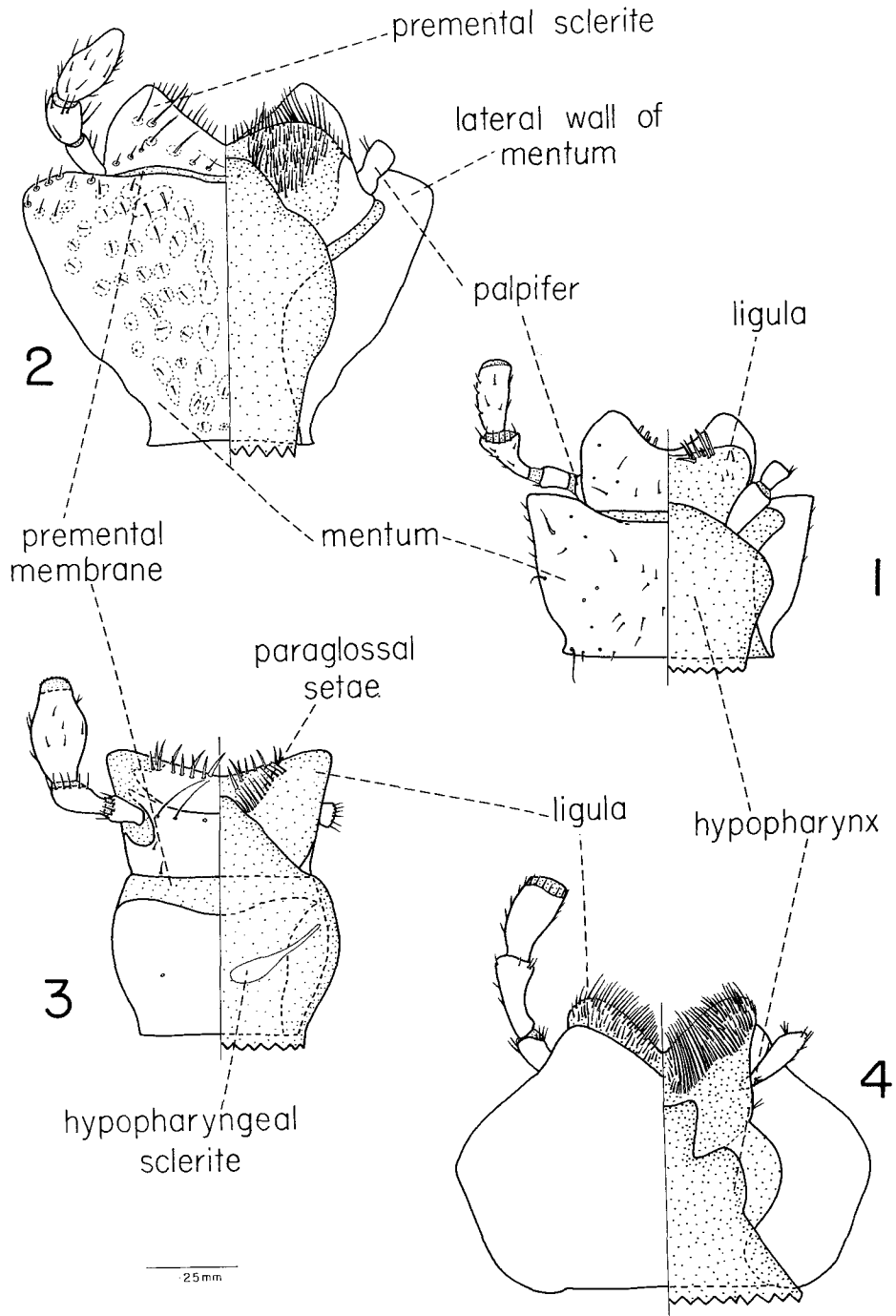


Fig. 1-4. Labial structures. The left side of each figure represents the ventral (external) surface. The right side represents the dorsal (internal) surface. 1, *Eusattus muricatus*; 2, *Branchus floridanus*; 3, *Praocis penai*; 4, *Zophosis plana*.

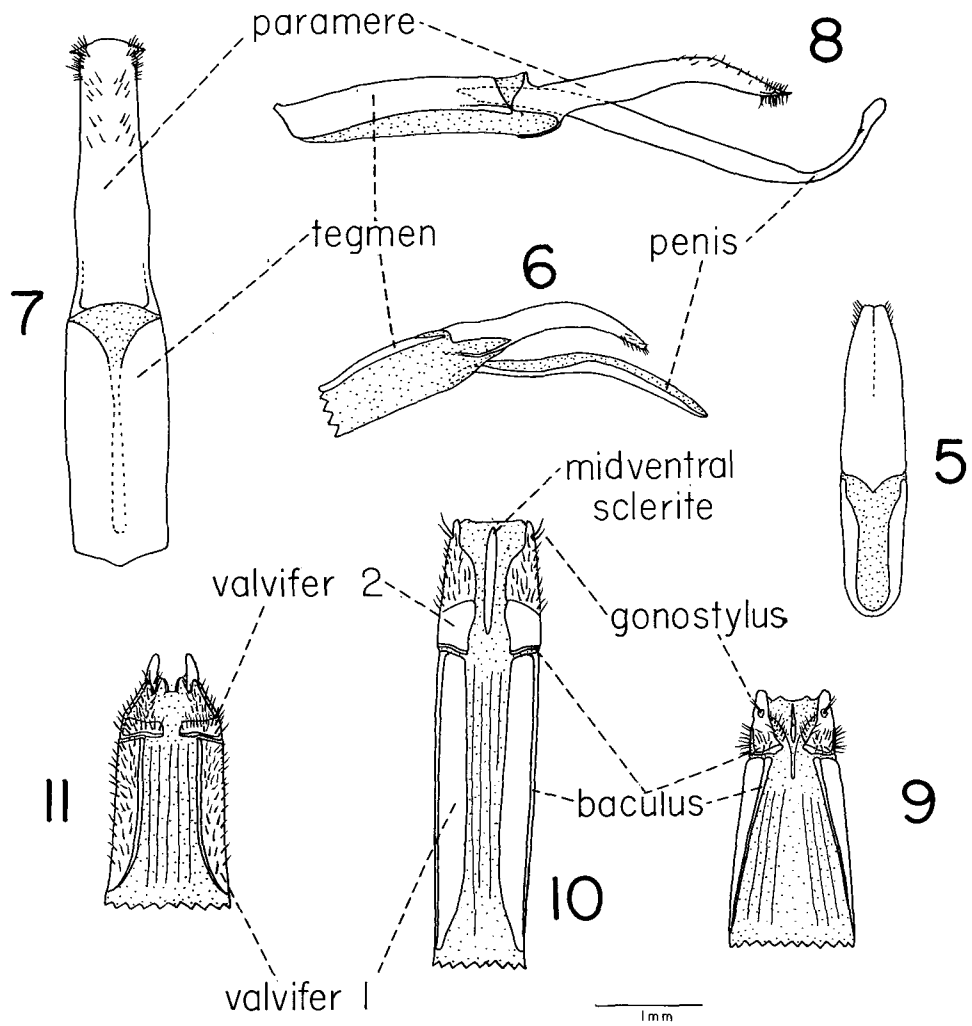


Fig. 5-8. Male genitalia. 5, *Eusattus reticulatus*, ventral aspect of aedeagus; 6, *Eusattus reticulatus*, lateral aspect of aedeagus and penis; 7, *Branchus floridanus*, ventral aspect of aedeagus; 8, *Branchus floridanus*, lateral aspect of aedeagus and penis. Fig. 9-11. Ventral aspect of ovipositors. 9, *Eusattus dubius*; 10, *Fraocis penai*; 11, *Zophosis plana*.

INTERNAL THORACIC STRUCTURE

Flightless tenebrionids and tentyriids illustrate extreme modifications of thoracic structure. Smith (1964) described reductions of flight musculature and the accompanying desclerotization and reduction in size of the metathoracic terga in a number of micropterous and apterous beetles. However, most of his examples appear to represent relatively early stages in the specialization for ambulatory life. Many groups of Tentyriidae have apparently been apterous for a very long time. In these the metanotum is completely membranous and the mesonotum is reduced to a narrow, leathery, transverse sclerite which extrudes externally as the scutellum. In highly modified forms (e.g., *Edrotes*, *Epiphysa*; Doyen, 1968) the mesonotum is further reduced, with no external indication of the scutellum, and the mesosterna and prosterna are fused by cuticular extensions of the sternal apophyses. These specializations are usually accompanied by elongation and thickening of the metendosternite, which frequently becomes fused with the mesocoxal inflexions and the mesopleura, especially in fossorial species.

Most of the skeletal adaptations described above are represented in the taxa discussed here. In the Coniointini, Coelini and Branchini the arms of the metendosternite are extremely elongate and approximated to the mesocoxal inflexions, or fused to the inflexions in more highly modified species (Fig. 12, Table 2). The arms extend to the vicinity of the mesepisterna, terminating in muscle disks which are fused with the episterna in the most specialized species. The mesapophyseal arms are relatively short, and may be expanded as vertically oriented flanges in fossorial species (Fig. 12). Structural details of the pterothorax of various species of these tribes are summarized in Table 2.

The Praocini, Nycteliini and Physogasterini share a distinct thoracic structure. The arms of the metendosternite are broadly fused with the mesocoxal inflexions, but terminate as short prongs without terminal muscle disks, and never approach the mesopleura (Fig. 13). The elongate, slender arms of the mesendosternite extend dorsolaterally almost to the dorsal margin of the mesepisternum. In *Nyctelia* and *Gyriosomus* the mesothorax and prothorax are rigidly joined by strong, ligamentous thickenings of the intersegmental membrane, while in *Praocis* and *Entomochilus* the prothorax is relatively mobile as in the Coniointini.

The thoracic modifications of *Zophosis* (Fig. 14) are strikingly similar to those of *Adesmia* and *Epiphysa* (see Doyen, 1968). The metendosternite is fused with the mesocoxal inflexions and the arms extend anterodorsally to the mesopleura, terminating in large muscle disks, but are not fused with the mesopleura. The mesendosternite consists of short, horizontal arms with large terminal muscle disks which are opposed to similar disks formed by the proapophyseal arms. The prothorax is attached to the pterothorax by a stout, ligamentous membrane, permitting little flexibility.

Zophosis has some other noteworthy structural modifications. The anterior three abdominal sternites, which are connate in all tenebrionids, are rigidly fused with the metasternum by continuous cuticular bands laterad of the metacoxal cavities. The pterothorax and abdomen thus become a single, rigid unit. In all other Tentyriidae, Tenebrionidae and other Coleoptera which have been examined, the mesothoracic-abdominal articulation is flexible, although in most apterous tenebrionids movement is prevented by interlocking joints between the elytra and the abdominal sternites and thoracic pleurites. In *Zophosis* there is a pair of sclerotized, dorsolateral projections from the region of the lateral metacoxal articulations. The function of these projections, which are unique among known Coleoptera, is uncertain, but they may help secure the elytra against the abdominal sternites.

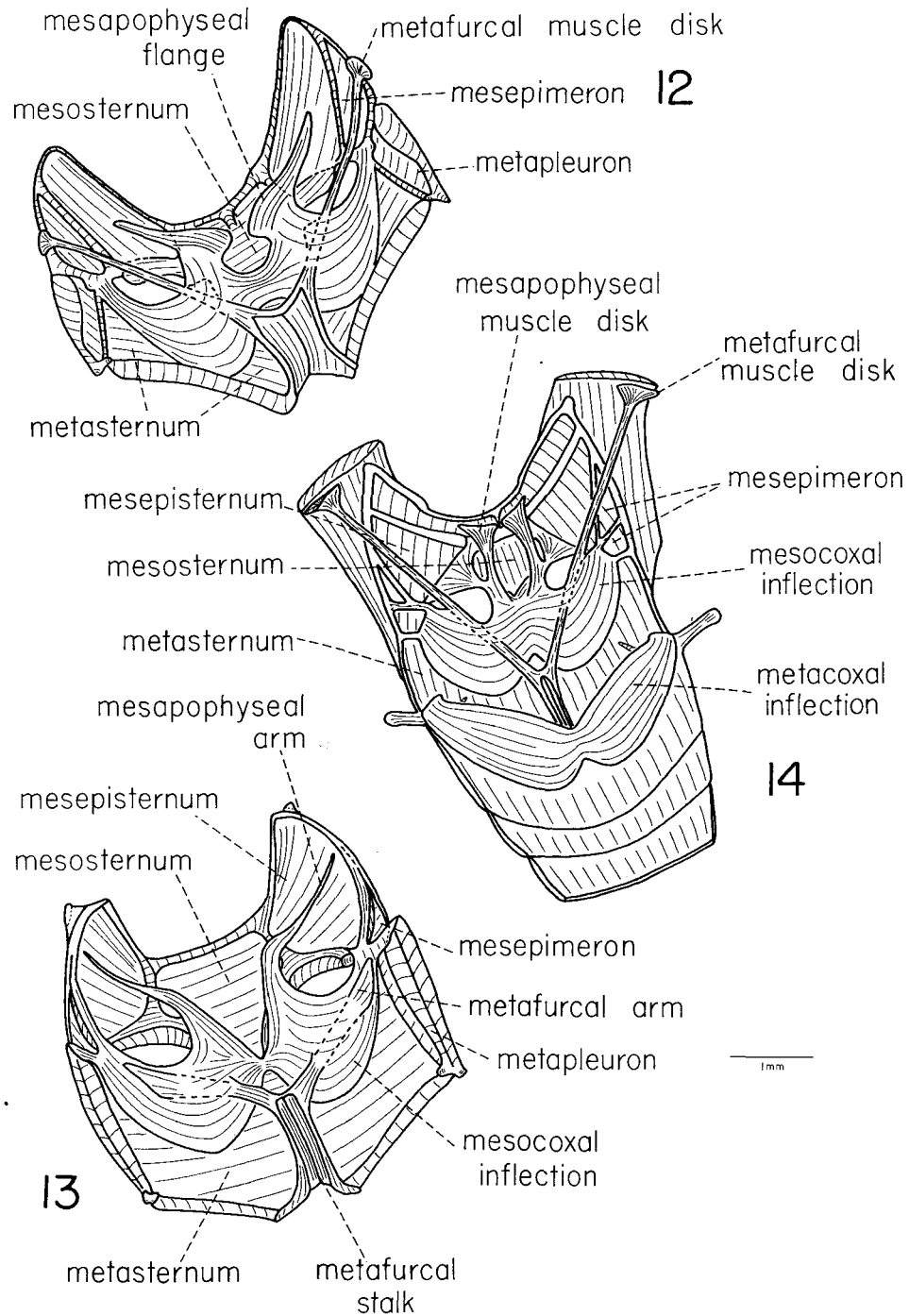


Fig. 12-14. Internal thoracic structures. The figures are from an oblique posterodorsal aspect, with the thoracic nota and dorsal abdominal membranes removed. 12, *Coelosattus fortineri*; 13, *Praocis penai*; 14, *Zophosis plana*.

Table 2. Comparison of certain thoracic features among selected species of Coniontini.*

	mentendosternite			mesapophyseal arms	
	(a) mesocoxal fusion	(b) muscle disks	(c) mesopleural fusion	(d) length	(e) basal flange
<i>Coelus ciliaris</i>	-	-	-	-	-
<i>Coelomorpha maritima</i>	-	-	-	-	-
<i>Coniontellus obesa</i>	-	-	-	-	-
<i>Coelotaxis punctulata</i>	-	+	-	-	-
<i>Coniontides latus</i>	-	+	-	-	-
<i>Coniontis viatica</i>	-	+	-	-	-
<i>Branchus floridanus</i>	-	+	-	+	-
<i>Oxinthas praocioides</i>	-	+	-	+	+
<i>Eusattus dubius</i>	-	+	+	-	-
<i>robustus</i>	-	+	+	+	-
<i>erosus</i>	-	+	+	+	-
<i>reticulatus</i>	-	+	+	+	+
<i>muricatus</i>	+	+	+	+	+
<i>Coelosattus fortineri</i>	+	+	+	+	+

*(a) Arms of metendosternite fused with mesocoxal inflection (+) or free (-); (b) arms terminated as enlarged muscle discs (+) or unmodified (-); (c) muscle disks fused with mesopleuron (+) or free (-); (d) mesapophyseal arms short, thick, extending no more than 1/2 the distance to the mesepisternal process (+) or more slender and extending at least 1/3 the distance to the mesepisternal process (-); (e) mesapophyseal arms expanded as flattened flanges basally (+) or unmodified (-). Taxa are arranged in order of increasing specialization, which has occurred in two ways. In *Branchus* and *Oxinthas*, the mesapophyseal arms are shortened and flanged, while the metafurcal arms are unmodified. Conversely, in all *Eusattus* the metafurcal arms are subject to fusions with other thoracic structures, while the mesapophyseal arms are modified only in fossorial species. Specialization in internal thoracic structures is not always concordant with trends in other characteristics. For example, the protarsi and antennae of *Coelus* and *Coelomorpha* are highly specialized for burrowing (Fig. 19-20).

Externally, *Zophosis* shows some other puzzling structural features. The metepisterna, which are separated from the metasterna by membranous clefts in winged Coleoptera, have apparently coalesced with the sterna. A pair of oblique grooves arising near the lateral metacoxal articulations and terminating near the mesocoxal inflections may represent the metepisternal sutures, but more likely are secondary grooves which strengthen

the metasternum. *Zophosis* also has a pair of "oblique sutures" running anterolaterad from the intercoxal process. These probably strengthen the metasternum. None of the beetles discussed here possess antecoxal grooves, which are almost universally present in winged forms. The antecoxal grooves run from the medial metacoxal articulation to the lateral metacoxal articulation, and probably reinforce the posterior sternal region.

The evidence described above indicates close affinities between geographically related taxa, but does not clarify the relationships among taxa in different zoogeographic regions. *Zophosis* shows clear relationships to *Adesmia* and *Epiphysa*, all inhabiting Africa and southern Eurasia. *Nyctelia*, *Gyriosomus*, *Praocis* and *Entomochilus*, all endemic to South America, share a strong structural consistency, particularly in internal thoracic features. Likewise the Coniontini, Coelini and Branchini (North America) are very similar morphologically. Intermediate forms between the African, South American and North American taxa are unknown, and the adaptations of each of these groups are so different that it is premature to speculate upon their affinities.

CLASSIFICATION OF THE CONIONTINI, COELINI AND BRANCHINI

Current tribal and generic classifications of these beetles largely follow the arrangement of Casey (1908, 1924) which emphasizes external differences in leg and antennal structure and size and shape of the epipleura. These features are variously modified to facilitate burrowing, and intermediate forms sometimes relate the specialized, fossorial species to the more generalized, ambulatory ones. This is especially evident in Casey's group *Eusattis*, as recognized by Triplehorn (1968), who synonymized all Casey's genera under *Eusattis*, greatly simplifying the previously arbitrary and unworkable classification. Several other generic and tribal changes are proposed here, based on adult characteristics. Larval features are largely concordant, and will be described elsewhere.

As indicated above, the morphological features of coniontine tentyriids strongly reflect their mode of life. Most species of *Coniontis* dwell on substrate surfaces, and the body is oval and relatively elongate. The arms of the metendosternite are elongate, but not fused with the mesocoxal inflexions (Table 2). *Coelotaxis*, distinguished by an elongate basal protarsomere and "minute" scutellum, is extremely similar to *Coniontis* in all other external and internal characters. There is considerable variation in the tarsal character, and some individuals are scarcely distinguishable from *Coniontis* (Fig. 15-18). Furthermore, the scutellum is relatively large, but is frequently hidden by the pronotum in pinned specimens. Therefore, *Coelotaxis* is placed as a synonym of *Coniontis*. *Coniontellus* is differentiated from *Coniontis* by having the eyes completely divided by a median canthus. However, there is considerable interspecific variation in the degree of constriction of the eyes in *Coniontis*, and in some specimens of *Coniontellus* the eyes are not completely divided. *Coniontides* and *Conisattus* differ from *Coniontis* only in minor body proportions. These three genera are also placed as synonyms of *Coniontis*. Detailed revisionary studies of *Coniontis* may show that some of these names should be recognized as subgenera, but even in the expanded sense proposed here *Coniontis* is much more monomorphic than *Eusattis* or *Praocis*.

The species of *Eusattis* are usually stouter bodied than *Coniontis*, and several are highly modified for burrowing in aeolian sand (*E. muricatus*, *E. ciliatus* Horn, *E. puberulus* LeC.). Within *Eusattis* (*sensu* Triplehorn) the degree of modification of internal thoracic structure ranges from the generalized condition in *E. dubius* to that in *E. muricatus* (Table 2). *Coelotaxis*, which was placed in the Coelini by Blaisdell (1927), differs from *E. muricatus* chiefly in having broadly expanded protibiae (Fig. 22-23) and strongly arcuate middle and hind

tibiae. It lacks the specialized tarsal and antennal characters of the Coelini, while the specialized internal thoracic structure (Fig. 12) is nearly identical to that of *E. muricatus*. The thoracic structure of *Coelus* and *Coelomorpha* is similar to that of *Coniontis*. For these reasons, *Coelosattus* is placed as a synonym under *Eusattus*.

The Coelini comprise a small, monomorphic group of fossorial species restricted to maritime sand dunes along the Pacific coast of North America. Superficially they greatly resemble certain species of *Praocis* (e.g., *P. pilula*), but show distinct differences in mouthparts and internal thoracic structures, as described earlier. The most important characters differentiating the Coelini from the Coniontini are the enlarged, spatulate basal protarsomeres (Fig. 19, 20) and the extremely short antennae. In all other characters they greatly resemble the Coniontini, particularly the fossorial species of *Eusattus*. That they apparently evolved independently, perhaps from *Coniontis*, is indicated by the generalized nature of the internal thoracic structures (Table 2). However, the general similarity to the Coniontini suggests that the Coelini should not be recognized as a separate tribe. This classification was also favored by LeConte (1866), LeConte and Horn (1883) and Horn (1870). One further point concerns the genera *Coelus* and *Coelomorpha*, which show very similar modifications in protarsal and antennal structure, but differ in the number of antennal segments (10 in *Coelomorpha*; 11 in *Coelus*). Because of their overall similarity, I propose that *Coelomorpha* be placed in synonymy under *Coelus*.

The Branchini were originally differentiated from the Coniontini by LeConte (1862). He felt that the anteriorly confluent gular sutures and abrupt basal expansion of the epipleura indicated an affinity to the Nycteliini and Praocini, respectively. Later, LeConte (1866:113) realized that most of the character states he used to separate these tribes were represented in the single genus *Eusattus*, and he suggested that the Nycteliini, Praocini and Branchini should possibly be placed in synonymy under the Coniontini. LeConte was unaware of the internal thoracic differences of the first two tribes, but his judgement concerning the Branchini was undoubtedly correct. The only major structural feature differentiating the Branchini is the absence of the submental sclerite (Fig. 24). However, the submentum is very small in some *Eusattus* (Fig. 25). For these reasons the Branchini are placed in synonymy under the Coniontini.

The taxonomic changes proposed here are intended to consolidate the classification of the Coniontini so that the degree of variation encompassed is similar to that of other differentiated tribes, such as the Adesmiini, Zophosini, Praocini and Eleodini. Extensive elucidation of the generic and tribal relationships will be necessary before the patterns of variation and affinity in the Tenebrionidae and Tentyriidae can be used to reach more general evolutionary and biogeographic conclusions.

The proposed taxonomic changes are summarized in the following checklist.

Tribe Coniontini

Coniontini Lacordaire, 1859:218; Horn, 1870:291; LeConte and Horn, 1883:371; Casey, 1908:55.

Coelini Casey, 1908:150.

Branchini LeConte, 1862:222.

Body stout, oval to subglobose, apterous. Mentum small, trapezoidal, weakly emarginate anteriorly; ligula large, sclerotized, projecting anteriorly beyond mentum; labial palps inserted dorsally on distinct palpifers; maxillae exposed laterad of labium, lacinia dentiform. Metendosternite with arms elongate, extending to region of metapleural wing process. Ovipositor with 1st valvifers elongate, weakly sclerotized; 2nd valvifers prolonged posteriorly

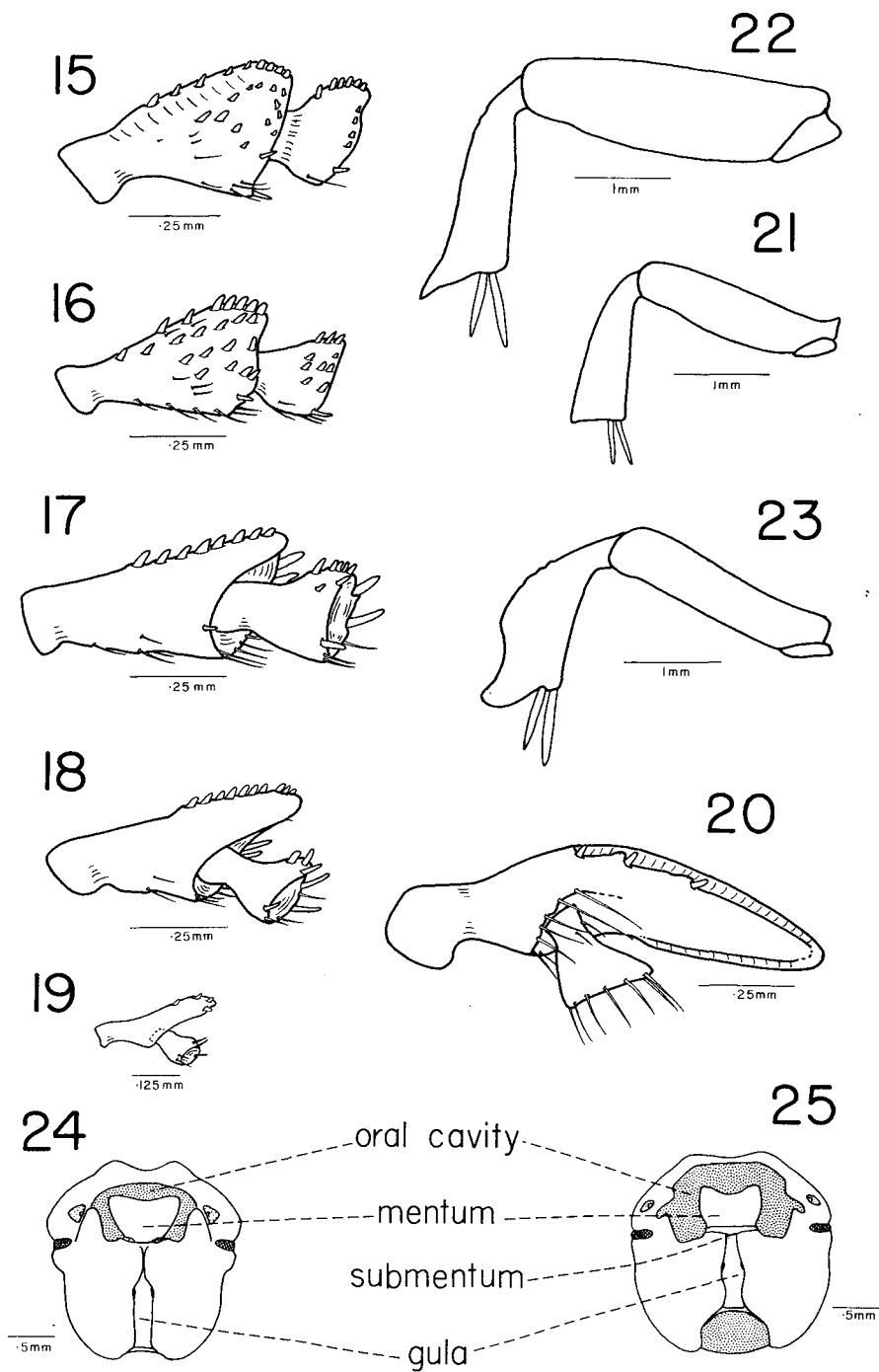


Fig. 15-20. Basal tarsomeres of forelegs, posteroventral aspect; 15, *Coniontis hoppingi* Blaisdell; 16, *Coniontides latus*; 17, 18, *Coelotaxis punctulata*; 19, *Coelomorpha maritima*; 20, *Coelus globosus*. Fig. 21-23. Posterior aspect of forelegs; 21, *Coniontides latus*; 22, *Eusattus reticulatus*; 23, *Coelosattus fortineri*. Fig. 24-25. Ventral aspect of crania; maxillae, mandibles, ligula and clypeus excised; 24, *Oxinthas praocioides*; 25, *Eusattus muricatus*.

as strongly sclerotized, spatulate prongs; gonostyli represented by several elongate setae inserted in membranous foramen situated medially on 2nd valvifers. Aedeagus inverted; tegmen with variable desclerotized area posteroventrally; paramere longer than tegmen, bearing several lateral setae at apex.

Coniontis Eschscholtz, 1829. Type species: *Coniontis viatica* Eschscholtz, Casey designation, 1908:57.

syn. *Coniontellus* Casey, 1890. Type species: *Coniontis obesa* LeConte, 1851, Casey designation, 1908:57.

syn. *Coniontides* Casey, 1908. Type species: *Coniontis lata* LeConte, 1866, by original designation, p. 57.

syn. *Conisattus* Casey, 1908. Type species: *Conisattus rectus* Casey, 1908:57, monobasic.

syn. *Coelotaxis* Horn, 1876. Type species: *Coelotaxis punctulata* Horn, 1876, Casey designation, 1908:57.

Eusattus LeConte, 1851.¹ Type species: *Eusattus difficilis* LeConte, 1852, Casey designation, 1908:56.

syn. *Eusattodes* Casey, 1908. Type species: *Eusattus laevis* LeConte, 1866, Casey designation, 1908:56.

syn. *Megasattus* Casey, 1908. Type species: *Eusattus erosus* Horn, 1870, by original designation, p. 56.

syn. *Nesostes* Casey, 1908. Type species: *Eusattus robustus* LeConte, 1866, by original designation, p. 56.

syn. *Sphaeriontis* Casey, 1908. Type species: *Eusattus muricatus* LeConte, 1851, by original designation, p. 56.

syn. *Coelosattus* Blaisdell, 1927. Type species: *Coelosattus fortineri* Blaisdell, 1927, monobasic.

syn. *Discodemus* LeConte, 1862. Type species: *Zophosis reticulata* Say, 1824, monobasic.

syn. *Conipinus* LeConte, 1862. Type species: *Eusattus dubius* LeConte, 1851, Gebien designation, 1938:284.

Coelus Eschscholtz, 1829. Type species: *Coelus ciliatus* Eschscholtz, 1829, monobasic.

syn. *Coelomorpha* Casey, 1890. Type species: *Coelomorpha maritima* Casey, 1890, Casey designation, 1908:151.

Branchus LeConte, 1862. Type species: *Branchus floridanus* LeConte, monobasic.

Oxinthas Champion, 1892. Type species: *Oxinthas praecioides* Champion, monobasic.

Anectus Horn, 1866. Type species: *Anectus vestitus* Horn, monobasic.

Detailed keys to species will be presented in future revisionary work on each genus. The genera are keyed below.

Key to the genera of Coniontini

1. Submentum clearly defined, though sometimes small, transverse (Fig. 25) 2
- Submentum extremely small, invisible externally (Fig. 24) 4
2. Basal protarsomere truncate or with process shorter than second tarsomere (Fig. 15-18) 3

¹ Generic synonymy for *Eusattus* is adapted from Triplehorn (1968) with the addition of *Coelosattus* Blaisdell.

- Basal protarsomere extending beyond second tarsomere as spatulate process (Fig. 19-20) *Coelus*
- 3. Protibia abruptly expanded apically as an acute process (Fig. 22-23) *Eusattus*
- Protibia gradually enlarged apically (Fig. 21) *Coniontis*
- 4. Intercoxal process of abdomen broadly rounded 5
- Intercoxal process of abdomen rectangularly truncate² *Anectus*
- 5. Protibia abruptly expanded apically as a short, acute process *Branchus*
- Protibia gradually enlarged apically *Oxinthas*

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² This couplet compiled from Horn, 1866.

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