

A revised subfamily classification of Tenebrionidae (Coleoptera)

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Existing classifications of Tenebrionidae are reviewed briefly. The inclusion of the families Alleculidae, Lagriidae, and Nilionidae in Tenebrionidae is confirmed. The splitting off from this complex of a family, Tentyriidae, by Doyen is discussed and rejected. Various taxa which had been included in Tenebrionidae are excluded, amongst which *Syrphetodes*, *Brouniphylax*, *Exohadrus*, *Arthropus*, *Cotulades*, *Docalis*, and *Latometus* (= *Elascus*) have not previously been formally excluded. A new family, **Archeocrypticidae**, is established and defined briefly for *Archeocrypticus*, *Sivacrypticus*, and *Enneboeus*.

Data from matrices based on adult and larval characters comparing Tenebrionidae with most other families of Tenebrionoidea (=Heteromera) are presented for derived characters in common, and for overall similarity. The families most closely related to Tenebrionidae according to these data are Zopheridae, Chalcodryidae, Merycidae, Archeocrypticidae, Synchronidae, Colydiidae, and Monommatidae; none is very close to Tenebrionidae, which has had a long independent history.

Characters of the subfamilies recognised are tabulated, and interpreted in a phylogenetic dendrogram. Phylogeny is discussed in relation to adaptive changes in the biology of the various subfamilies, which are Zolodininae new subfamily, Pimeliinae new sense (including Tentyriinae), Toxicinae new sense, Phrenapatinae new sense (including Archeoglenini new tribe), Diaperinae new sense, Gnathidiinae, Tenebrioninae new sense, Alleculinae, Nilioninae, Lagriinae new sense, Cossyphinae, and Cossyphodinae new status.

Biology, economic importance, copulation, orientation of the aedeagus, and distribution are discussed briefly.

Definitions of the family and subfamilies and a key to subfamilies are given, and keys to tribes are included for the smaller subfamilies. The previously unknown larvae of the genera *Zolodinus*, *Menimus*, *Archeoglenes*, *Lepisilus*, and *Nyctoporis* are described in detail. Pupae of *Zolodinus* and *Nyctoporis* are described. Keys to larvae include many other genera which were hitherto unknown or poorly known.

INTRODUCTION

The family Tenebrionidae is one of the largest in the animal kingdom, comprising approximately 15 000 described species (considerably exceeding the known species of birds). Great superficial diversity is exhibited by adult tenebrionids, and some are often wrongly identified in preliminary sorting as they closely resemble members of other families (e.g., Carabidae, Chrysomelidae). Larvae tend to be more uniform and easily recognisable superficially, although they also include some highly specialised and aberrant forms.

Relatively few Tenebrionidae are of great economic importance (notably the stored products pests and the false wireworms of arid and semi-arid areas). Perhaps because of this, the family has attracted less attention than the other vast families of Coleoptera (Curculionidae, Chrysomelidae, Carabidae, etc.). Most systematic work has been at the specific and generic levels, and few have attempted to improve the higher classification within the family. This still largely comprises a synthesis of the classifications of Lacordaire (1859) and Leconte & Horn (1883), which were based entirely on adults.

There is a marked lack of congruence between classifications based on adults (e.g., Reitter 1917, Gebien 1937-44, Koch 1955, Arnett 1963) and those based on larvae (e.g., Schiödt 1878, van Emden 1947, Skopin 1964a). Larval classifications appear on the whole to be more satisfactory, partly because useful larval characters are more obvious, and partly because larvae have been studied rather less superficially than adults. Existing classifications of Tenebrionidae were reviewed critically by Watt (1966), and a classification based largely on Skopin's system, but including Lagriidae and Nilionidae, was favoured.

Doyen (1972) has proposed a subfamily classification of "Tenebrionoidea" (= Tenebrionidae, Alleculidae, Lagriidae, Nilionidae, and Monommidae of Crowson 1955) which is similar to that of Koch (1955) in dividing traditional Tenebrionidae into two major groups. One of these Doyen elevates to family rank (Tentyriidae). In his Tenebrionidae he includes the remaining Tenebrionidae of Gebien (1937-44) (in a single subfamily, Tenebrioninae), and the old families Alleculidae, Lagriidae, and Nilionidae (as subfamilies). The inclusion of these last three groups in Tenebrionidae was suggested by Skopin (1964a), and proposed by Watt (1965, 1966). Doyen justifies his elevation of Tentyriidae to family rank on the following adult characters: absence of visible intersegmental membranes between visible sternites 3, 4, and 5 (except in Pimeliini); inverted aedeagus; and absence of abdominal defensive ("repugnatorial") glands. In his Tentyriidae the larval mandibles each have a membranous dorsolateral elevation bearing numerous coarse setae; in other Tenebrionidae having such an elevation there are only a few setae, as noted by Watt (1966).

Cossyphini lack visible intersegmental membranes between the abdominal sternites and lack defensive glands, but the aedeagus is normally orientated (as noted by Doyen). In the Amarygmini [regarded as Tenebrioninae by Leconte & Horn (1883), Gebien (1937-44), Koch (1955), and others] the aedeagus is inverted, but there are exposed intersegmental membranes between visible abdominal sternites 3, 4, and 5 (Ardoin 1962), and abdominal defensive glands are present. In the new subfamily Zolodininae (not studied by Doyen) the aedeagus is inverted, abdominal defensive glands are absent, and the membranes between the visible abdominal sternites are concealed, but the larva has no membranous, dorsolateral setose elevation on the mandibles, or any other character which would associate it with larvae of Tentyriinae rather than with other Tenebrionidae. In the tribe Dysantini, abdominal intersegmental membranes are concealed but the aedeagus is not inverted (*see* Table 3).

Thus, the distinction between Doyen's Tentyriidae and Tenebrionidae is not as clear-cut as he believed. Doyen's Tentyriidae is almost exactly equivalent to my Pimeliinae (Pimeliariae Latreille, [1802] having priority over Tentyrites Solier, 1834). As this group is not equivalent to the Tentyriinae of any of the earlier authors, because it includes Pimeliini and Platyopini, the change of name is, if anything, desirable. Doyen has made a major contribution to understanding of tenebrionid classification by emphasising the importance of the presence or absence of defensive glands.

The present classification is based on both adults and larvae. Although perhaps not entirely satisfactory, it should at least provide a sounder basis than has been available in the past on which to build a consistent phylogenetic classification. It is compared with Doyen's and Skopin's classifications in Table 1.

With such an enormous number and diversity of species, it was obviously not possible to examine more than a small fraction of the known world fauna in detail. Any shortcomings of the classification proposed here are due in part to my reliance on published

TABLE 1—Comparison of classifications of Tenebrionidae (*Groups not mentioned by Doyen, but which from the references to other classifications in his table 1 may be inferred to be included in his Tenebrioninae)

This paper	Doyen 1972	Skopin 1964a
Zolodininae	*[not mentioned]	[not mentioned]
Toxicinae	*[not mentioned]	[not mentioned]
Diaperinae	*[not mentioned]	Diaperimorpha (part)
Gnathidiinae	*[not mentioned]	[not mentioned]
Phrenapatinae	*[not mentioned]	Phrenapatimorpha
Tenebrioninae	Tenebrioninae (part)	Tenebrimorpha + Blapimorpha + Ulomimorpha (part)
Alleculinae	Alleculinae	Ulomimorpha (part)
Lagriinae	Lagriinae	Pycnocerimorpha + Lagriidae
Nilioninae	Nilioninae	Nilionidae
Pimeliinae	Tentyriidae	Tentyromorpha + Asidomorpha
Cosyphinae	Tenebrioninae (part)	[not mentioned]
Cosyphodinae	*[not mentioned]	[not mentioned]

information for the placing of genera which I was not able to examine in cleared preparations, as larvae, or at all.

All taxa mentioned in the text are listed in a terminal index for ease of reference.

MATERIALS AND METHODS

Larvae and adults of Tenebrionidae and related families were macerated in hot 10% caustic potash (KOH) solution, dehydrated in glacial acetic acid, cleared in beechwood creosote, and mounted in Canada balsam. Large specimens were stored in glycerol after dehydration. Wings of adults were detached and then macerated in cold KOH solution, as hot KOH renders flecks and even venation invisible. Adult mouthparts and one antenna were removed and mounted separately under an unsupported coverslip, and the rest of the beetle was pulled apart (by separating head, prothorax, meso- and metathorax, and abdomen from each other, removing elytra, one front coxa, and meso- and metanota, and exserting genitalia) and mounted in a cell on a slide or placed in glycerol. Larval mandibles, labrum-epipharynx, and often part of the abdominal wall containing spiracles were mounted separately under an unsupported coverslip, the head was detached and mounted dorsal side up, and the body was mounted on its side in a cell.

Certain structures, such as larval spiracles, epipharynges, and hypopharynges and adult metendosternites, procoxal cavities, and mouthparts, can be seen accurately only in cleared specimens. The keys and definitions were based as far as possible on study of both whole and cleared material. The detailed structure of larval spiracles, which is of considerable value in classification, can often be appreciated only under a compound microscope, at a fairly high magnification ($\times 100$ – 400), although peripheral air-tubes and crenulations are usually easily seen in whole specimens with a stereoscopic microscope.

All drawings were made with the aid of a squared eyepiece graticule or a camera lucida. Cleared convex structures were usually drawn before mounting, but wings and flat mouthparts were drawn after mounting.

Some of the material examined was collected or reared by me, but most was borrowed or received in exchange from museums and individuals (*see Acknowledgments*).

In addition to the specimens studied in detail, many adults and larvae were examined superficially to check the validity of the externally visible characters used in keys and definitions. It was possible to examine only a fraction of adults of the known genera, but at least one member of each tribe of the classifications set out in standard catalogues was examined (except for a few small tribes of Pimeliinae).

In lists of larvae examined, H.W. = head width.

No attempt was made to study non-chitinised structures ('soft parts') comparatively, although a few dissections were made. It has been shown (e.g., Watt 1971, 1974) that the chitinised internal parts of the female genitalia may provide very useful taxonomic characters, especially above the generic level. However, too few taxa have yet been examined to include female genitalia in the diagnoses and descriptions.

LIMITS OF TENEBRIONIDAE

Perhaps because of the superficial diversity of Tenebrionidae, they were grouped into several families by such pioneers of family classification as Latreille [1802]. The "Tenebrionides" of Lacordaire (1859) coincides fairly closely with the usual traditional view of the family. Lacordaire included in his "Famille Tenebrionides" a "Tribu Zopherides", and the genera *Boros* and *Penthe*, which have subsequently been shown by Böving & Craighead (1931) to have larvae differing in several important respects from tenebrionid larvae. However, *Boros* and Zopherini were still included in the latest world catalogue of Tenebrionidae of Gebien (1937-44). Studies of adults have confirmed the necessity for removing these taxa from Tenebrionidae (Crowson 1955).

Since Lacordaire, other extraneous, tenebrionid-like beetles were included in Tenebrionidae and listed there in Gebien's world catalogue. St. George (1939) established a family, Perimylopidae, for *Perimylops* and *Hydromedion*, to which Watt (1967) added *Chanopterus* and *Darwinella*. A family, Tretothoracidae, was established by Lea (1910) for the peculiar myrmecophilous Australian genus *Tretothorax*, which was later associated with the Dacoderini and included in that tribe under Tenebrionidae. However, Watt (1967) showed that Dacoderini cannot be retained in Tenebrionidae, and established a family, Dacoderidae, which he considered most closely related to Salpingidae.

Crowson (1955) suggested that the tribe Usechini should perhaps be included in Zopheridae, and this was confirmed by Kamiya (1963). The genus *Synercticus* was removed from Tenebrionidae by Crowson (1955) and placed in Boridae, but later Crowson (1967) stated that the larva of *Synercticus* is definitely pythid. Crowson (1955) also transferred the tenebrionid tribe Heterotarsini to the family Lagriidae.

In Crowson's (1955) key to the families of Heteromera, Tenebrionidae runs out in the same section as Nilionidae, Lagriidae, and Alleculidae. The characters these families share, and which separate them from all other Heteromera, are as follows. **Adult:** tarsal formula 5-5-4 (very rarely 4-4-4); sub-cubital fleck (if present) not placed across end of anterior anal vein; abdomen with sternites 1-3 connate, 4 and 5 more-or-less movable; tarsal claws simple or pectinate, never appendiculate; metendosternite very rarely hylecoetoid; if middle coxal cavities completely closed outwardly by sterna, antennae without a distinct three-segmented club; aedeagus of normal heteromeroid type; mesepisterna not nearly meeting each other in front of mesosternum. **Larva:** molar part of mandibles ridged or toothed, its armature not extending on to ventral surface; maxillary cardo undivided;

mandibles with well-developed mola; head with clypeus delimited posteriorly by a well-marked suture; gular area well defined; thoracic and abdominal sclerites distinctly sclerotised all round, form usually cylindrical, urogomphi (if present) simple.

Although Crowson stated that his key to Heteromera is artificial, it does define numerous natural groups. My study of representatives of most heteromeran families shows that Tenebrionidae, Alleculidae, Lagriidae, and Nilionidae form a natural, monophyletic group clearly distinguishable from all other families of Heteromera (better and more formally called Tenebrionoidea) by the larval characters quoted above, and by slight modifications and additions to the adult characters. In all taxa with this type of larva, the adults have each antennal insertion concealed from above by a lateral, shelf-like expansion of the frons, which usually forms a 'canthus' that encroaches on the front border of the eye, and the prosternal intercoxal process (usually strongly) convex from side to side, and not expanded laterally behind the coxae. With only two generic exceptions, all members of this group also have the front coxal cavities closed behind by inward extensions of the propleura.

The question thus arises whether this monophyletic group should be treated as several separate families, as in the past, or as a single family. If the group is to be divided into several families, there should be systematically significant 'gaps' between each, in both larval and adult characters.

If the Lagriidae of only the Holarctic region are considered, then a separate family is perhaps justified on phenetic grounds. When the Lypropini (= Heterotarsini except *Heterotarsus*), Adeliini, Goniaderini, and Pyncocerini are considered, however, the apparent gap disappears. These tribes were regarded as typical Tenebrionidae in all the older treatments of adults, although their close relationship to Lagriidae has been recognised by most larval systematists. None of the adult characters traditionally used to distinguish Lagriidae as a separate family (projecting front coxae, absence of lateral pronotal explanations or carinae, lobed penultimate tarsal segments) is common to all these forms, yet all are obviously related, with a fairly complete series of intermediate forms.

The family Alleculidae (= Cistelidae of older literature) has always been thought to be closely related to Tenebrionidae, and the only constant character separating the adults is the possession of pectinate tarsal claws by the former. Alleculid larvae have an elongate anterior extension of the hypopharyngeal sclerome, but this is found also in the typical tenebrionid *Uloma*. The parabolic form of abdominal segment 9 characteristic of alleculid larvae is found also in *Uloma*, *Ulomotypus*, *Aphthora*, *Lepispilus*, and a few other tenebrionid genera.

Perhaps the most distinct 'family' is Nilionidae, which on purely phenetic grounds might justifiably be separated from Tenebrionidae. The only constant character separating adult Nilionidae from Tenebrionidae, which also includes convex, *Coccinella*-like beetles (e.g., *Hemicyclus*, *Tetraphyllus*), is the possession of non-heteromeroïd anterior trochanters. The greatly reduced, membranous antennal segment 2 of nilionid larvae seems not to be found in any traditional tenebrionid.

There is no doubt that Nilionidae is a specialised offshoot from more generalised Tenebrionidae, and in a phylogenetic classification must be included in Tenebrionidae. The same applies to Lagriidae and Alleculidae, which would be referred to Tenebrionidae also in a phenetic classification in which both adult and larval characters were considered, because of the absence of gaps between them and Tenebrionidae. One may note that Cossyphinae

and Cossyphodinae would have to be treated as separate families in a phenetic classification so ranking Nilionidae, but both are obviously specialised offshoots of more generalised Tenebrionidae.

If we wish to continue to accept Tenebrionidae in its traditional sense, then the old families Alleculidae, Lagriidae, and Nilionidae must be included in it in a phylogenetic (and also in a consistent phenetic) classification. The alternative would be to elevate most, if not all, of the subfamilies recognised here to family rank. This inflation would be undesirable, especially as the broader family Tenebrionidae recognised here is no more diverse than the great phytophagous families (Chrysomelidae, Cerambycidae, Curculionidae).

Consistency would almost certainly require the merging of some of the smaller families of Tenebrionoidea (e.g., Pythidae with Pyrochroidae, Salpingidae with Dacoderidae, and perhaps Inopeplidae with Prostomidae). This will be considered more fully in a later paper.

Apart from Alleculidae, Lagriidae, and Nilionidae, a few taxa not originally included in Tenebrionidae belong there. The family Cossyphodidae includes specialised myrmecophilous beetles which are Tenebrionidae as recognised here (*see below*, subfamily Cossyphodinae). Lawrence (1971) has confirmed that *Petria*, which was originally placed in a distinct family, Petriidae, is actually a specialised omophline alleculid, a position assigned to it by Oglobin & Znoiko (1950). *Platycotylus* is a flattened, subcortical beetle originally described as a cucujid, but transferred to Tenebrionidae by Crowson (1955). *Archeoglenes*, which has tetramerous tarsi, was originally described as a colydiid, but a new tribe, Archeoglenini, is established for it in Phrenapatinae (*see below*).

Although numerous extraneous forms were excluded from Tenebrionidae by Böving & Craighead (1931) and Crowson (1955), there still remain several genera listed in Gebien's catalogue which must be removed from Tenebrionidae as defined here. The genera *Parahelops*, *Syrphetodes*, *Brouniphylax*, *Exohadrus*, and *Arthropus* and the tribe Ulodini all resemble Zopheridae in the prosternal intercoxal process, which is flat transversely and expanded posteriorly behind the coxae to partly close the front coxal cavities, and in the aedeagus, which has a simple, lightly sclerotised tegmen with setose parameres and without the inflected alae characteristic of Tenebrionidae. In *Syrphetodes* and *Brouniphylax* the internal female genitalia are quite unlike the usual tenebrionid form (e.g., Watt 1971), but rather similar to that found in Perimylopidae (Watt 1970). The adults also differ from Tenebrionidae in the completely exposed antennal insertions. Known larvae of this group resemble Zopheridae (and differ from Tenebrionidae) in the divided cardo, fused frontoclypeal region, lyre-shaped frontal sutures, and presence of hypostomal rods.

The genera discussed in the preceding paragraph differ from Zopheridae in having middle coxae with exposed trochantins, middle coxal cavities closed laterally partly by the mesepimera, exposed antennal insertions, and the aedeagus not inverted. Their inclusion in Zopheridae may appear to conflict with the definition of that family, but the larvae show fewer and less striking differences, and the family Colydiidae shows similar variation in the same adult characters. Thus, it seems best to expand the family Zopheridae to include these forms.

The New Zealand genera *Chalcodrya*, *Onysius* (= *Malacodrya*), and *Philpottia* were originally referred by their authors to either Melandryidae (*Chalcodrya*, *Onysius*) or Tenebrionidae (*Malacodrya*, *Philpottia*). Crowson (1955) placed them tentatively in Tenebrionidae, but they cannot remain there, having the zopherid type of closure of the front

coxal cavities, exposed antennal insertions, and the basal four abdominal sternites weakly connate. *Sirrhias* (= *Notolea*) from Tasmania has only three connate abdominal sternites, but otherwise agrees with the New Zealand genera. Watt (1974) has established a new family, Chalcodryidae, for these genera.

The Australian genera *Cotulades*, *Docalis*, and *Latometus* (= *Elascus*) were included in Tenebrionidae by Carter (1926) and Gebien, but they are typical Zopheridae in the restricted sense of Crowson (1955). They differ from previously recognised zopherids, however, in having fully developed wings, striate elytra, and the aedeagus lightly sclerotised.

Abdullah (1966) established a subfamily, Anaplopinae, in Tenebrionidae for the Australian genus *Anaplopus*. It is most certainly not a tenebrionid, and Crowson (1973) has transferred it to his family Phloeostichidae (*Cucujoidea sensu stricto*).

Abdullah (1966) also suggested a close relationship of the family Merycidae to Tenebrionidae, but gave no convincing reasons. *Meryx* shows a fairly close relationship to Ulo-dini in both adult and larval stages, and a strong case could be made for including it in Zopheridae, but certainly not in Tenebrionidae. As noted by Abdullah, a subcubital fleck is present in the wing of *Cryphaeus* (and also in several other relatively primitive Tenebrionidae), but this is characteristic also of winged Zopheridae (and numerous other Tenebrionoidea).

Abdullah (1974) has published a new key to families of Heteromera, and has summarised the adult characters of the families he recognises. Some of the information included appears to have been taken, without acknowledgment, from my unpublished thesis (Watt 1965), especially my table 1. Abdullah treats Nilionidae as a separate family, but includes Alleculidae and Lagriidae in Tenebrionidae. *Archaeoglenes* and *Rhipidandrus* (tarsal formula 4-4-4) would run to Merycidae in his key. The following family-group names within Tenebrionidae are wrongly attributed: "Diaperidae Leach, 1815" for Diaperialae Latreille, [1802]; "Helopidae Latreille, 1825" for Helopii Latreille, [1802]; "Pimeliidae Leach, 1815" for Pimeliariae Latreille, [1802]. There are minor errors in several of the characters which he attributes to Tenebrionidae: the antennal insertion is always at least partly covered by a small canthus when viewed from above (cf. Abdullah's character No. 10); the eyes have fine facets in diurnal species and coarse facets in nocturnal species (cf. No. 16); cervical sclerites are always absent (cf. No. 18); the pronotum has a foliate anterior margin covering the head in Cossyphinae (cf. No. 28); the mesocoxal trochantins are exposed in at least 50% of known genera (cf. No. 31). No. 59 appears twice, the first time apparently as a misprint for No. 50.

It is obvious from Kaszab's description and figures that the genus *Szekessya* Kaszab, 1955 is not a tenebrionid. It is referred tentatively to Prostomidae by Lawrence (1971), although its tarsal formula is 5-5-4. I have not yet examined any examples of this genus.

The genus *Enneboeus* has always previously been regarded as tenebrionid. However, the adult differs from all known Tenebrionidae in that the front coxae lack substantial concealed lateral extensions; only the first two visible abdominal sternites are connate; the aedeagus is lightly sclerotised, has setose parameres, and lacks inflected alae; the prosternal intercoxal process has substantial lateral extensions behind, which partly close the coxal cavities and embrace the coxae; and in the female genitalia a spermathecal gland appears to be lacking, and the spermatheca is a bulb connected to the bursa by a very long, thin duct.

In the larva, antennal segment 3 is relatively larger and more elongate than in Tenebrionidae; the head has ventral hypostomal rods; the maxillary cardo is divided; and the mandibular mola is asperate, with the asperities extending on to the ventral surface (as in Mycetophagidae and Colydiidae).

The adult seems to have more in common with Tenebrionidae and Zopheridae than with other families, but cannot find a place in either. The larva, on the other hand, seems to show stronger affinities with Mycetophagidae and Colydiidae, but differs from them and agrees with Tenebrionidae in the distinct clypeus. This is no doubt a primitive character, however. *Enneboeus* and its probable relatives [*Archeocrypticus* and *Sivacrypticus*, associated tentatively in an undefined tribe, Archeocrypticini, by Kaszab (1964)] must be removed from Tenebrionidae. They require a new family, **Archeocrypticidae** new status, which will be defined more fully in a later paper.

Groups which were referred to Tenebrionidae in the Junk Coleopterorum Catalogus, or by other authors more recently, and which have been excluded from Tenebrionidae, are listed in Table 2.

RELATIONSHIPS AND PHYLOGENY OF TENEBRIONIDAE

Characters which have been used to define families or subfamilies of Tenebrionoidea, plus some hitherto unrecorded characters, were listed for most known families, including all those thought to be related to Tenebrionidae. From these, 28 adult and 28 larval characters were tabulated as primitive or derived states. Matrices were constructed, based on overall similarity and on derived characters only. I have considerable reservations about the validity of this method when used uncritically. It can, however, provide useful indications of real phylogenetic relationships, as phyletically closely related taxa usually have more characters in common than do more distantly related taxa. This is especially true of derived characters in common.

The results for both derived-character and overall-similarity matrices for Tenebrionidae are recorded in Table 3. In Zopheridae, for example, 5 of the 28 adult characters considered are derived, and 3 of these are shared with Tenebrionidae, so there are 3/5 derived characters shared by the two families, i.e., 60%. Eight of the 28 larval characters considered are derived, and 4 of these are shared with Tenebrionidae, so there are 4/8 (i.e., 50%) derived characters shared by the two families. The possible number of derived character matches between each family and Tenebrionidae is the greater number of derived characters, hence the larger figure was the divisor in each instance.

Comparisons with families having only one (Mycetophagidae) or no (Tetratomidae) derived adult characters are not very useful, but in both the larvae have several derived characters. The mean of the adult and larval percentages is given in the column headed "Derived Mean (%)", and the families have been ranked from highest to lowest on the basis of these figures.

The overall similarity figures were calculated as in the following example. In Zopheridae, 23 out of 28 adult characters (82%) and 19 out of 28 larval characters (68%) are shared with Tenebrionidae. The mean of these percentages is 75%.

It is interesting to note that the families closest to Tenebrionidae on derived characters all have relatively high overall-similarity indices, but there are minor differences in sequence.

TABLE 2—Groups referred to Tenebrionidae in the Junk Coleopterorum Catalogus or more recently which must be excluded (T, Tenebrionidae; ..., not included)

Group	Junk Catalogue	Gebien (1937-44) (T only)	Present position	Authority
<i>Boros</i>	T: Tenebrioninae	Tenebrionini	Boridae	Böving & Craighead, 1931
<i>Perimylops</i>	T: Helopinae	...	Perimylopidae	St. George, 1939
<i>Hydromedion</i>	"	...	"	" "
<i>Darwinella</i>	"	...	"	Watt, 1967 "
<i>Chanopteris</i> (= <i>Chitoniscus</i>)	"	...	"	" "
<i>Tretothorax</i>	Tretothoracidae	Helopini	"	" "
<i>Dacoderus</i>	T: Dacoderinae	Dacoderini	Dacoderidae	" "
<i>Zopherinae</i>	T: Zopherinae	Zopherini	Zopheridae	Böving & Craighead, 1931
<i>Usechinae</i>	T: Usechinae	Usechini	"	Hayashi, 1962
<i>Cotulades</i>	T: Stenosinae	Stenosini	"	This paper
<i>Docalis</i>	T: Nyctoporinae	"	"	" "
<i>Latometus</i> (= <i>Elascus</i>)	T: Bolitophaginae	Bolitophagini	"	" "
<i>Ulodinae</i>	T: Ulodinae	Ulodini	"	Watt, 1967
<i>Syrphetodes</i>	T: Opatrinae	Adeliini	"	This paper
<i>Brouniphylax</i> (= <i>Paraphylax</i>)	T: Opatrinae	"	"	" "
<i>Exohadrus</i>	"	"	"	" "
<i>Arthropus</i>	T: Helopinae	Helopini	"	" "
<i>Parahelops</i>	"	"	"	Watt, 1967
<i>Chalcodrya</i>	Chalcodryidae	Watt, 1974
<i>Philpottia</i>	"	" "
<i>Onysius</i> (= <i>Malacodrya</i>)	T: Serropalpidae	...	"	" "
<i>Sirrhax</i> (= <i>Notolea</i>)	T: Cnodaloninae	Cnodalonini	"	" "
<i>Szekessya</i>	"	" "
<i>Synercticus</i>	T: Tenebrioninae	...	Prostomidae?	Lawrence, 1971
<i>Anaplopus</i>	Pedilidae	...	Pythidae	Crowson, 1967
<i>Enneboeus</i>	T: Diaperinae	Diaperini	Phloeostichidae	Crowson, 1973
<i>Archeocrypticus</i>	Archeocrypticidae	This paper
<i>Sivacrypticus</i>	"	" "
<i>Bancous</i>	"	" "
<i>Synopticus</i>	...	Rhysopaussini	Cucujoidea	Paulian, 1947
			Melandryidae?	Ardoin, 1962

In derived characters there is a 10% gap (between Perimylopidae and Ciidae), but there is no such gap in overall similarity.

It would be a dangerous oversimplification to state that, on the basis of Table 3, Zopheridae is the family most closely related to Tenebrionidae. There is no doubt, however, that those families at the top of the table are more closely related to Tenebrionidae than those further down.

The family Tenebrionidae as defined here is not closely related to any other family, and has had a long, independent evolutionary history. The first known fossil assigned to the family with high probability is *Eodromus agilis*, from the Middle Eocene Brown Coal of Geiseltal, Germany (Crowson *et al.* 1967). Several other genera from the same beds were assigned to Tenebrionidae (Haupt 1950), but only *E. agilis* is represented by sufficiently adequate material to make its attribution to the family reasonably certain. *Paropiophorus* and *Rhinohelaetes* are definitely not tenebrionids.

Eodromus agilis has 10-striate elytra with a scutellary striole, but there are no other characters in Haupt's description which would enable it to be placed in a subfamily. Haupt compares it with *Camitaria* (Tenebrioninae), but *Eodromus* would be excluded from Tenebrioninae by its 10-striate elytra. In general appearance it is closer to certain Pimeliinae

TABLE 3—Derived character and overall similarity matches between Tenebrionidae and other families (A, adult characters; L, larval characters; No., number of derived characters (out of 28) for each family; —, nil; ..., not applicable)

Family	Derived					Overall		
	A(%)	No.	L(%)	No.	Mean(%)	A(%)	L(%)	Mean(%)
Tenebrionidae	100	4	100	6	100	100	100	100
Zopheridae	60	5	50	8	55	82	68	75
Chalcodryidae	33	6	71	7	52	68	82	75
Merycidae	44	9	57	7	51	79	64	72
Archeocrypticidae	43	7	50	5	47	79	64	72
Synchroidae	50	6	38	8	44	71	64	68
Colydiidae	50	6	29	7	40	79	68	74
Monommatidae	50	8	30	10	40	75	75	75
Melandryidae	25	3	50	6	38	61	71	66
Perimylopidae	25	3	44	9	35	68	71	70
Ciidae	17	6	43	7	25	64	71	68
Oedemeridae	—	8	50	8	25	50	79	65
Anthicidae	10	10	40	10	25	54	71	63
Tetratomidae	—	—	43	7	22	68	64	66
Cephaloidea	10	10	33	9	22	54	61	57
Dacoderidae	22	9	22	61	...	61
Prostomidae	21	14	17	12	19	61	46	54
[Byturidae]	14	7	17	4	16	61	57	59
Mycetophagidae	—	1	30	10	15	64	64	64
Salpingidae	22	9	8	13	15	71	43	57
Boridae	17	6	10	10	14	68	46	57
Mycteridae	6	15	18	11	12	50	61	56
Othniidae	14	7	8	13	11	75	39	57
Pythidae	—	7	20	15	10	61	43	52
Pyrochroidae	—	8	17	12	9	50	50	50
Inoepelidae	8	12	8	13	8	64	43	54

(Epitragini) than to *Camitaria*. Epitragini are among the most primitive Pimeliinae, being fully winged and some having distinctly striate elytra.

The fossil record of Tenebrionoidea (Heteromera) is rather poor, and of little help in deducing phylogeny; *Eodromus agilis* is in fact the first known fossil of the superfamily. Probably the superfamily originated in the Jurassic, and the family Tenebrionidae may have arisen not long afterwards, and certainly before the separation of New Zealand from Australia in the mid Cretaceous (Raven & Axelrod 1972).

Characters of the subfamilies of Tenebrionidae recognised here are given in Tables 4 and 5. In the phylogenetic diagram (Fig. A), based on the data presented in these tables, the sequence of branching is reasonably clear-cut up to "e". A likely sequence for the remaining subfamilies (Toxicinae to Alleculinae) is suggested by the arrangement of horizontal bars. Further study may provide additional information which will enable the sequence of branching to be determined.

On the basis of adult character 1 (A1) and larval character 1 (L1) it could be argued that Zolodininae split off from the ancestral stem before Pimeliinae, but for both characters Zolodininae exhibit the primitive character state. Zolodininae and Pimeliinae are synapomorphic in the sense of Hennig (1966) for A2 and A3. These two subfamilies are zoogeographical sister groups, in that Zolodininae are confined to Australia and New Zealand, whereas Pimeliinae occur in all except these regions (Table 6). Apparently Zolodininae retained their primitive characters and the habit of living in rotten wood, following the isolation of Australia and New Zealand. Pimeliinae probably evolved soil-inhabiting larvae very early in their evolution, as existing pimeliine larvae are much more specialised and more

TABLE 4—Selected characters of subfamilies of Tenebrionidae: adults (—, primitive state of character; +, derived state of character; †, primitive state predominates; ±, derived state predominates; *, rare exceptions occur; 0, structure (wing, elytral striae) absent in all known genera)

Derived state of character	ZOLODININAE	TOXICINAE	DIAPERINAE	GNATHIDINAE	PHRENAPATINAE	TENEBRIONINAE	ALLECULINAE	NILIONINAE	LAGRIINAE	PIMELINAE	COSSYPHINAE	COSSYPHODINAE
1. Front coxal cavities closed behind	—	+	+	+	+	+	+	+	+	+	+	+
2. Aedeagus inverted	+	—	—	—	—	*	—	—	—	—	—	—
3. Abdominal defensive glands present	—	+	+	+	+	+	+	+	+	+	—	—
4. Intersegmental membranes of abdomen exposed	—	—	†	†	†	†	†	†	†	†	—	+
5. Elytra, if striate, with less than 10 striae	—	+	+	+	+	+	+	+	—	—	0	0
6. Wings, if present, without subcubital flecks	—	—	+	0	+	+	+	+	+	+	+	0
7. Mandibular mola without fine transverse ridges	†	+	+	—	+	*	+	+	+	+	+	+
8. Lacinia without apical hook or tooth	—	—	+	+	+	†	+	+	†	†	+	+
9. Middle coxae without exposed trochantins	—	—	—	+	†	†	—	+	*	†	+	+
10. Middle coxal cavities closed laterally by meso- and metasterna	—	—	—	+	—	—	—	—	*	†	+	+
11. Outer margins of tibia carinate	—	—	—	—	—	*	—	—	—	—	—	—
12. Antennae 10-segmented and clubbed	—	—	—	+	—	—	—	—	—	—	—	—
13. Mandible tridentate at apex	—	—	—	—	+	—	—	—	—	—	—	—
14. Elytra, if striate, without scutellary striole	—	—	—	—	+	—	—	—	—	—	0	0
15. Tarsal claws pectinate	—	—	—	—	—	—	+	—	—	—	—	—
16. Labrum elongate	—	—	—	—	—	—	—	+	—	—	+	—
17. At least anterior trochanters not heteromeroid	—	—	—	—	—	—	+	—	—	—	—	—
18. Penultimate tarsal segments lobed	—	—	—	—	—	*	†	+	†	—	—	—
19. Postcoxal processes of propleura meet in middle	—	—	—	—	—	—	†	—	—	—	+	—
20. Prothorax with foliate anterior margin covering head	—	—	—	—	—	—	—	—	—	—	+	—
21. Antennae geniculate, retractable into pouches	—	—	—	—	—	—	—	—	—	—	—	+

TABLE 5—Selected characters of subfamilies of Tenebrionidae: larvae (symbols as for Table 4; larvae of Cossyphinae and Cossyphodinae are unknown)

Derived state of character	ZOLODININAE	TOXICINAE	DIAPERINAE	GNATHIDINAE	PHRENAPATINAE	TENEBRIONINAE	ALLECULINAE	NILIONINAE	LAGRIINAE	PIMELINAE
1. Maxillary mala without uncus	—	+	+	+	+	+	+	+	+	+
2. Hypopharyngeal sclerome not tridentate anteriorly	—	+	+	+	+	†	*	+	+	+
3. Mandibular mola with fine transverse ridges	—	—	—	+	+	—	*	—	—	—
4. Spiracles without ring of peripheral air-tubes	—	—	—	—	+	+	+	+	+	+
5. Urogomphi absent	—	—	—	—	+	+	+	+	—	†
6. Antenna with less than 3 segments	—	—	—	—	—	—	*	—	—	—
7. Dorsal surface of mandible with knob or tubercle	—	—	+	—	—	—	—	+	—	—
8. Tergite 9 and sternite 9 about equal, anus terminal	—	—	—	—	+	—	—	—	—	—
9. Gula absent, gular sutures confluent	—	—	—	—	—	+	—	—	—	—
10. Pleurosternal sutures of abdomen absent	—	—	—	—	+	—	†	—	—	—
11. Legs specialised for digging ("Pedobionta")	—	—	—	—	—	+	†	—	—	+
12. Head capsule visible between antennal and mandibular bases	—	—	—	—	—	—	*	—	+	—
13. Antennae pubescent	—	—	—	—	—	—	—	+	+	—
14. Mandible with membranous elevation bearing numerous setae	—	—	—	—	—	—	—	—	—	+
15. Hypopharyngeal sclerome with elongate anterior extension	—	—	—	—	—	—	+	—	—	—

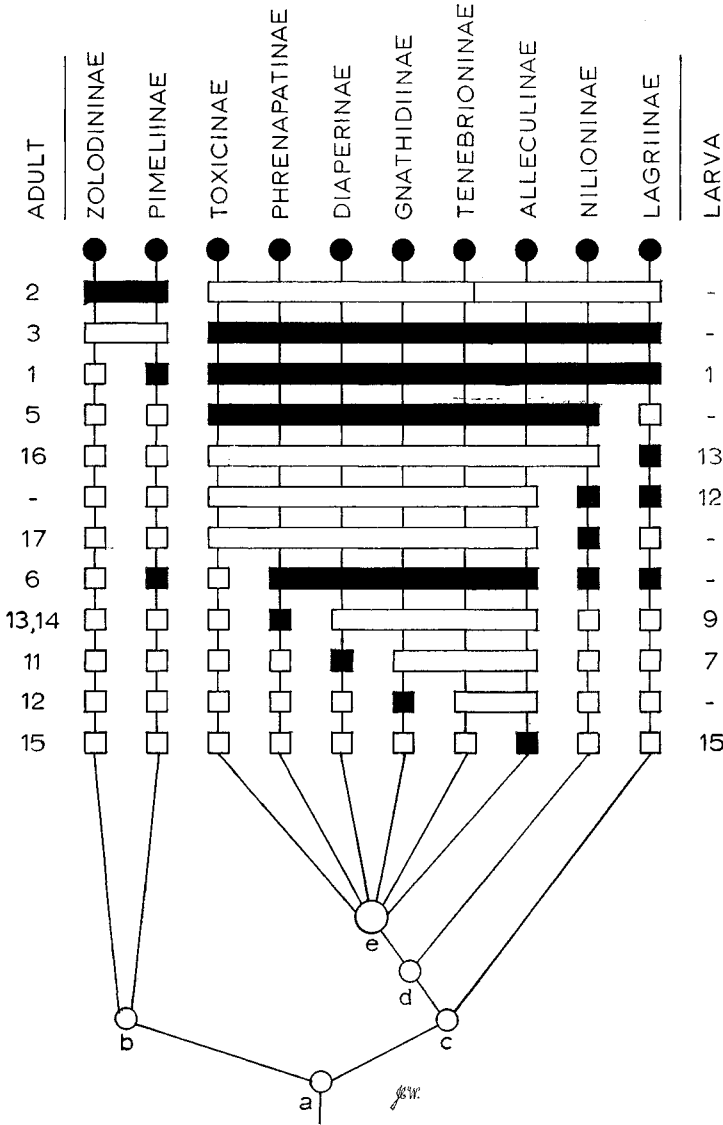


FIG. A.—Probable phylogeny of the subfamilies of Tenebrionidae; adult and larval characters given in Tables 4, 5 respectively. White bars and squares indicate the primitive state, and black bars and squares the derived state, for each character or complex of characters.

diverse than soil-inhabiting larvae of other subfamilies (Tenebrioninae, Alleculinae), which all conform to the false wireworm form. Perhaps the most primitive Pimeliinae are the winged Epitragini. Pimeliinae are most diverse in the Ethiopian Region, where they may have originated (Koch 1955). There are endemic tribes in each of the main arid areas of the world except that of Australia.

Note the distribution of the derived state of characters A1 and A6, which suggests preadaptation, with parallelism resulting in their independent evolution in Pimeliinae and the remainder of the higher Tenebrionidae. Alternatively, the interpretation illustrated by

TABLE 6—Distribution of subfamilies of Tenebrionidae (+, present)

	ZOLODININAE	TOXICINAE	DIAPERINAE	GNATHIDIINAE	PHRENAPATINAE	TENEBRIONINAE	ALLECULINAE	NILIONINAE	LAGRIINAE	PIMELINAE	COSSYPHINAE	COSSYPHODINAE
New Zealand	+			+	+	+	+		+			
Australia	+	+	+		+	+		+	+		+	
Oriental region		+	+	+	+	+	+	+	+	+	+	+
Ethiopian region		+	+	+	+	+		+	+	+	+	+
Malagasy		+	+		+	+	+	+	+	+	+	
Palearctic region		+	+		+	+	+		+	+	+	
Nearctic region					+	+			+	+		
Neotropical region			+		+	+	+	+	+	+		

Fig. A may be wrong, in that Pimeliinae may have diverged after the ancestral line separated from Zolodiniinae, but this is less probable.

The subfamily Lagriinae was apparently an early offshoot, and is readily characterised by the combination of 10-striate elytra (A5), elongate labrum-ephiparynx (A16), and 2-segmented, pubescent larval antennae (L13). The larvae appear to have adopted a leaf-litter habitat at an early stage of lagriine evolution, although some larvae of Adeliini are found in rotten wood. However, this may be a secondary reinvasion of the habitat.

Nilioninae share some characters with Lagriinae (notably L12), and similarly have larvae inhabiting leaf litter. Their geographical distribution, with one tribe in South America and the other in the Old World tropics and Australia (Table 6), is partially relict.

Beyond Nilioninae, tenebrionid phylogeny is less certain. By far the largest and most diverse subfamily is Tenebrioninae, even after splitting off Toxicinae, Phrenapatinae, Diaperinae, and Gnathidiinae, which were included in Tenebrioninae in the traditional classifications, and by inference in Doyen's classification.

Despite the fact that Alleculinae were treated as a separate family for so long, they are at least as close to Tenebrioninae as the other subfamilies recognised here. Some Amarygmini and Strongyliini are very similar to Alleculinae as adults, but the resemblance is less apparent in their larvae. Larvae of *Uloma* share with Alleculinae a hypopharyngeal sclerome with an elongate anterior extension, and a paraboloid tergite 9, but no close affinity is apparent in adults. The resemblance between the larvae in this instance may be due to convergence, as both *Uloma* and primitive alleculine larvae live in rotten wood.

Toxicinae are the most primitive close relatives of Tenebrioninae in the characters tabulated, but both adults and larvae have several derived characters (*see* keys). Phrenapatinae, Diaperinae, and Gnathidiinae each have a complex of primitive and derived characters justifying their separation from Tenebrioninae, and by implication their divergence antedates the origin of tribes within Tenebrioninae itself. Phrenapatinae are associated with rotten wood, Diaperinae with 'brackets' of polypore fungi, Gnathidiinae with rotten wood previously attacked by polypore fungi, and Toxicinae with polypore fungi or rotten wood.

The subfamily Tenebrioninae as recognised here may still be polyphyletic. Groups with anomalous characters which should be investigated and considered further include *Cnemeplatia*, *Choerodes* and its relatives, *Uloma*, *Hypophloeus*, *Cataphronetis*, and the Rhysopausini (which have been said [e.g., Wassmann 1921] to be Amarygmini specialised for myrmecophily or termitophily).

Among the most primitive Tenebrioninae are the Tenebrionini themselves, which mostly inhabit rotten wood, apart from a few which, like *Tenebrio*, have adapted themselves to stored products, possibly via the lairs of food-storing mammals. Several other tribes have larvae inhabiting rotten wood, but the adults are short-lived, active, long-legged beetles which fly readily (Amarygmini, Strongyliini, many Cyphaleini), and have paralleled Alleculinae. Cyphaleini are primitive in having wings with subcubital flecks. Others have become associated with polypore fungi (many Platydemini). Specialised soil-inhabiting larvae have evolved independently in at least two lines within Tenebrioninae (Helaeini-Nyctoziolini in Australasia, and Skopin's "Blapimorpha" in the rest of the world). Larvae of Cyphaleini, Helaeini, and Nyctoziolini have spiracles with crenulate peritremes. Many Triboliini and a few Platydemini have become associated with stored products, probably via subcortical habitats. Some Tenebrioninae inhabit the galleries of wood-borers, or follow subcortical workings, where they probably feed on moulds. *Artystona* and its relatives in New Zealand feed on lichens.

Cossyphodinae appear to be related to Tenebrioninae, though not particularly closely. The affinities of Cossyphinae are not clearly towards either the pimeliine or the tenebrionine branches, and the subfamily probably arose near the base of the tenebrionid stem. As their larvae are unknown, Cossyphodinae and Cossyphinae have been omitted from Fig. A.

BIOLOGY

Primitive Tenebrionidae are relatively large, and both larval and adult life is usually long. In some of the more specialised groups, larval life is fairly long, but the period of adult emergence and life is short, and the adults themselves are very active (e.g., Alleculinae, Lagriini, Strongyliini, Amarygmini). In the soil-inhabiting groups, larval and adult life is primitively long (Helaeini-Nyctoziolini, many "Blapimorpha", some Pimeliinae). In the more specialised Pimeliinae and a few "Blapimorpha" adapted to arid conditions, larval development is very rapid and the adults are very long-lived. Adults will oviposit only in a damp substrate (normally after rain), and the rapid larval development is obviously an adaptation to make the best use of ephemeral moisture. The adults appear to be much more resistant to desiccation than the larvae.

Tenebrionidae characteristically feed on dead vegetable or (sometimes) animal matter. Soil-inhabiting larvae will feed on living plant tissue, especially during droughts, as will the adults.

Most tenebrionid larvae are cannibalistic if overcrowded in the laboratory. It is not uncommon to find chitinous exoskeleton fragments in the gut contents of larvae inhabiting rotten wood, but some of these may be exuviae, and most of the others reflect accidental ingestion rather than active predation. *Hypophloeus* spp. were thought to prey upon the Scolytidae with which they are usually associated, but Struble (1930) reared *Hypophloeus substriatus* Leconte entirely on a diet of cultured moulds. Few normally predacious Tenebrionidae are known.

Adult Tenebrionidae with abdominal defensive glands produce a repugnatorial secretion which has been shown in some to contain benzoquinones (Eisner & Meinwald 1966). This apparently serves to protect them from most predators. Some such beetles can spray fine jets of secretion from the defensive glands.

The biology of Tenebrionidae *sensu stricto* has been reviewed by Butler (1949) from a rather different viewpoint. More detailed biological information is included in the systematic section below.

ECONOMIC IMPORTANCE

In regions with moderate to high rainfall the soil-inhabiting Tenebrionidae are of little economic importance, and usually restricted to well-drained, sandy soils. In semi-arid and arid areas, however, soil-dwelling larvae may do considerable damage to roots or seedlings of agricultural crops. The adults live on the surface of the ground and gnaw the stems of plants, and sometimes eat leaves and buds (*see* Butler 1949 for references). In the Palaearctic region the most serious pests are Opatrini, Platyscelini, Pedinini, and Blaptini ("Blapimorpha"), though in North America their place is taken by Eleodini and *Blapstinus* ("Pedinini"), and in the drier parts of both regions they tend to be replaced by Pimeliinae. In Africa a similar pattern exists. In Australia, the only record of a tenebrionid attacking agricultural crops is of *Cestrinus punctatissimus* Pascoe (Adeliini) damaging germinating wheat, but it is likely that some damage attributed to wireworms is in fact caused by larvae of Helaeini and Nyctoziilini. The vernacular name for larvae of "Blapimorpha" is 'false wireworms', which indicates their superficial resemblance to wireworms *per se*.

Some Tenebrionidae are pests of stored grain and grain products. The most important of these are the flour beetles *Tribolium confusum* Duval and *T. castaneum* Herbst, which cause considerable damage to stored cereals, especially in temperate climates. Other pests of stored grain are the mealworms *Tenebrio molitor* and *T. obscurus*, other *Tribolium* spp., *Gnathocerus* spp., *Latheticus oryzae*, *Palorus* spp., *Alphitobius* spp., *Alphitophagus bifasciatus*, and *Martianus* spp. (*see* Cotton 1956 for references). Most of these are cosmopolitan.

In recent years, *Tribolium castaneum* and *T. confusum* have been used extensively in studies of population dynamics and in genetical studies (Sokoloff 1966). They are particularly suitable for such research because of their short life cycle and the ease with which they can be reared in the laboratory. *Tenebrio molitor* has been used for many years for physiological research.

DISTRIBUTION

Tenebrionidae are strongly represented in tropical and subtropical regions and in both hot and cold deserts, but are not numerous in damp, cool-temperate climates. In the British Isles, for example, only 27 species are definitely established and occur naturally, away from artificially heated environments, and the majority are confined to southern England. Many of these species, and others, occur much further north in continental Europe, where the summers are more reliable than in Britain. For example, *Scaphidema metallicum* and 10 other Tenebrionidae occur north of the Arctic Circle in Sweden (Klefbeck & Sjöberg 1960).

In the Southern Hemisphere, a single tenebrionid occurs on Campbell Island (52°30'S), and several occur slightly further south (to 55°S) on Tierra del Fuego. Few Tenebrionidae have reached oceanic islands.

Detailed distribution is discussed under each subfamily. Generally speaking, the most primitive Tenebrionidae occur in Australia, New Zealand, and the Old World tropics including Malagasy. The Palaearctic and Nearctic regions are not rich in primitive forms. The New Zealand tenebrionid fauna is closely related to that of Australia, and there is no indication of any special relationship between these faunas and that of southern South America.

COPULATION AND ORIENTATION OF THE AEDEAGUS

The aedeagus is inverted (i.e., tegmen ventral, median lobe dorsal) both when retracted into the abdomen and when exerted in Zolodininae and Pimeliinae (Figs 16, 17). In Coleoptera generally, this feature is associated with 'back-to-back' copulation, whereas when the aedeagus is normally orientated the male climbs on to the female's back.

I have observed copulation in the field and/or in the laboratory in the Pimeliinae *Pimelia cribra* Solier, *Akis acuminata* Fabricius, and *Tentyria schauimi* Kraatz, and in the following species with a normally orientated (uninverted) aedeagus: *Scaurus striatus* Fabricius, *Micrositus semicostatus* Mulsant & Rey, *Tenebrio molitor* Linnaeus, *Tribolium confusum* Duval, *Mimopeus opaculus* (Bates), and *Isomira murina* (Linnaeus). In both groups the male climbs on to the female's back, and the aedeagus and terminal abdominal segments are extended and curved around beneath the abdomen (see Fig. 37). According to Fiori (1954) the aedeagus in *Pimelia angulata* Fabricius is turned through 180° as it is extended, so that it becomes normally orientated morphologically as in forms with an uninverted aedeagus (Fig. 37). During my observations of *Tentyria schauimi*, the aedeagus remained morphologically inverted (i.e., topographically uninverted) during copulation. Copulation in Pimeliinae (and other Tenebrionidae) obviously requires further study.

FEMALE GENITALIA

The study of internal female genitalia in Tenebrionoidea is in its infancy. Work already done shows that very useful characters at the family and lower levels of classification can be found in these structures.

Female genitalia of representatives of four of the subfamilies recognised here are illustrated in Figs 93–97 (Zolodininae—*Zolodinus*, Pimeliinae—*Tentyria*, Lagriinae—*Pheloneis*, Tenebrioninae—*Tenebrio*). All are characterised by a long, tubular spermatheca, and all except *Tentyria* have a fine-branched, tubular spermathecal gland. Dissection of a fresh *Tenebrio* confirms the identification of the spermatheca, which has a thick, muscular wall; the spermathecal gland has only a thin, probably non-muscular, wall.

In *Zolodinus* and *Tentyria* the spermatheca is gradually expanded towards its apex, but in *Pheloneis* and other Lagriinae, and in *Tenebrio* and other (but not all) Tenebrioninae, it is a thin tube throughout its length (see also Watt 1971, figs 59–62, *Pseudhelops*). This greatly elongated, usually tubular spermatheca has not been found in any other Tenebrionoidea examined so far (e.g., Zopheridae, Archeocrypticidae, Perimylopidae; see Watt 1970), and may be diagnostic of Tenebrionidae. The anus opens beneath the proctiger, and the vulva is situated between the coxites in these taxa.

The female genitalia (like the pupal gin-traps found in all tenebrionid pupae except Lagriinae and Nilioninae) further confirm the inclusion of Zolodininae and Pimeliinae within Tenebrionidae.

Family TENEBRIONIDAE

- Tenebrionites Latreille, [1802], Hist. nat. Crust. Ins. 3: 165.
 Diaperiales Latreille, [1802], *op. cit.*: 161.
 Cossyphores Latreille, [1802], *op. cit.*: 164.
 Pimeliariae Latreille, [1802], *op. cit.*: 165.
 Helopii Latreille, [1802], *op. cit.*: 176.
 Cisteleniae Latreille, [1802], *op. cit.*: 181 (= Alleculidae auct.).
 Lagriariae Latreille, 1825, Fam. nat. Regne anim.: 381.
 Tentyrites Solier, 1834, Ann. Soc. ent. Fr. 3: 501.
 Nilionidae Champion, 1888, Biol. C. Amer. Col. 4(1): 470.
 Alleculidae Seidlitz, 1891, Fauna Balt. ed. 2: 49.
 Petriidae Semenow, 1893, Bull. Acad. Imp. Sci. St. Petersburg (n.s.) 3(35): 607.
 Rhysoaussidae Wasmann, 1896, Ann. Mus. Stor. Nat. Genova (2)16: 613.
 Cossyphodidae Wasmann, 1899, Dtsch. ent. Z. 1899: 161.

ADULTS. Antennae inserted under lateral expansions of frons (Fig. 44: canthus) which conceal at least base of scape from above and almost always extend back to anterior margins of eyes, on which they usually encroach. Antennae filiform or (occasionally) perfoliate, distinctly clubbed or bluntly serrate, very rarely flabellate. Terminal segments of palpi securiform or not. Lacinia often armed at apex with inwardly directed, sclerotised tooth (Fig. 34). Head not sharply constricted behind eyes to narrow neck.

Prothorax usually carinate or explanate laterally. Procoxal cavities almost always closed behind by postcoxal extensions of propleura (Fig. 72), not closed partly by curved, posterior, lateral extensions from prosternal intercoxal process. Procoxae without exposed trochantins, set almost at 90° to body axis, with concealed lateral extensions. Procoxal cavities partly open (Fig. 4) or closed internally (Figs 71, 72). Mesocoxae with or without exposed trochantins, their cavities closed laterally partly by mesepimera or entirely by sterna. Elytra usually with distinct epipleura; if striate, usually with 9 striae, sometimes 10, rarely more or fewer; usually with scutellary striae, or at least with sutural striae diverging distinctly at base. Metasternum usually with median longitudinal suture. Metacoxae with (Fig. 3) or without internal flanges. Metendosternite usually with stalk, sometimes without anterior median process (Figs 3, 35), sometimes with 'laminae', anterior tendons usually borne on arms (Figs 43, 46, 47), rarely on anterior median process (Fig. 35). Wings (if present) rarely with subcubital flecks (Fig. 14), usually with complete heteromerous venation except in small beetles. All trochanters heteromeroid (Fig. 36) except in Nilioninae (Fig. 40). Tibial spurs simple, sometimes very small. Tarsal formula almost always 5-5-4, very rarely 5-4-4 (Cossyphodini) or 4-4-4 (*Rhipidandrus*, *Archaeoglenes*); tarsal segments usually not lobed below; tarsal claws usually simple, pectinate in Alleculinae (Fig. 39), never toothed, appendiculate, cleft, or with long appendages below them.

Abdomen always with visible sternites 1-3 connate, 4 and 5 movable, rarely with more than five sternites normally visible. Aedeagus inverted or not; tegmen divided into apical and basal parts, rarely in one piece or with intermediate sclerites between apical and basal pieces, moderately to strongly sclerotised, parameres parallel, fused almost to apex, not divergent (Fig. 17), without long apical setae; median lobe usually simple, occasionally with lateral processes ("lacinia" of Koch 1956). Ovipositor usually elongate (Fig. 38), usually with styli, coxites usually partly fused with valvifers (Fig. 38), paraprocts and proctiger often with rod-like thickenings.

LARVAE. Cylindrical, subcylindrical, strongly convex, or onisciform, very rarely strongly depressed.

Antennae two- or three-segmented, sometimes pubescent; sensorium at apex of segment 2 very variable, but most often an incomplete ring partly surrounding segment 3; latter

much smaller than segment 2. Basal membranes of antenna and mandible usually contiguous, partly obscuring very narrow strip of head capsule between them; strip sometimes broader, clearly visible, occasionally very broad (Nilioninae). Clypeus clearly delimited posteriorly by distinct transverse suture (Fig. 82). Epicranial suture not very short. Frontal sutures characteristic (Fig. 82), never lyre-shaped. Endocarina absent. Mandibular molae distinct, usually sculptured with irregular tubercles and cusps (Figs 5, 6), but occasionally with fine, transverse grooves (Fig. 59). Maxillary cardo not divided; maxillary mala broadly or narrowly rounded at apex, without anterior indentation, rarely with uncus (Fig. 13), bearing usually two, sometimes one or more than two longitudinal rows of stout bristles on inner surface; maxillary palpi three-segmented. Hypopharynx with bracon (Fig. 30), almost always with distinct, sclerotised sclerome. Labial palpi two-segmented. Distinct gula almost always present (Fig. 81), often not distinctly divided from submentum. Hypostomal rods absent.

Legs well developed, all usual parts present, usually bearing some bristles or articulated spines on inner surface; each tarsungulus often apparently divided into two (in soil-inhabiting larvae), with a strongly sclerotised apical part and a weakly sclerotised base (Figs 88, 89). Coxae contiguous to fairly widely separated, but not arising on lateral margins of thorax.

Abdomen usually with pleurosternal sutures, sometimes with distinct pleura, without laterotergites. Tergite 9 usually with extensive ventral surface (Figs 7, 58), anus opening below it, occasionally without ventral surface, anus subterminal (Fig. 32); urogomphi present or absent. Sternite 10 usually produced into a pair of weakly to moderately sclerotised pseudopods (e.g., Figs 7, 61, 68, 69), tergite 10 rarely distinct.

Spiracles circular or oval, occasionally with complete ring of peripheral air-tubes (Figs 9, 24, 26) or crenulate peritreme (Fig. 60), usually with filter consisting of bars projecting into atrium and bearing complex of setae (Fig. 60).

PUPAE. Insufficient is known of tenebrionid pupae to enable the family to be defined on pupal characters. The most important studies are those of Schiödte (1878, 1880) and Daggy (1947). All known tenebrionid pupae have more-or-less extensive lateral lamellae, or occasionally club-shaped processes, projecting from the sides of the anterior abdominal terga (Figs 1, 2, 70). In the vast majority there are lateral gin-traps (Hinton 1946) or curved spines between some of the lateral lamellae (Figs 2, 85, 86). The pupae of *Zolodinus* and *Nyctoporis* (a primitive pimeliine) are described below.

CYTOLOGY. The basic chromosome formula for the family is $9AA + Xy_p$, according to Smith (1952), who summarises the existing cytological data on Tenebrionidae, Zopheridae, and Melandryidae.

PRIMITIVE CHARACTERS

The following characters are almost certainly primitive for Tenebrionidae; an asterisk (*) indicates that the character is almost certainly primitive for Tenebrionoidea also.

ADULTS. *Antennae 11-segmented. Antennae inserted under canthi (substantial, lateral, shelf-like extensions of frons). Prothorax with carinate or explanate lateral margins. *Procoxal cavities open externally. Procoxal cavities partially open internally. *Mesocoxae with exposed trochantins, mesocoxal cavities closed laterally partly by mesepimera. *Elytra 10-striate, with scutellary striole. *Elytra with distinct epipleura extending to apex. *Metacoxae strongly transverse, with internal flanges. *Metendosternite with stalk, laminae, and

anterior median process. *Wings with complete heteromeroid venation and subcubital flecks. *All trochanters heteromeroid. *Tarsal segments and tarsal claws simple. *Tarsal formula 5-5-4. *Aedeagus normally orientated.

LARVAE. Form cylindrical or subcylindrical. *Antennae three-segmented. *Antennae not pubescent. *Antennal sensorium a projecting, cone-like structure. Epipharynx with posterior, sclerotised, masticatory processes. *Mandible without membranous, dorsolateral, setose elevation. Maxillary mala with uncus. *Distinct gula present. *Ocelli five. *Legs all similar, not modified for digging. *Abdomen with pleurosternal sutures. *Abdominal spiracles in one plane in pleural region. *Abdominal tergite 9 bearing urogomphi.

In addition to the characters listed above, the following are probably primitive, but the evidence is inconclusive.

ADULTS. Antenna with distinct club. Terminal segments of palpi not securiform. Apex of lacinia with sclerotised tooth. Abdomen lacking exposed intersegmental membranes between visible sternites (this character is exhibited by all Zolodininae and Toxicinae, some Diaperinae, most Pimeliinae, all Cossyphinae, and Belopini; it is usually associated with certainly primitive characters such as 10-striate elytra or wings with subcubital flecks).

LARVAE. Strip of head capsule between antennal and mandibular bases visible but narrow. Hypopharyngeal sclerome depressed and tridentate anteriorly. Abdominal tergite 9 with distinct ventral surface, or at least vertical posterior surface; anus below it, not subterminal. Abdominal sternite 10 produced into a pair of short, fleshy pseudopods. Spiracles each with complete peripheral ring of air-tubes. (The last-mentioned character is present in the larvae of Zolodininae, Toxicinae, Diaperinae, and most Phrenapatinae, the first three of which are undoubtedly primitive in other respects. Similar spiracles are found in Ciidae, Boridae, Mycteridae, Pythidae, and Pyrochroidae – possibly this is the primitive type of larval spiracle for Tenebrionoidea.)

ARTIFICIAL KEY TO SUBFAMILIES OF TENEBRIONIDAE

ADULTS

1. At least anterior trochanters as in Fig. 40, not of heteromeroid type. Form very convex, nearly hemispherical, *Coccinella*-like. Mesocoxae without exposed trochantins.....NILIONINAE
—Trochanters all of heteromeroid type (Fig. 36). Form very rarely nearly hemispherical, if so then mesocoxae with exposed trochantins..... 2
2. Procoxal cavities open behind (Fig. 4). Wings with subcubital flecks (Fig. 14). Aedeagus inverted (Figs 16, 17). Elytra 10-striate (New Zealand and Tasmania).....ZOLODININAE
—Procoxal cavities closed behind (Figs 71, 72). Other characters not all present together..... 3
3. Postcoxal processes of propleura meeting in middle behind intercoxal process (Fig. 76). Prothorax with anterior margin foliate, semicircular, completely covering head (Fig. 76), lateral margins of prothorax and elytra also foliate. Strongly depressed.....COSSYPHINAE
—Postcoxal processes of propleura not meeting in middle behind intercoxal process (e.g., Fig. 72). Anterior margin of prothorax not foliate, very rarely covering head, lateral margins of prothorax and elytra usually not foliate. Rarely strongly depressed..... 4
4. Margins of head, prothorax, and elytra foliate, outline of head semicircular (Fig. 77). Antennae geniculate, completely concealed in pouches on underside of head when retracted (Fig. 77). Myrmecophilous.....COSSYPHODINAE
—Margins of head not foliate, its outline not semicircular. Antennae not geniculate, antennal pouches absent..... 5
5. Tarsal claws pectinate (Fig. 39).....ALLECULINAE
—Tarsal claws simple..... 6
6. Aedeagus inverted when withdrawn into abdomen and when exerted (i.e., median lobe dorsal, tegmen ventral – Figs 16, 17). Abdomen without exposed intersegmental membranes between visible sternites except in the Palaeartic tribes Pimeliini and Platyopini.....PIMELIINAE
—Aedeagus not inverted. Abdomen usually with exposed intersegmental membranes between visible sternites 3-5 (Fig. 37)..... 7

7. Elytra striate, scutellary striae absent, sutural striae parallel to base. Each mandible tridentate at apex..... PHRENAPATINAE
—Elytra, if striate, with scutellary striae, or at least with sutural striae diverging distinctly at base. Mandibles bidentate, unidentate, or truncate at apex..... 8
8. Labrum (when dissected out) elongate, or at most weakly transverse. Epipharynx and tormae characteristic (Fig. 75). Elytra, if striate, each with 10 striae. Penultimate segments of tarsi frequently lobed below, at least weakly (Fig. 41)..... LAGRIINAE
(See also Belopini, tribe *incertae sedis*)
—Labrum moderately to strongly transverse. Epipharynx and tormae not as above (see, e.g., Fig. 53). Elytra each with fewer than 10 striae. Penultimate segments of tarsi rarely lobed below, if so then elytra nine-striate..... 9
9. Outer surface of each tibia with a shallow, longitudinal groove or median carina, and with anterior and posterior margins of outer surface carinate (Fig. 22). Antennae characteristic, with last six to eight segments bluntly serrate to flabellate on inner margin, and bearing sensilla on the projections (Fig. 20). Tarsal formula sometimes 4-4-4 (*Rhipidandrus*). Body strongly convex..... DIAPERINAE
—If tibiae so formed, then body strongly depressed (*Catapiestus*). Antennae not as above. Tarsal formula 5-5-4..... 10
10. Antennae 10-segmented, with a 3- or 4-segmented club, terminal segment oval (Fig. 18). Mesocoxae without exposed trochantins, their cavities closed laterally by sterna. Molar part of mandibles with fine, transverse ridges. Mandibular prosthema small, slender, projecting upwards from anterior end of mola (Fig. 21)..... GNATHIDIINAE
—Antennae 11-segmented, or if 10-segmented then not clubbed. Mesocoxae usually with exposed trochantins, their cavities always closed laterally partly by mesepimera (Fig. 36). Molar part of mandibles without fine transverse ridges, prosthema larger (Figs 48, 49)..... 11
11. Antennae with distinct, four-segmented, flattened club (Fig. 19). Wings with subcubital flecks (Fig. 14)..... TOXICINAE
—Antennae not thus. Wings without subcubital flecks except in the Australian tribe *Cyphaleini*..... TENEBRIONINAE

LARVAE

(N.B. Larvae of Cossyphinae and Cossyphodinae are unknown.)

1. Distinct gula absent, gular sutures confluent. Mandibular mola with fine, transverse ridges (Fig. 59). Antennal sensorium occupying most of distal half of ventral surface of segment 2 (Fig. 54). Larvae elongate, cylindrical, abdomen without pleurosternal sutures..... PHRENAPATINAE
—Gula present, gular sutures separate (Fig. 81). Antennal sensorium not as above. Other characters not all present in combination..... 2
2. Spiracles each with a complete ring of peripheral air-tubes (Figs 9, 24, 26)..... 3
—Spiracles without a complete ring of peripheral air-tubes, occasionally with crenulate peritreme..... 5
3. Basal part of dorsolateral surface of each mandible with a conspicuous knob- or tooth-like tubercle (Fig. 23). Body weakly sclerotised, without distinct sclerites. Inhabiting bracket fungi (Polyporaceae)..... DIAPERINAE
—Mandibles without such tubercles. Body strongly sclerotised, at least dorsally..... 4
4. Maxillary mala with a small projection (uncus) on inner edge near apex (Fig. 13). Hypopharyngeal sclerome well developed, tridentate anteriorly (Fig. 12). Urogomphi conical (Fig. 7), without basal grooves. Spiracles as in Fig. 9..... ZOLODININAE
—Maxillary mala without uncus. Hypopharyngeal sclerome small and saucer-shaped (Fig. 27), a flat, transverse band, or absent. Urogomphi approximately as in Fig. 28, with longitudinal grooves at base. Spiracles approximately as in Fig. 26..... TOXICINAE
5. Antennal and mandibular bases separated by at least length of antenna (Fig. 78). Form very broad and convex..... NILIONINAE
—Antennal and mandibular bases separated by much less than length of antenna. Form less broad and convex..... 6
6. Body weakly sclerotised, without distinct sclerites. Antennae two-segmented, segment 1 very short, segment 2 conical (Fig. 33), not pubescent. Tergite 9 about same length as sternite 9; anus terminal (Fig. 32)..... GNATHIDIINAE
—Body usually moderately to strongly sclerotised. Antennae not as above. Tergite 9 longer than sternite 9; anus not terminal..... 7
7. Antennae pubescent, two-segmented (Fig. 63), sometimes with a small, convex sensorium at apex of segment 2 (antennae pubescent, three-segmented — cf. Belopini, tribe *incertae sedis*). Antennal and mandibular bases separated by a visible, though narrow, strip of head capsule..... LAGRIINAE
—Antennae not pubescent, rarely two-segmented. Strip of head capsule between antennal and mandibular bases almost always partly concealed by basal membranes..... 8

8. Legs modified for digging: tarsungulus divided into a heavily sclerotised apical lobe and a weakly sclerotised base (Figs 88, 89). Front legs much stouter and with a different setal pattern to others. Hypopharyngeal sclerome usually concave anteriorly, rarely convex (Fig. 79), never tridentate, dorsal surface smooth. Dorsolateral surface of mandible with a membranous elevation bearing numerous setae (Fig. 82). Urogomphi absent.....PIMELIINAE
- If legs so modified, then hypopharyngeal sclerome tridentate anteriorly and raised posteriorly (Fig. 12), or with long anterior extension (Fig. 67). If dorsolateral surface of mandible with a membranous elevation, latter bears only a few setae..... 9
9. Hypopharyngeal sclerome with elongate anterior extension (Fig. 67). Abdominal segment 9 approximately parabolic in outline (Figs 68, 69). Sternopleural sutures of abdomen all absent (Omophlini) or all present (Alleculini).....ALLECULINAE
- Hypopharyngeal sclerome rarely with elongate extension (*Uloma*), if so then sternopleural sutures lacking on abdominal segment 8, but present on others. Abdominal segment 9 rarely parabolic in outline.....TENEBRIONINAE

ZOLODININAE new subfamily

ADULTS. Elongate, moderately convex.

Antennae 11-segmented, filiform, inserted under canthi, which encroach on front margins of reniform eyes. Labrum weakly to moderately transverse, basal membrane exposed. Terminal segments of maxillary palpi fusiform or weakly securiform, those of labial palpi broadly oval, apically truncate. Epipharynx membranous, bearing two longitudinal groups of punctiform sensilla on disc. Mandibles approximately as in Fig. 48, each bifid at apex, molae with (*Tanylypa*) or without fine transverse ridges, without distinct cusps at apex of left mola. Lacinia with small, apical, mesally directed, sclerotised hook.

Prothorax carinate laterally. Front coxal cavities partly open externally and internally (Fig. 4). Mesosternum slightly depressed anteriorly. Mesocoxae contiguous internally, with exposed trochantins; mesocoxal cavities closed laterally partly by mesepimera. Arms of mesendosternite (Fig. 3: mesofurca) branched. Elytra 10-striate, with scutellary striole, and distinct epipleura extending to apex. Metasternum with median longitudinal suture extending more than half distance from posterior to anterior border. Metacoxae oval, slightly oblique, approx. $1.25 \times$ broader than long, narrowly separated, each with internal flange in outer part, continued as internal ridge. Metendosternite with long, slender stalk, without 'laminae' but with anterior median process extending in front of arms, from which it is indistinctly divided (Fig. 3). Wings with subcubital flecks (Fig. 15), somewhat reduced and non-functional in *Zolodinus*. All trochanters heteromeroid. Femora and tibiae unarmed except for apical spurs of latter. Tarsi setose below, segments and claws simple; tarsal formula 5-5-4.

Intersegmental membranes between abdominal sternites 3-5 concealed. Aedeagus (Fig. 17) inverted, parameres completely fused to apex, bearing some fine, preapical setae. Ovipositor elongate, moderately sclerotised, margins of proctiger and paraprocts with rod-like thickenings ('baculi'), valvifer divided from coxite, which is undivided.

LARVAE. See description of *Zolodinus zealandicus* below.

BIOLOGY. *Zolodinus* adults and larvae live under the bark of decaying trees or in rotten logs, mainly in *Nothofagus* forest. The macerated gut contents of one larva examined consisted mainly of wood particles, and some insect fragments. Nothing is recorded of the habits of *Tanylypa*.

REMARKS. This subfamily contains *Zolodinus* Blanchard from New Zealand and *Tanylypa* Pascoe from Tasmania. *Zolodinus* has always been included in Tenebrionidae. The strong

superficial resemblance to *Tenebrio* apparently blinded even such eminent coleopterists as Lacordaire (1859) and Seidlitz (1898) to the fact that the front coxal cavities are open posteriorly, which probably would have caused them to exclude the genus from Tenebrionidae as then recognised. *Tanylypa* was included in Tenebrionidae, "subfamily Borinae", by its author (Pascoe 1869), who correctly described its open anterior coxal cavities.

Both genera differ from Boridae (see Table 1) and agree with Tenebrionidae in the front coxae, which are set at approximately 90° to the longitudinal axis of the body, have substantial, concealed, lateral extensions, and lack exposed trochantins; laterally carinate prothorax; abdomen with three basal, visible sternites connate; and aedeagus with tegmen simple (Fig. 17), i.e., without long, morphologically dorsal projections from apical piece as in *Boros* (Fig. 15). Each lacinia bears a sclerotised hook at its apex, a character frequent in Tenebrionidae but unknown in Boridae. The larva of *Zolodinus* is typical of Tenebrionidae, and quite unlike that of Boridae as described by St. George (1931).

In adult Zolodininae, the only obviously derivative characters in relation to other Tenebrionidae are the inverted aedeagus and the absence of 'laminae' on the metendosternite. The larva of *Zolodinus* has few certainly derivative characters in comparison with other tenebrionid larvae. The pupa is quite similar to those of other Tenebrionidae, and is specialised in lacking functional spiracles on abdominal segment 6.

KEY TO GENERA OF ZOLODININAE (ADULTS)

1. Exposed part of labrum approx. 3 × broader than long. Prothorax transverse. Elytral intervals strongly convex. Mandibular mola without fine, transverse ridges. Apical piece of aedeagal tegmen with almost rectangular apex, latter with small median projection. (New Zealand)..... *Zolodinus*
 —Exposed part of labrum approx. 1.7 × broader than long. Prothorax as long as broad. Elytral intervals almost flat. Mandibular mola with fine, transverse ridges. Apical piece of aedeagal tegmen tapering gradually to apex (Fig. 17). (Tasmania)..... *Tanylypa*

Zolodinus zealandicus Blanchard

LARVA (Figs 5–13). Elongate, cylindrical, moderately sclerotised both dorsally and ventrally, in general appearance like *Tenebrio* larvae. Colour cream, more strongly sclerotised parts brown.

Head moderately convex, slightly transverse, top with three long setae on each side towards base of epicranium, two behind base of antenna, and one just within tentorial pit. Clypeus strongly transverse, with three medium setae on each side and a transverse row of four very small setae on disc. Labrum about half as wide as clypeus, rounded anteriorly, with two moderately long, stout setae on upper surface on each side, and three on each anterolateral edge. Antennae three-segmented, glabrous except for terminal setae, ratio of segment lengths (from base) 4.4 : 4.7 : 1, segment 1 slightly stouter than 2, which is much stouter than 3. Sensorium at apex of segment 2 lens-shaped in profile, reniform in end view (Fig. 10). Epipharynx as in Fig. 11, asymmetrical, surface membranous except laterally and posteriorly. Mandibles as in Figs 5 and 6, apically bidentate, outer dorsolateral edge carinate and bearing three setae, mola and teeth strongly sclerotised. Hypopharyngeal sclerome (Fig. 12) strongly sclerotised, prominent posteriorly, tridentate and somewhat depressed anteriorly. Membranous part of hypopharynx produced into four setose lobes, two before and two beside sclerome (Fig. 12). Maxillary mala (Fig. 13) with small uncus at apex of inner edge, upper surface bearing two rows of stout bristles near inner edge and fine, short setae elsewhere. Maxillary articulating area convex, obliquely divided near outer posterior angle (Fig. 13). Ligula projecting between labial palpi beyond apex of segment 1

of latter, bearing a few very small setae on upper surface of apex. Prementum transverse, bearing two setae; mentum bearing four setae. Submentum and gula completely fused, latter distinct from epicranium, about as long as broad. Strip of head capsule between antennal and mandibular bases very narrow, partly obscured by basal membranes. Ocelli five, arranged in two rows as in Fig. 8.

Thoracic sclerotisations strikingly similar to those in *Tenebrio* (St. George 1929), but coxae slightly more widely separated. Legs about equal in length, which slightly exceeds depth of thorax, front pair slightly stouter. Femora with four to five spiniform setae in a longitudinal row on inner surface, and some fine setae. Each tibia with a row of four spiniform setae on inner surface, and two on posterior surface. Tarsunguli moderately sclerotised, each with a short, anterior, spine-like seta and a longer, very slender, posterior seta on inner surface.

Abdominal tergites 1–8 with a transverse row of four long setae near posterior margin. Tergites 4–8 with a transverse group of conspicuous punctures near base, and some smaller punctures behind them. Pleurosternal sutures distinct, spiracles situated just above them. Sternite 1 with two discal anterior setae, two in each anterior corner, and one on each side behind middle; sternites 2–7 each with two pairs of lateral setae; sternite 8 with one seta on each side near base and a transverse row of four near apex. Abdominal tergite 9 (Fig. 7) ending in a pair of sharp, upturned urogomphi. Sternite 9 curved around sternite 10 (Fig. 7), which is produced into a pair of slender, curved, lightly sclerotised processes.

Spiracles (Fig. 9) oval, cribriform, each with a complete peripheral ring of small air-tubes.

MATERIAL EXAMINED. Two larvae, Reservoir Bush, Cass, Canterbury, N.Z., under rotten log, 20.i.1956, R. L. C. Pilgrim (1 cleared in glycerine, with mouthparts, spiracles, etc. on slide; H.W. 2.00, 1.92 mm). Four adults reared from larvae, some coll. data, emerged 9.v.1956 (1) and ii.1957 (3). About 30 larvae from various other localities, not reared. All in Entomology Division collection, DSIR, Auckland.

PUPA (Figs 1, 2). Elongate, approximately parallel-sided, cream, with sclerotised parts dark brown. Length 19.5–21 mm, width of prothorax 4.2–4.4 mm, greatest width (abdominal segment 4) 4.7–4.8 mm.

Head with a few small, fine setae, without tubercles except two small ones just above each eye. Antennae glabrous. Tips of mandibles sclerotised.

Anterior edge of pronotum with a transverse row of four large, spinous tubercles on each side near middle, with other, smaller tubercles laterally, at anterior and posterior angles, and on lateral margins; also some even smaller tubercles scattered on disc. Remaining thoracic (and abdominal) terga bearing areas of rather sparse pubescence, some of the fine setae of which arise from small tubercles. Legs with a few small setae on outer surfaces. Elytra bare. Metathoracic wings slightly shorter than elytra, and normally almost entirely concealed by them.

Abdominal terga 1–6 have prominent, laterally projecting plates (Fig. 2: lateral lamella), each with strongly sclerotised anterior and posterior spines; plates of terga 3–6 very similar to each other. Tergal plates 7 and 8 much less prominent, with much smaller spines (Fig. 1). Urogomphi as for larva, slightly separated at base, slightly curved, erect, sharp, strongly sclerotised. Genital characters of usual tenebrionid type (viz., male with short, female with longer papillae projecting from sternite 10). All tubercles bear setae arising proximal to

their apices (Fig. 2). Sternopleural sutures absent except on segments 8 and 9. Functional spiracles confined to segments 1–5, spiracles of segment 6 vestigial.

MATERIAL EXAMINED. Two pupae collected as larvae, Cass, Canterbury, N.Z., rotten *Nothofagus* stump, viii.1957, x.1957, R. L. C. Pilgrim (Entomology Division collection).

Subfamily TOXICINAE

Toxicides Lacordaire, 1859, Gen. Col. 5: 341.

Nycteropides Lacordaire, 1859, *op. cit.*: 388 (provisional position).

No definition of this subfamily is given here, as its constitution is not yet certain. The diagnostic characters are given in the key to subfamilies.

It is apparent that the genera *Toxicum* and *Cryphaeus* should be removed from Tenebrioninae. The Malagasy tribe Nycteropini agrees with Toxicini in adult structure in the four-segmented, flattened, antennal club (Fig. 19), the basic structure of the mouthparts, the wings with subcubital flecks, and the aedeagus, in which the apical piece of the tegmen is approximately as long as the basal piece, and the basal half of the median lobe is supported by lateral, sclerotised strips. Nycteropini differ from Toxicini in the presence of exposed intersegmental membranes between visible abdominal sternites 3–5, in the presence of 'laminae' on the metendosternite (otherwise known only in Ulomini and Platydemiini amongst Tenebrionidae), and in the absence of horns or angular projections on the head. The lacinia in Nycteropini is said by Lacordaire (1859) to be unarmed, but in fact it bears a small but quite distinct apical hook, as in Toxicini. Both Nycteropini and Toxicini were included in "Tenebrionini" by Gebien (1938–42).

A new study of larvae of Nycteropini is required before the tribe can be assigned with certainty to Toxicinae. Despite the length of Xambeu's (1904) unillustrated descriptions of *Nycteropus* larvae, they omit such essential information as the detailed structure of the spiracles, epipharynx, hypopharynx, mandibular molae, and antennal sensoria. The general appearance, terminal abdominal segments, and urogomphi differ from those of *Cryphaeus* and *Toxicum* larvae.

Recently the larvae of *Cryphaeus cornutus* Fischer (Byzova 1958) and *Cryphaeus* sp. (Abdullah 1964) have been described. Byzova states that the antennae are four-segmented, but it is obvious from her drawing of this and other larvae that she counts the basal membrane as a segment. Abdullah states that the antennae are two-segmented, but examination of his specimen shows that the short basal segment is retracted and concealed by the basal membrane. Neither author mentions the detailed structure of the spiracles. These have a complete ring of peripheral air-tubes, within which are complex, secondary crenulations and processes (Fig. 26). The filter mechanism consists of a complex system of fine, curved, interdigitating bars. The hypopharyngeal sclerome is a strongly transverse, anteriorly concave structure (Fig. 27), a simple transverse band, or absent. The antennal sensorium on the apex of segment 2 is annular and surrounds segment 3, except for a short dorsolateral gap. Each tarsungulus bears two fine, equal setae on the inner surface.

The characters of the larvae keyed below suggest the desirability of a new genus for the *Toxicum* sp. *A* from Sarawak. *Toxicum* and *Cryphaeus* have never been revised, and the need for a thorough review of the world fauna of Toxicini is evident. The tribe is absent from America although represented in all the other continents, and is most numerous in species in the Oriental region, especially on the islands of Indonesia. It is absent from New Zealand, however.

KEY TO KNOWN LARVAE OF TOXICINAE

1. Sensorium at apex of antennal segment 2 a strongly crenulate, incomplete ring. Peripheral air-tubes of spiracles very small, scarcely or not visible at 25× magnification. Large (H.W. up to 6.9 mm) (Sarawak) *Toxicum* sp. *A*
 — Sensorium at apex of antennal segment 2 a simple, incomplete ring. Peripheral air-tubes of spiracles larger, at least those of thoracic spiracles clearly visible at 25× magnification. Smaller..... 2
2. Abdominal sternite 9 with four conspicuous setae in a transverse row near posterior border, and a few small setae. (New South Wales)..... *Toxicum* sp. *B*
 — Abdominal sternite 9 with at least 16 conspicuous setae in a transverse row near posterior border *Cryphaeus* spp.

MATERIAL EXAMINED. Larvae of: *Cryphaeus duellicus* Lewis – Kikuna-machi, Kohuku-ku, Yokohama, Japan, in fungi and under bark of dead wood, 12.vi.1964, N. Hayashi; *Cryphaeus taurus* Fabricius – Ukurewe I., Lake Victoria, E. Africa, P. A. Conrads (van Emden Coll., El 2950; “Statirinae”); *Cryphaeus* sp. – (see Abdullah 1964); *Toxicum* sp. *A* – Sarawak, foot of Mt. Dulit, junction of rivers Tinjar and Lejok, in fungus on rotten wood, 23.viii.1932, Oxford Univ. Exp., B. M. Hobby & A. W. Moore (B.M. 1933 – 254); *Toxicum* sp. *B* – Bellbird Corner, Kurrajong, Blue Mountains, N.S.W., Australia, dead standing eucalypt, 16.iv.1957, R. A. Crowson.

Subfamily DIAPERINAE new sense

Diaperialae Latreille, [1802], Hist. nat. Crust. Ins. 3: 161.
 Bolitophagiens Mulsant, 1854, Hist. nat. Col. Fr. 5, Latigènes: 218.
 Rhipidandrinae Sharp, 1905, Biol. C. Amer. Col. 2(1): 690.
 Dysantinae Gebien, 1922, Trans. linn. Soc. Lond. Zool. 18: 289.

ADULTS. Moderately or strongly convex, fairly stout. Frequently coarsely sculptured, bearing tubercles and gibbosities, often with horns on head and/or prothorax.

Antennae (Fig. 20) 11-segmented (rarely 10-segmented), bluntly serrate to flabellate, inserted under canthi, which encroach on front margins of eyes, sometimes dividing them completely. Epistomal suture usually distinct. Labrum fairly small, strongly transverse; basal membrane exposed, but concealed from above by clypeus, and visible only from the front. Each mandible bidentate at apex, the left with a long dorsal cutting edge, the right with a dorsal, preapical tooth; molar parts with fine, transverse ridges (visible usually only at high magnification), without cusps, not strongly receding at apex. Epipharynx with two areas of dense pubescence posteriorly above inner projections of tormae, arms of tormae very short. Terminal segments of palpi fusiform or cylindrical. Lacinia without apical tooth. Anterior margin of gena marked by a prominent ridge behind base of mandible and maxilla, usually with a deep antennal groove between ridge and eye.

Prothorax strongly transverse, explanate laterally. Procoxal cavities closed externally, closed internally by a transverse bar (Fig. 71); exposed part of front coxae more-or-less strongly transverse, scarcely projecting. Mesosternum strongly depressed anteriorly, intercoxal processes prominent. Mesocoxal cavities closed laterally partly by mesepimera, contiguous; mesocoxae transverse, their trochantins exposed. Metendosternite with long, slender, usually unbranched arms. Elytra often striate, each with nine striae and scutellary striole, with distinct epipleura and epipleural carinae, which usually reach apex. Metasternum strongly transverse, with distinct median suture. Metacoxae strongly transverse, narrowly separated, each with internal flange running from outer angle to at least middle. Metendosternite of two distinct types: Y-shaped, without anterior median process, with long slender arms bearing anterior tendons near their extremities (*Bolitophagus*); or, arms diverge strongly, and an anterior median process bears anterior tendons (*Eledona*, *Diaperis*) (Fig. 35); ‘laminae’ absent in both types. Wings with only first three anal veins reaching near margin, fourth greatly abbreviated or absent; subcubital flecks absent. All trochanters heteromeroid. Femora flattened on ventral surfaces. Each tibia (Fig. 22) with outer anterior

and posterior edges carinate, a longitudinal groove or median carina between them; tibial spurs short to very short. Tarsal claws and segments simple, latter clothed below with sparse, fine setae; tarsal formula 5-5-4 (4-4-4 in *Rhipidandrus*).

Abdomen usually with intersegmental membranes exposed between visible sternites 3-5. Aedeagus normally orientated. Ovipositor rather variable, short to fairly elongate, without distinct rods, with or without styli.

LARVAE. Cylindrical, weakly sclerotised (except head), tapering somewhat posteriorly, colour generally cream.

Antennae three-segmented, bearing a few setae; sensorium at apex of segment 2 a strongly projecting conical process, a short dome-shaped structure, or a transverse strip (each situated below segment 3), or an incomplete ring surrounding segment 3. Antennal and mandibular bases separated by a narrow, curved strip of head capsule, rarely concealed by basal membranes. Labrum weakly transverse, approximately semicircular. Tormae with prominent backward projections, posterior part of epipharynx with asymmetrical masticatory processes. Mandibles with a single apical tooth, a ventral preapical tooth, and a dorsal cutting edge, which is dentate on the right mandible; dorsolateral surface bearing a large tubercle near base (Fig. 23); molar parts with fine transverse ridges, left mola with a prominent, blunt, triangular projection at apex, right mola slightly receding at apex. Maxillary mala usually broadly rounded at apex, without uncus; bristles of inner surface relatively short and slender. Hypopharynx as in *Menimus* (Fig. 30), but anterior lobe with fewer, shorter setae, and sclerome often more concave anteriorly or almost square. Gular sutures distinct, parallel or diverging posteriorly.

Ventral thoracic sclerotisations weak, confined to episterna, epimera, and sometimes middle parts of sterna. Coxae never contiguous, usually separated by at least a coxal width. Legs slender, similar, bearing some fine setae, without stout bristles. Setae of inner surfaces of tarsunguli usually equal and slender.

Abdomen with pleurosternal sutures. Spiracles situated in line on pleura. Abdominal tergite 9 short, curved downwards to apex, without ventral surface; anus subterminal, short urogomphi frequently present. Tergite 10 membranous, often not distinguishable. Sternite 10 produced into a pair of very short, blunt, membranous lobes.

Spiracles (Fig. 24) with a complete ring of peripheral air-tubes, thoracic spiracles oval, abdominal spiracles circular.

PUBLISHED DESCRIPTIONS OF LARVAE. See Gebien (1938-42: 509-25). Van Emden (1947) keyed the British species, introducing characters previously overlooked. Hayashi (1959) described and figured *Bolitoxenus bellicosus* Lewis and *Diaperis lewisi* Bates.

BIOLOGY. All species of known biology breed in dead brackets of Polyporaceae.

DISTRIBUTION. Cosmopolitan except New Zealand and oceanic islands, most numerous in genera and species in the Oriental region.

REMARKS. This subfamily includes the tribes Bolitophagini, Rhipidandrini, and Dysantini as listed by Gebien (1938-42), and the genus *Diaperis* Geoffroy. This grouping has long been recognised by specialists in larval taxonomy (Schiödt 1878, van Emden 1947), but has not previously been proposed as a formal taxon. Certain adults of Platydemiini (= Diaperini auct. except *Diaperis*) are strikingly similar to adult *Diaperis*, but their larvae are quite

different, and are obviously related to certain Ulomini (e.g., *Alphitobius*). Adults of these genera (*Platydema*, *Ceropria*, etc.) differ from *Diaperis* in their rounded, non-carinate tibiae, perfoliate or sharply serrate antennae, securiform maxillary palpi, and metendosternite with 'laminae' and with anterior tendons borne laterally on arms. *Platydema* spp., like *Diaperis*, inhabit dead bracket fungi (Polyporaceae), and the resemblances between the adults are no doubt due to convergence in similar habitats.

Dysantini are anomalous, lacking exposed intersegmental membranes between the abdominal sternites, and having weakly carinate tibiae and antennae with a basically three-segmented, flattened club, which often becomes two-segmented with fusion of segments 10 and 11. I have not been able to make cleared preparations of any adults, and larvae are unknown, so the tribe's inclusion in Diaperinae is tentative. Dysantini appear to be intermediate in some respects, e.g., antennal structure, between Diaperinae and Toxicinae.

Rhipidandrus adults are strikingly similar to *Eledona* except in their 4-4-4 tarsal formula. Their larvae are unknown, but the genus is almost certainly correctly included in the Diaperinae. The basal segments of pro- and mesotarsi in *Eledona* are small, and not as distinctly divided from the second segments as the remaining segments are from each other. The flabellate antennae of some *Rhipidandrus* no doubt developed from the lateral sensory projections characteristic of normal diaperine antennae, and in some species of the genus the antennae are no more than strongly serrate. Rhipidandrini as defined below includes only *Rhipidandrus*, as *Eledona* and *Bolitolaemus*, referred by Gebien (1938-42) to this tribe, are transferred to Bolitophagini. This simplifies defining the tribe, and on present knowledge is as likely to be phylogenetically correct as Gebien's system.

KEY TO TRIBES OF DIAPERINAE (ADULTS)

1. Abdomen lacking exposed intersegmental membranes between sternites. Antennae 11-segmented with 3-segmented, flattened club, or 10-segmented with 2-segmented club..... **Dysantini**
—Abdomen with exposed intersegmental membranes between sternites 3-5. Antennae with at least six-segmented, bluntly serrate club, or flabellate..... 2
2. Tarsal formula 4-4-4..... **Rhipidandrini**
—Tarsal formula 5-5-4..... 3
3. Sculpture strong, frequently irregular, surface dull, brown or black..... **Bolitophagini**
—Sculpture weak, regular, surface shining, variegated with light markings..... **Diaperini**

KEY TO KNOWN LARVAE OF DIAPERINAE

(*Genus or species examined by me.)

1. Antennal sensorium at apex of segment 2 an incomplete ring surrounding segment 3. Anterior margin of frons produced on each side into a prominent, triangular projection outside clypeal condyle and projecting over base of antenna. Most tergites each bearing a transverse row of small granules (Diaperini)..... ***Diaperis**
(**D. boleti*, *D. lewisi*, **D. maculata*)
—Antennal sensorium at apex of segment 2 a conical projection or small, transverse strip beneath segment 3. Anterior margin of frons not so produced. Tergites without transverse rows of granules (Bolitophagini) 2
2. Urogomphi absent 3
—Urogomphi present..... 4
3. Antennal sensorium longer than segment 3 (see Schiödte 1878)..... ***Eledonoprius armatus***
—Antennal sensorium shorter than segment 3..... ****Eledona agricola***
4. Frons bearing a pair of more-or-less prominent tubercles. Antennal sensorium very short..... 5
—Frons without tubercles. Antennal sensorium about as long as segment 3, conical..... ****Bolitophagus***
(**B. reticulatus*, **B. corticola*)

5. Frontal tubercles approximately as large as dorsolateral projections of mandibles..... 6
 —Frontal tubercles much smaller than dorsolateral projections of mandibles..... 7
6. Distance between frontal tubercles slightly less than distance between tubercle and side of head, when viewed from above.....**Bolitotherus cornutus*
 —Distance between frontal tubercles greater than distance between tubercle and side of head (see Candeze 1861).....*Bolitonaeus quadridentatus*
7. Each frontal tubercle with an indistinct ridge running from it to anterior margin of frons, area between them somewhat depressed with irregular, transverse wrinkles.....**Megeleates sequoiarum*
 —Frons without ridges, depressed area, or transverse wrinkles (see Hayashi 1959).....*Bolitoxenus bellicosus*

Subfamily GNATHIDIINAE

Gnathidiinae Gebien, 1920: Arch. Naturg. 86 A6: 41.

ADULTS. Broadly oval, moderately convex.

Antennae 10-segmented, with distinct, flattened, 3- or 4-segmented club, segments of club with distinct, relatively large, circular sensoria on their apices, terminal segment elongate-oval (Fig. 18). Antennal insertions concealed from above under canthi, which do not encroach on front borders of small and obliquely oval eyes. Head broad, scarcely narrowed behind eyes. Exposed part of labrum transverse, semicircular, basal membrane not exposed. Epipharynx membranous, with anterior median area of punctiform sensilla, on each side of which is an elongate group of relatively long, stout setae. Tormae curved, their inner processes each covered with a dense, longitudinal row of fine setae, and with a dense area of smaller setae between them, behind which is a row of punctiform sensilla. Mandibles (Fig. 21) characteristic, with short, transversely ridged mola, small, narrow, setose protheca, long cutting edge, single, sharp, apical tooth, and often a small, blunt, preapical tooth. Maxillary palpi fusiform or weakly securiform, labial palpi fusiform. Lacinia very slender, without apical tooth.

Prothorax strongly transverse with narrow, explanate margins. Procoxal cavities closed externally, completely closed internally by a transverse bar. Intercostal processes with posterior projection. Mesosternum scarcely depressed anteriorly, strongly transverse, mesocoxal cavities closed laterally by sterna, trochantins concealed. Arms of mesofurca simple, slender, strongly diverging. Elytra each with nine rows of punctures and a short scutellary row, or non-striate, epipleura and epipleural carina distinct, but not reaching apex. Wings usually absent. Metasternum strongly transverse. Metacoxae very slightly oblique, strongly transverse, without internal flanges. Metendosternite with short stalk and long, slender arms, which bear anterior tendons at one-third from apex, without lamina or anterior median process. Femora and tibiae simple, tibial spurs short. Tarsal segments not lobed, bearing a few relatively long, fine setae below; tarsal claws simple; tarsal formula 5-5-4.

Intersegmental membranes exposed between visible sternites 3-5. Aedeagus orientated normally. Ovipositor moderately elongate, with strengthening rods in paraprocts but not proctiger; coxites not divided; styli apical, with prominent setae.

LARVAE. See description of *Menimus* spp. below.

BIOLOGY. In New Zealand, *Menimus* spp. occur in rotten logs, leaf-litter, and dead *Fomes* brackets. The Fijian species are associated with rotten logs and dead branches (Kaszab 1955).

DISTRIBUTION. Tropical West Africa (*Gnathidium*), Japan, Oriental region, islands of western Pacific, New Zealand.

REMARKS. This subfamily is equivalent to the tribe Gnathidiini as listed by Gebien (1938-42). The majority of the species are included in *Menimus* Sharp, which is strongly represented in New Zealand. *Menimus* adults are very similar to *Gnathidium* in their fundamental structures so, although larvae of *Menimus* only are known at present, it is probable that those of *Gnathidium* are basically similar.

The larvae resemble those of Diaperinae in their weakly sclerotised body and sub-terminal anus, but lack the characteristic dorsal mandibular processes, and have simple spiracles and a number of obviously derivative characters, such as tergal glands and two-segmented antennae, unknown in any Diaperinae as defined here. The adults similarly lack the diagnostic derivative characters of Diaperinae, and have a number of derivative characters of their own unknown in Diaperinae (e.g., mesocoxae without trochantins, their cavities closed laterally by sterna).

Gnathidiinae appear to be as closely related to Phrenapatinae as to Diaperinae, perhaps more closely.

Menimus spp.

There are 19 species of *Menimus* described from New Zealand, and until these have been revised it will not be possible to assign specific names to the larvae with certainty. The following description of larvae is based on slide-mounts of two species and a superficial examination of three others associated with adults with reasonable probability.

LARVAE. Elongate, sub-cylindrical, slightly depressed, weakly sclerotised, cream.

Antennae two-segmented (Fig. 33); basal segment very short, segment 2 approx. $7\times$ as long, tapering gradually, with a large, convex, nearly hemispherical sensorium occupying the entire apex, a few short, stout setae laterally, and a single, long seta above and just behind sensorium. Strip of head capsule between antennal and mandibular bases very narrow, partly obscured by basal membranes. Epicranial and frontal sutures rather faint. Clypeus with two short, relatively stout setae on each side, and a few very small, fine setae between and behind them. A small seta behind each posterior angle of clypeus on frons, two large, conspicuous setae on each side behind base of antenna, and one on each side below base of antenna; remainder of head capsule with only some very fine, short setae, which form a sparse pubescence on dorsal and lateral surfaces. Ocelli small, in two groups, the anterior of three and the posterior of two, contiguous in each group and not always distinguishable from each other. Labrum prominent, weakly transverse, with two stout setae and some very small, fine ones on disc, two near middle behind anterior margin, and three on each lateral margin. Epipharynx as in Fig. 31, almost symmetrical, membranous, with asymmetrical, sclerotised masticatory structure posteriorly; tormae as in Fig. 31. Mandibles each with a single, sharp apical tooth and ventral preapical tooth, right mandible with a dorsal preapical tooth, left one with a dentate cutting edge. Molar parts with fine, transverse ridges, chevron-shaped on left mandible, apex of mola of left mandible prominent, that of right receding (as in *Archaeoglenes*, Fig. 59). Outer dorsolateral surface of each mandible rounded, bearing one relatively long seta and a few fine, short setae. Maxillary mala (Fig. 29) elongate, narrow, with two rows of stout bristles on inner surface and a row of fine setae parallel to them on upper surface; uncus absent. Stipes with three setae near base of palp, the seta near each posterior angle, and a few small setae between these. Maxillary articulating area transverse, weakly convex, not distinctly divided. Palpi slender. Ligula not projecting at all, bearing two setae on its upper surface. Hypopharyngeal

sclerome (Fig. 30) symmetrical, anterior margin slightly concave, oral surface almost flat, hypopharynx produced in front of sclerome as a prominent, setose lobe. Prementum with two setae. Mentum with four setae, indistinctly divided from submentum, latter distinctly divided from gula. Gular sutures rather indistinct, gula widening somewhat posteriorly, almost as broad as long.

Each thoracic and abdominal tergite with two long setae arising from each side. Pronotum as long as meso- and metanota combined. Ventral parts of thorax without distinct sclerotisations. Legs all similar, slender, longer than depth of thorax, with a few fine setae, especially on inner surface; each tarsungulus with two minute, equal setae on inner surface. Coxae inserted laterally, separated by more than own diameter.

Each thoracic tergite, and abdominal tergites 1-8, with paired lateral glands, staining with carbol fuchsin in cleared preparations, and visible as faint, brown, oval patches in complete specimens, each situated diagonally above and behind spiracle (except, of course, on pro- and metathorax).

Abdominal spiracles lateral, each just in front of long lateral setae. Pleurosternal sutures present, but not easily visible except in cleared specimens. Each abdominal sternite except first with two long discal setae. Terminal abdominal segments as in Fig. 32; anus sub-terminal, tergite 9 scarcely longer than sternite 9, tergite 10 short, usually concealed under 9, sternite 10 membranous.

Spiracles circular, simple; walls of atrium with small, papilla-like processes; filter apparatus appears to consist of a cribriform plate, but exact structure difficult to interpret even at higher magnifications because of small size of spiracles.

MATERIAL EXAMINED. Many larvae of several New Zealand species.

Subfamily PHRENAPATINAE new sense

Phrépatides [*sic*] Solier, 1834: Ann. soc. ent. Fr. 3: 487.

Phrenapatides Lacordaire, 1859. Gen. Col. 5: 312.

ADULTS. Moderately to strongly convex.

Antennae usually 11-segmented (10 in *Archaeoglenes*) with 2- or 3-segmented club, inserted under canthi, which do not encroach on front borders of usually circular eyes. Labrum transverse, basal membrane exposed or concealed. Each mandible tridentate at apex, molar part of at least right mandible with fine, transverse ridges. Palpi fusiform or oval, never securiform. Lacinia without apical hook.

Front coxal cavities closed externally, completely closed internally by transverse bar (Fig. 71). Exposed part of front coxa transversely oval. Prosternal intercoxal process usually narrow and declivous posteriorly. Mesocoxae closed laterally partly by mesepimera, with or without exposed trochantins. Arms of mesendosternite branched anteriorly. Elytra each 9-striate (10-striate in *Archaeoglenes*), without scutellary striole, distinct epipleuron and epipleural carina extend to apex. Metasternum usually with median longitudinal suture. Hind coxae strongly transverse, narrowly separated. Metendosternite with short stalk and long, slender arms bearing anterior tendons near apices, without distinct median anterior process. Wings, if present, without subcubital flecks. All trochanters heteromeroid. Tarsal segments and claws simple; tarsal formula 5-5-4 (4-4-4 in *Archaeoglenes*).

Abdomen with exposed intersegmental membranes between visible sternites 3-5. Aedeagus orientated normally. Ovipositor fairly short, without styli.

LARVAE. Elongate, cylindrical, white or cream, weakly sclerotised.

Antennae three-segmented, segment 2 with one or more fine, short setae, 3 with three apical setae. Antennal sensorium a large, irregularly oval, membranous area, occupying distal half of lower surface of segment 2 (Fig. 54). Strip of head capsule between antennal and mandibular bases very narrow, but not obscured by basal membranes. Each mandible with a single apical tooth and two preapical teeth, one dorsal and one ventral; molar part with fine, transverse ridges. Molar part of left mandible prominent, that of right regularly curved and receding to apex (Fig. 59). Hypopharyngeal sclerome nearly quadrate in dorsal view, oral surface flat, hypopharynx produced in front of sclerome as a dome-shaped, setose projection. Maxillary mala without uncus, with two rows of stout bristles on dorsal surface near inner edge. Mentum distinctly divided from submentum. Distinct gula absent, gular sutures confluent.

Legs fairly short and slender; coxae almost contiguous, their chaetotaxy similar; each tarsungulus with two short, equal setae on inner surface.

Abdomen without distinguishable sternopleural sutures, segments regularly cylindrical with smooth surface. Abdominal tergite 9 paraboloid (Fig. 57), or with a pair of sclerotised spines arising on upper surface near base and curving backwards over an extensive excavation. Segment 10 membranous, produced into a short, pygopod-like structure.

Spiracles circular, with a complete peripheral ring of small air-tubes (as in Diaperinae, Fig. 24), or simple (*Archaeoglenes*).

PUBLISHED DESCRIPTIONS OF LARVAE. The larva and pupa of *Phthora crenata* were described by Perris (1857: 361-4), and the larva of *Tagalus cavifrons* was described by Gebien (1922: 296). The larva of *Dioedus punctatus* is similar to these, as noted by van Emden (1947). Ohaus (1909: 73) says that larvae of *Phrenapates ohausi* resemble mealworms in the form of the body, but are milk white. This brief description has some value, as it is probable that Ohaus would have noted any features as characteristic as the spines of abdominal tergite 9 of *Phthora* and its relatives, a condition quite unlike that found in mealworms.

BIOLOGY. *Phrenapates ohausi* exhibits parental care (Ohaus 1909). Adults cut galleries in dead stems of *Bombax*, and the larvae develop in lateral chambers, feeding on fine shavings of the wood provided by the adults. The larvae die when deprived of the wood shavings, apparently being unable to tear away the wood themselves. All other known phrenapatine larvae live in rotten wood.

REMARKS. As defined here, Phrenapatinae comprises the genera of the tribe Phrenapatini listed by Gebien (1938-42: 562-6), and the New Zealand genus *Archaeoglenes* Broun, 1893, which has the tarsal formula 4-4-4 and was referred to Colydiidae by its author. Both adults and larvae of *Archaeoglenes* agree with Tenebrionidae, and especially with Phrenapatinae, in their basic structure. All the adults examined so far have been females, so the structure of the aedeagus is unknown.

KEY TO TRIBES OF PHRENAPATINAE

ADULTS

1. Elytra 10-striate. Antennae 10-segmented. Tarsal formula 4-4-4. Sides of head and anterior part of prothorax with deep grooves for antennae..... **Archaeoglenini**
—Elytra 9-striate. Antennae 11-segmented. Tarsal formula 5-5-4. Sides of head and prothorax without deep grooves for antennae..... **Phrenapatini**

LARVAE

1. Abdominal tergite 9 parabolic in outline (Fig. 57), spiracles simple.....**Archaeoglenini**
 —Abdominal tergite 9 with two sclerotised spines near base, on dorsal surface, which curve backwards over an excavation (except perhaps in *Phrenapates*). Spiracles with a complete peripheral ring of small air-tubes.....**Phrenapatini**

Archaeoglenini new tribe

This is known to contain only *Archaeoglenes costipennis* Broun, although it is possible that other members of the tribe remain to be recognised as Tenebrionidae. The resemblance between the larva of *Archaeoglenes* and those of *Phthora*, *Tagalus*, and *Dioedus* in basic features is so strong that it is unlikely to be due to convergence. The simple spiracles of the larva and reduced tarsal formula of the adult may perhaps result from the small size of *Archaeoglenes*. The larva is sufficiently characterised in the subfamily definition and keys above.

MATERIAL EXAMINED. About 30 larvae from dead twigs, Waipoua Forest, N. Auckland, and decaying *Nothofagus* stump, Third House, Nelson.

Tribe Phrenapatini

On adult structure, this falls into two distinct groups. *Phrenapates* and *Delognatha* have mesocoxae with exposed trochantins and large, strongly projecting mandibles. The remaining genera have mesocoxae without exposed trochantins, and less prominent mandibles. The differences are probably of at least subtribal value, but this requires further study.

The tribe is strongly represented in the Neotropical region, and occurs in all the other major regions except the African mainland. There are two endemic genera in Malagasy, and *Tagalus* spp. occur on islands in the Pacific and Indian Oceans.

MATERIAL EXAMINED. Larvae of *Dioedus punctatus*, *Tagalus cavifrons*, and *Tagalus* sp. (Japan; slide).

Subfamily TENEBRIONINAE new sense

Tenebrionites Latreille, [1802], Hist. nat. Crust. Ins. 3: 165, 170.
 Helopii Latreille, [1802], *op. cit.*: 176.

ADULTS. Antennae 11-segmented, filiform, gradually thickened or perfoliate, rarely distinctly clubbed; if so, not as in Figs 18–20. Labrum distinctly, usually strongly, transverse (Fig. 52). Maxillary palpi at least weakly securiform. Procoxal cavities closed externally, usually closed internally by a transverse bar, but almost always with at least a small posterior opening behind it (Fig. 71). Mesocoxal cavities closed laterally partly by mesepimera. Elytra, if striate, each with no more than nine striae and scutellary striae. Metendosternite with anterior tendons usually borne on arms (Figs 43, 46, 47). Wings, if present, without subcubital flecks except in the Australian tribe Cyphaleini. Abdomen with intersegmental membranes exposed between visible sternites 3–5. Aedeagus orientated normally (i.e., not inverted). All trochanters heteromeroid. Tarsal segments usually simple, sometimes lobed, but penultimate segment not lobed. Tarsal claws simple.

LARVAE. Body usually moderately to strongly sclerotised. Antennae three-segmented, rarely two-segmented, glabrous or with a few setae, not pubescent. Antennal and mandibular bases not widely separated. Mandible without dorsolateral tubercle, often with membranous setose elevation in its place. Hypopharynx variable, with sclerome, latter with elongate anterior extension only in *Uloma*. Gula present. Legs all similar, or front legs longer and stouter than others; if so, then tarsungulus usually with a strongly sclerotised apical lobe and weakly sclerotised base (Fig. 88). Tenebrionine larvae with the latter type of tarsungulus

("Blapimorpha", Skopin 1962) have a hypopharyngeal sclerome tridentate anteriorly, with raised posterior part (Fig. 12). Sternopleural sutures present on abdominal segments 1-7 and (usually) 8. Urogomphi frequently present. Abdominal tergite 9 with a distinct posterior or ventral surface, rarely paraboloid; anus usually situated ventrally, rarely subterminal. Sternite 10 usually produced into a pair of more-or-less prominent, usually weakly sclerotised pseudopods. Spiracles without complete peripheral air-tubes, but sometimes with peripheral crenulations (Fig. 60), cribriform.

PUBLISHED DESCRIPTIONS OF LARVAE AND PUPAE. See Gebien (1937-44). General works on larvae of regional tenebrionid faunas published since Gebien, and containing much new data on larvae of Tenebrioninae, are Korschefsky (1943), van Emden (1947), Hayashi (1959, 1966, 1968), and Ghilarov (1964). Our knowledge of "Blapimorpha" has recently been increased considerably by Skopin (1960a, Blaptini), Keleinikova (1961, "Opatrinae"), and Schulze (1962, 1963, Opatrini; 1964, Platynotini; 1968, Drosochrini; 1969, Scaurini). Marcuzzi & Rampazzo (1960) described several larvae of Tenebrioninae (mainly "Blapimorpha"). Other important recent papers are Skopin (1964b, *Pseudhelops tuberculatus posticalis* Broun), Byzova & Ghilarov (1956, Helopini), and Ghilarov & Svetova (1963, Helopini). Daggy's (1947) study of tenebrionid pupae deals with Diaperinae and Tenebrioninae. Spilman (1966) described the larvae and pupa of *Amarygmus morio* (Fabricius).

REMARKS. This very large subfamily, even after the removal of such tribes as Adeliini, Pycnocerini, and Bolitophagini, contains about half the species of Tenebrionidae. The diversity of the included forms is great, but at present no satisfactory basis is apparent for further subdividing the subfamily into groups of status equivalent to the other subfamilies recognised here.

Blapimorpha, Tenebriomorpha, Diaperimorpha, and Ulomimorpha of Skopin's (1964a) larval classification are included here. The case for separating his Blapimorpha as a separate subfamily may appear strong on larval characters, but no satisfactory characters for distinguishing all adults of this group from other Tenebrioninae have been found. Larvae of Helaeini and Nyctozoilini agree with Blapimorpha in leg structure, but with more primitive Tenebrioninae in the absence in many of them of membranous, dorsolateral, setose elevations on the mandibles, and especially with Cyphaleini in their essential structure. The larvae of *Tenebrio* and other Tenebrionini have the front legs longer and stouter, and the apex of the tarsungulus considerably more strongly sclerotised than the base, although the distinct division characteristic of Blapimorpha is lacking. In larvae, as in adults, there is a series of forms intermediate between the most specialised Blapimorpha and *Tenebrio*, so that it is not desirable to split Blapimorpha off as a separate subfamily. The "Opatrinae" of Koch (1956) and others are Blapimorpha with a deeply emarginate clypeus in the adult. They may be a monophyletic group, but are not worthy of subfamily status.

The resemblances between the larvae of *Uloma* and Alleculinae are probably due to convergence. In *Uloma* the hypopharyngeal sclerome has a long, narrow, anterior process (e.g., Fig. 67), pleurosternal sutures are absent or reduced on abdominal segment 8, and tergite 9 is paraboloid with an apical point. *Uloma* larvae live in damp, rotten wood, as do many larvae of Alleculinae, and this is probably the primitive larval habitat of the latter subfamily. The larva of *Aphthora rufipes* Sharp, which, like that of *Uloma*, inhabits rotten wood, is even more like alleculine larvae in general appearance, but lacks the long anterior process of the hypopharyngeal sclerome, and has complete pleurosternal sutures. When other characters are taken into account, *Aphthora* provides a link between *Uloma* and

Platydemini rather than Alleculinae. There are no characters of adult *Uloma* or *Apthora* which could justify placing them in a different subfamily from such genera as *Alphitobius*, *Tribolium*, and *Platydema*.

The last three genera are members of Skopin's "Diaperimorpha". Apart from *Diaperis*, which of course belongs to Diaperinae (q.v.), members of this group are not satisfactorily separable from the other Tenebrioninae on adult characters. Skopin (1964a) separates Diaperimorpha from Tenebriomorpha on the structure of the hypopharyngeal sclerome, which is anteriorly flat or concave, with a smooth dorsal surface. This may be diagnostic within Tenebrioninae of the tribes concerned (Triboliini, Alphitobiini, Hypophloeini, Platydemini), but it is not by itself sufficient to exclude them from the subfamily.

Certain Tenebrioninae are distinguishable in the adult stage by the exposed basal membrane of the labrum (some Misolampini and Cnodalonini, all Helopini, Helopinini, Amarygmini (including Meracanthini) and Strongyliini). No means of associating them nor of separating them from other Tenebrioninae, on larval characters, are apparent. The larva of *Emyon tristis* Fahraeus (Helopinini) seems from Jack's (1918) description to have the characters of Blapimorpha. Larvae of Helopini are readily recognised by the characteristic long, recurved urogomphi and declivous tergite 8 (e.g., Byzova & Ghilarov 1956, van Emden 1947). *Meracantha contracta* and most Amarygmini have larvae with tergite 9 with a regular, oval, dorsal excavation (Böving & Craighead 1931, pl. 57), but some species of the Australian genus *Chalcopteroides* Strand lack this, and have short urogomphi borne on an oblique projection. Strongyliini have larvae with tergite 9 armed with complex urogomphi, tubercles, and teeth (Böving & Craighead, pl. 57). The larva of *Pseudhadrus seriatus* Kolbe is essentially similar (Gebien 1922). Although these larvae are individually characteristic and easily recognisable, they have the basic characters of Tenebrioninae.

The tribe Tenebrionini has been used as a dumping-ground for distantly related primitive forms. Gebien's (1938-42) tribe of this name includes another family (Boridae), two other subfamilies (Zolodininae and Toxicinae), the tribe Belopini (see tribes *incertae sedis*, below) and other genera whose close relationship to *Tenebrio* is open to serious doubt (e.g., *Pseudhadrus*, *Catapiestus*, *Arthrodactyla*, *Osphyoplesius*, *Iscanus*).

Adelonia (= *Rhacius*), *Alaephus*, *Eupsophulus*, and the American species "*Bius*" *estriatus* (but not the type species *B. thoracicus*) lack exposed intersegmental membranes between visible abdominal sternites 3-5 (Arnett 1963, pp. 659-61). These are referred to Pimeliinae, but require further study.

The Australian tribe Cyphaleini is included here because it has not been possible to discover any satisfactory characters for separating it from all Tenebrioninae in the adult stage. Cyphaleini have wings with subcubital flecks, but this is a primitive character, and derivative characters which could be used for separating the tribe from Tenebrioninae are not apparent. The larvae (described below) may be distinguished, with those of Helaeini and Nyctofoilini, by the small, regular crenulations of the spiracular peritreme (probably derived from peripheral air-tubes). In this and other respects larvae of the Australian genera *Meneristes* and *Asphalus*, usually placed in Tenebrionini, agree with Cyphaleini. A few other Tenebrioninae have crenulate spiracles, but the crenulations are irregular, are in the walls of the atrium, and do not affect the peritreme.

The tribe Cnodalonini as listed by Gebien (1938-42) includes a large number of poorly studied, mainly tropical genera, many of which are probably not closely related to *Cnodalon*.

Larvae of these genera are virtually unknown. That of *Phaedis helopioides*, described by Hayashi (1959, p. 478), is of the form characteristic of Helopini, so *Phaedis* should be transferred to the latter tribe. Certain Australian and New Zealand genera previously referred to Cnodalonini (e.g., *Artystona*, *Titaena*) should be removed, probably to a new tribe. The larva of *Artystona* is primitive, similar in some respects to larvae of Diaperinae and Toxicinae, but lacking their diagnostic characters. Its nearest relative among known larvae is that of *Pseudhelops*, described by Skopin (1964b), but the relationship is not very close. *Pseudhelops* has previously been attributed erroneously to Adeliini (Lagriinae), but the adult, like the larva, shows an affinity to *Artystona* (Watt 1971). The New Zealand genus *Cerodolus*, also attributed erroneously to Adeliini, is intermediate between *Pseudhelops* and *Artystona* in some characters of both adults and larvae.

The most necessary task remaining in the major classification of Tenebrionidae is the construction of a satisfactory tribal classification of Tenebrioninae. This cannot be done at present because of inadequate knowledge of adults, and the complete absence of knowledge of larvae of a high proportion of genera. Some genera now remaining in Tenebrioninae may have to be removed to other subfamilies.

KEY TO MAJOR GROUPS OF LARVAE OF TENEBRIONINAE

1. Spiracular peritreme with distinct, regular, more-or-less semicircular crenulations (Fig. 60). (Australia and New Zealand)..... 2
—Spiracular peritreme without crenulations..... 3
2. Legs modified for digging, front legs much stouter and somewhat longer than others, tarsunguli each with a strongly sclerotised apex. Urogomphi absent, dorsal surface of tergite 9 weakly to moderately concave before apex (Fig. 61). Outer dorsolateral edge of mandible with at least two setae near base. Larvae usually in soil, sometimes in rotten wood..... **Helaeini, Nyctozoilini**
—Legs not modified for digging and urogomphi present, or (*Lepispilus*) with legs modified for digging and urogomphi absent, but dorsal surface of tergite 9 convex, and outer dorsolateral edge of mandible with only a single seta near base. Larvae in rotten wood..... **Cyphaleini**
3. Legs modified for digging (see couplet 2), each tarsungulus divided into a strongly sclerotised apical lobe and weakly sclerotised base (as in Fig. 88). Outer dorsolateral edge of mandible with a membranous, setose elevation near base. Urogomphi absent. Larvae in soil..... **"Blapimorpha"**
[Scaurini to Crypticini inclusive of Gebien (1938-42), except Pimeliini, Platyopini, Physogasterini, Praocini, Branchini, Coniointini, Coelini.]
—Legs not or little modified for digging, sometimes with front legs longer and stouter than others, but tarsunguli evenly sclerotised. Mandible very rarely with a membranous, setose elevation on dorsolateral edge. Urogomphi frequently present. Larvae rarely in soil..... 4
4. Antennal and mandibular bases separated by a clearly visible, though narrow, strip of head capsule..... **Artystona, Cerodolus, Pseudhelops**, and probably some Australian genera
—Strip of head capsule between antennal and mandibular bases very narrow, depressed, partly to almost completely concealed by basal membranes..... 5
5. Hypopharyngeal sclerome with an elongate anterior extension, as in Alleculinae (Fig. 67). Sternopleural sutures absent on segment 8. Abdominal tergite 9 paraboloid, with an apical point..... **Uloma**
—Hypopharyngeal sclerome without an elongate anterior extension. Sternopleural sutures present on segment 8. Abdominal tergite 9 not as above..... 6
6. Hypopharyngeal sclerome straight or concave anteriorly, dorsal surface flat. Dorsal surface of body usually much more strongly sclerotised than ventral surface.....
Platydemini, Triboliini, Alplitobiini, Hypophloeini sensu
Reitter (1917) [= Diaperini except *Diaperis* and *Ulomini* except *Uloma* of Gebien (1938-42)]
—Hypopharyngeal sclerome tridentate or trilobed anteriorly, anterior part of dorsal surface depressed, usually concave, posterior part raised. Body fairly evenly sclerotised, dorsal surface not much more strongly sclerotised than ventral surface..... 7
7. Abdominal tergite 8 declivous posteriorly. Tergite 9 short; urogomphi longer than it, sharp, recurved, and pointing forwards..... **Helopini**
—Abdominal tergite 8 not declivous posteriorly. Tergite 9 longer; urogomphi shorter than it, not pointing forwards, or absent..... 8
8. Body strongly depressed. Urogomphi bearing a number of hook-like tubercles at their bases on dorsal and lateral surfaces (Gardner 1932)..... **Catapiestus**
—Body not, or weakly, depressed. Urogomphi with different or without armament, or absent..... 9

9. Dorsal surface of tergite 9 with a prominent, transverse elevation on each side, bearing several sharp, curved teeth. Each urogomphus with a hook-like tubercle on inner surface near base (see Böving & Craighead 1931, pl. 57)..... **Strongyliini and Pseudhadrus**
—Tergite 9 and urogomphi with different or without armament..... 10
10. Dorsal surface of tergite 9 with a large, regular, oval excavation OR (some Australian larvae) urogomphi short, borne on a process projecting obliquely upwards..... **Amarygmini** (including **Meracanthini**)
—Dorsal surface of tergite 9 without a regular, oval excavation. Urogomphi (if present) arise directly from tergite 9..... **Tenebrionini sensu stricto, Coelometopini, Misolampidus**, and probably other Misolampini

LARVAE OF CYPHALEINI

It is necessary to include here larvae of some Australian genera formerly included in Tenebrionini (*Asphalus*, *Meneristes*, and probably others). These larvae are similar to those of undoubted Cyphaleini in so many respects that it is undesirable to separate them in different tribes. The adults of *Meneristes*, like those of all Cyphaleini studied, have strong subcubital flecks in their wings, a character not found in true Tenebrionini. *Asphalus* adults are wingless, but resemble *Meneristes* adults in general appearance. As will be noted in the key above, the larva of *Lepispilus* is not easily separated from those of Helaeini and Nyctoziolini.

KEY TO AUSTRALIAN CYPHALEINE LARVAE EXAMINED

1. Urogomphi absent, abdominal tergite 9 paraboloid, bearing four short, articulated spines just before apex (Fig. 58). Front legs much stouter, and with a different setal pattern to other legs. Antennal sensorium a long, vertically elongate, sinuous strip on an extensive, oblique, membranous area below base of segment 3 (Fig. 55)..... **Lepispilus**
—Urogomphi present, articulated spines absent from tergite 9. Front legs very slightly or not stouter than others, setal patterns of all legs similar. Antennal sensorium a U-shaped or horizontally sinuous strip on apex of segment 2 below segment 3..... 2
2. Abdominal tergite 9 with two small, dentate tubercles on each dorsolateral margin anterior to urogomphi. Antennal sensorium with several situations..... 3
—Abdominal tergite 9 with only one or without dentate tubercles on dorsolateral margin. Antennal sensorium nearly U-shaped, but usually with long arms..... 6
3. Urogomphi contiguous at base. Anterior lateral angles of frons raised and produced slightly over antennal insertions..... **Asphalus**
—Urogomphi distinctly separated at base. Anterior lateral angles of frons not raised and produced over antennal insertions..... 4
4. Lower surface of abdominal tergite 9 with two prominent spines below urogomphi and two granules on each side in line with the spines..... **Genus B**
—Lower surface of abdominal tergite 9 without such armament..... 5
5. Each urogomphus with a prominent, obtuse, angular projection on its inner surface near base. Spiracular crenulations very numerous, exceeding 30 in abdominal spiracles..... **Genus A**
—Urogomphi without projections. Spiracular crenulations few..... **Meneristes**
6. Abdominal tergite 9 with one dentate tubercle on each side..... **Trisilus**
—Abdominal tergite 9 without dentate tubercles..... **Genera indet.**

MATERIAL EXAMINED. Larvae of: *Lepispilus rotundicollis* Blackburn – Ebor, N.S.W., under log in gum forest, 1.xii.1963, B. P. Moore No. 30 (reared in wood mould, emerged iii.1964; exuviae); *Lepispilus sulcicollis* Boisduval – Healesville, Victoria, 4.v.1958, B.P.M. No. 3 (H.W. 3.88 mm); Mt. Macedon, Vict., 14.ix.1958, B.P.M. No. 7 (H.W. 3.92, 4.28 mm); Cape Otway, Vict., 9–15.x.1952, E.M. (National Museum of Victoria; H.W. 4.4 mm); *Trisilus punctipennis* Carter – Federal Highway, N.S.W., in large, soft, dry log, 28.ix.1963, B.P.M. No. 13 (pupa reared; H.W. 1.56, 2.28, 2.36, 2.72, 2.80 mm); *Asphalus ebeninus* Pascoe – 1 adult, 6 larvae, Walcha, N.S.W., in damp log in scrub, xi.1963, B.P.M. No. 24 (H.W. 2.72–2.80 mm); *Meneristes australis* Blessig – Tharwa, A.C.T., 6.x.1963, B.P.M. No. 20 (identity confirmed by rearing; H.W. 2.48, 2.68, 3.04 mm); *Meneristes latior* Carter – Tooloom Range, N.S.W., in very wet log in rain forest, ix.1963, B.P.M. No. 28 (adult + exuviae) and 29 (H.W. 2.20, 3.32 mm); **Genus A** – Barrington Tops, N.S.W., ix.1963, B.P.M. No. 22; Eagle Mountains, SE Queensland, 23.iii.1955, S. B. Gunn (Queensland Museum); **Genus B** – Homebush, Queensland, boring in mangroves, 6.viii.1932, F. J. Gay No. 29 (Australian National Insect Collection; H.W. 1.16, 1.29 mm). Some undetermined larvae are not included in this list.

Lepispilus spp. larvae (Figs 55, 56, 58, 60)

(The following description is based on both species listed above, which are very similar.)

Elongate, cylindrical, strongly sclerotised, brown.

Antennae (Fig. 55) three-segmented, glabrous except for apical setae, ratio of segment lengths about 8:8:1, segments 1 and 2 about equally stout, 3 minute. Antennal sensorium an elongate, strongly sinuous strip on elongate, oblique, membranous area below segment 3. Upper surface of head with two long setae on each side, the first above posterior group of ocelli, the second at level of divergence of epicranial sutures. Frons with a single pair of smaller setae on anterior margin towards sides. Clypeus with two setae on each side near lateral margin. Labrum with two conspicuous setae on disc, three on each side, and four small setae on front margin. Epipharynx as in Fig. 56. Mandibles bidentate at apex, with a long, curved, dorsal cutting edge. Molae prominent, that of left mandible projecting at apex, that of right receding somewhat, surfaces of both slightly irregular. Apical teeth, cutting edges, and molae strongly sclerotised. Outer dorsolateral edge of each mandible bluntly carinate, bearing a single seta near base. Maxillary mala broadly rounded anteriorly, with two distinct rows of stout bristles on inner surface, other, short, rows beside them, and a parallel pubescent area on dorsal surface. Stipes with three setae at base of palp and one near posterior angle. Maxillary articulating area extensive, convex, longitudinally divided. Hypopharynx without anterior or lateral lobes, with distinct, slightly asymmetrical sclerome which is tridentate anteriorly; dorsal surface of sclerome depressed and somewhat concave anteriorly. Ligula projecting as far as apex of segment 1 of labial palp, without setae. Prementum and mentum each with two setae on each side. Mentum distinctly divided from submentum, which bears one seta on each side near base of cardo, not divided from gula. Gular sutures rather faint, gula slightly transverse, barrel-shaped. On each side of gula, behind cardo, is a sparsely pubescent area and two conspicuous setae behind outer angle of cardo. Ocelli arranged in two groups, the first containing three in an almost vertical line behind base of antenna, the second above and behind these, comprising two contiguous ocelli. Behind lowest ocellus are two conspicuous setae on side of head, and a vertical line of three in front of them, just behind base of antenna and mandible.

Pronotum almost as long as meso- and metanota combined, with six long setae behind anterior margin and six before posterior margin. Meso- and metanotum each with a long seta near each anterior lateral angle, and a transverse row of six near posterior margin. Ventral part of thorax without distinct sclerotisations except for small presterna, episterna, and epimera. Thoracic spiracles large, oval, peritreme with small crenulations. Front legs distinctly longer and stouter, front femora more than twice as wide as others. Coxae almost contiguous. Trochanter with two stout bristles on inner surface, femur with two parallel rows of similar bristles on inner edge and two on posterior surface; tibia with two rows of stout bristles on inner surface and a few small ones on posterior surface. Tarsungulus strongly sclerotised at apex, more weakly at base, but without a definite division between, setae of inner surface about equal, one-third length of tarsungulus. Middle and hind legs more slender, with only a single row of fine bristles on inner surface of femur.

Abdominal terga 1-8 with a distinct, internal, longitudinal ridge on each side, spiracles situated near anterior of 'pleura' just below this line, sternopleural sutures distinct. Arrangement of setae on terga 1-8 as for meso- and metanota. Sterna 1-8 each with a seta near each lateral angle, sternum 1 with another pair near middle of anterior edge, sternum 8 with a pair near middle of posterior edge. Tergite 9 paraboloid, with four small, articulated spines on edge of dorsal surface near apex (Fig. 58). Sternite 9 short (only one-seventh the length of tergite 9), transverse, with a transverse row of six setae near posterior margin. Tergite 10 and sternite 10 completely membranous.

Abdominal spiracles oval, peritreme of each with small, semicircular crenulations (Fig. 60); walls of atrium grooved, bearing numerous minute setae, especially in grooves. Filter apparatus a complex of closely intermeshed setae, arising from transverse bars.

Subfamily ALLECULINAE

Alleculidae Seidlitz, 1891, Fauna Balt. ed. 2: 49.

Cisteleniae Latreille, [1802], Hist. nat. Crust. Ins. 3: 187 (based on *Cistela* Fabricius, 1775 not Müller, 1764).

Petriidae Semenow, 1893, Bull. Acad. Imp. Sci. St. Petersbourg (n.s.) 3(35): 607.

This subfamily is exactly equivalent to the family Alleculidae of authors, and requires no definition here. The name Alleculinae is "a widely accepted family-group name that was established before 1961 under a different procedure" from that stated in Article 39 of the International Code of Zoological Nomenclature (1961). Thus, as provided in the Code, there is no need to alter it to a name based on *Gonodera* Mulsant, 1856 (= *Cistela* Fabricius, 1775).

Larvae of only the Palaearctic Alleculinae are moderately well known. The most important recent studies of these are Oglobin & Znoiko (1950, Omophlini), Korschefsky (1943), and Striganova (1961, Alleculini).

Probably the most primitive Alleculinae on adult characters are the tropical American genera *Prostenus*, *Lystronychus*, and *Xystropus*. Crowson (1955) states that the metendosternite of *Prostenus* resembles that of *Meryx* and *Penthe*. This probably approximates to the primitive condition for Tenebrionidae. Unfortunately the larvae of these American genera are unknown. Undetermined larvae from North America and Australia, and *Tanychilus* (Figs 67–69) and *Xylochus* from New Zealand, are fairly close to larvae of known Palaearctic Alleculini.

Alleculini have a worldwide distribution, including certain oceanic islands, and are most numerous in the tropics. The genus *Labetis* contains the only Tenebrionidae occurring naturally on the Hawaiian Islands. Omophlini are almost exclusively Palaearctic in distribution. The highly specialised *Petria* is apparently on omophline (Lawrence 1971). The pectinate claws of adult Alleculinae are evidently an adaptation which assists walking on foliage, where they are usually found.

KEY TO TRIBES OF ALLECULINAE

ADULTS (partly after Seidlitz 1920)

1. Canthi over antennal insertions reaching and encroaching on anterior margins of eyes. Metacoxae recessed in distinctly margined cavities formed by anterior depressions of visible abdominal sternite 1. Tarsal segments frequently lobed below..... **Alleculini**
- Canthi very small, scarcely covering base of scape, not reaching back to anterior margins of eyes. Anterior part of visible abdominal sternite 1 indistinctly depressed, not forming distinct, margined cavities. Tarsal segments simple..... **Omophlini**

LARVAE

1. Abdomen with distinct sternopleural sutures. Legs rarely modified for digging. Sternite 10 produced into a pair of usually long, curved, slender pseudopods (Fig. 68). Larvae living in rotten wood, rarely in soil..... **Alleculini**
- Abdomen without sternopleural sutures. Legs modified for digging; front legs much longer and stouter than others, and with a different arrangement of setae; tarsunguli strongly sclerotised, with unequal setae, one of them displaced on to inner lateral surface. Sternite 10 not produced into pseudopods. Larvae living in soil..... **Omophlini**

MATERIAL EXAMINED. Larvae of: *Prionychus ater*, *Pseudocistela ceramboides*, *Allecula rhenana*, *Isomira murina*, *Tanychilus sophorae* (Figs 67–69), *T. metallicus*, *Xylochus* sp., *Hymenorus* sp., *Ctenopus flavus*, *Omophilus lepturoides*.

Subfamily LAGRIINAE new sense

Lagriariae Latreille, 1825, Fam. nat. Regne anim.: 381.
Lagriidae auctorum.

ADULTS. Antennae 11-segmented, filiform, rarely moniliform, sometimes with indistinct, three-segmented club. At least base of scape concealed from above by canthus, which encroaches on anterior margin of reniform eye (but eye small, circular in *Laena*). Epistomal suture faint or absent, clypeus relatively short. Labrum elongate to slightly transverse, never strongly transverse (except exposed part, which often is), basal membrane exposed or not. Tormae and epipharynx (Fig. 75) characteristic. Mandibles strongly (Pycnocerini) or weakly bidentate or truncate at apex (Fig. 74), sclerotisation of molar part of at least one mandible characteristically triradiate or triangular (Fig. 73), except in some Pycnocerini. Apex of lacinia without sclerotised hook, except in Pycnocerini.

Prothorax with explanate lateral margins, or carinate laterally, or completely rounded laterally (Lagriini). Procoxae usually weakly or not projecting and contiguous internally, sometimes projecting strongly and contiguous externally (Lagriini). Procoxal cavities closed behind externally, and completely closed internally (Fig. 71) by an oblique bar or plate. Mesocoxae with exposed trochantins, except in *Lorelus*. Mesocoxal cavities closed laterally partly by mesepimera, except in *Lorelus*, contiguous internally. Elytra, if striate, with scutellary striole and 10 striae, usually with distinct epipleura and epipleural carina, which may extend to apex. Metasternum with at least a short median longitudinal sulcus. Hind coxae variable, but usually moderately separated, with or without internal flange. Metendosternite with slender arms bearing anterior tendons near their apices, usually with an anterior median process, without 'laminae' (cf. Crowson 1938, pl. 1, fig. 10 - *Luprops*; pl. 2, fig. 2 - *Lagria*). Wings, if present, without subcubital flecks. All trochanters heteromeroid. Tarsal claws simple; penultimate tarsal segment lobed below at least weakly (Fig. 41), with terminal segment arising above and before its apex, except in Pycnocerini; tarsal segments usually clothed below with dense, fine pubescence, almost glabrous with a few bristles or small spines in some Pycnocerini.

Abdomen with intersegmental membranes exposed between visible sternites 3-5. Aedeagus orientated normally. Ovipositor elongate, with long, divided coxites bearing the long styli apically; apical divisions of coxites slender and pubescent like styli, so that superficially the styli appear two-segmented (Tanner 1927, figs 139, 140). Proctiger and paraprocts usually with strengthening rods ('baculi').

LARVAE. Sub-depressed or depressed, fusiform or onisciform.

Antennae pubescent, two-segmented; segment 2 considerably longer than 1, club-shaped, with a group of sensilla or a dome-shaped or sinuous sensorium (Fig. 64) at apex. Antennal and mandibular bases separated by a clearly visible though usually narrow strip of head capsule. Epipharynx variable, more-or-less strongly asymmetrical, with tormae connected and with a pair of asymmetrical, sclerotised masticatory processes posteriorly near middle (e.g., Fig. 66). Mandibles bidentate at apex, sometimes with one dorsal pre-apical tooth, rarely two; molar parts well developed, strongly sclerotised, without fine, transverse grooves, left mola with slightly to strongly prominent cusp(s) at apex. Maxillary mala broad, bluntly rounded at apex, without uncus, bearing two longitudinal rows of stout, curved bristles on dorsolateral inner surface. Hypopharynx with strongly sclerotised, asymmetrical sclerome (e.g., Fig. 65), which may be tridentate, bidentate, or irregularly

TABLE 7 — Genera erroneously included in Adeliini by Gebien (1942–44)

Genus	Correct position	Reference
<i>Anamphidora</i> Casey	Alleculini	Spilman (1958)
<i>Cratidus</i> Leconte	Amphidorini	Blaisdell (1939)
<i>Trichoderulus</i> Blaisdell	"	" "
<i>Amphidora</i> Eschscholtz	"	" "
<i>Ectyche</i> Pascoe	"	Carter (1926)
<i>Micrectyche</i> Bates	"	" "
<i>Phaennis</i> Champion	"	" "
<i>Stenotrichus</i> Leconte	Helopini	Blaisdell (1939)
<i>Prolabrus</i> Fairmaire	Ulomini	Ardoin (1959)
<i>Pseudhelops</i> Guerin	near <i>Artystona</i> Bates	new position
<i>Cerodolus</i> Sharp	" "	" "
<i>Brouniphylax</i> Strand (= <i>Paraphylax</i> Broun)	Zopheridae	" "
<i>Exohadrus</i> Broun	"	" "
<i>Syrphetodes</i> Pascoe	"	" "

truncate anteriorly; hypopharynx without setae or prominent lobes. Maxillary articulating area convex, obliquely divided into two parts. Gula triangular, separated from submentum by a transverse depression.

Body moderately to strongly sclerotised, especially dorsal surface. Coxae moderately separated, never contiguous. Legs similar in size and chaetotaxy, well developed, fairly slender, sometimes considerably elongated, frequently pubescent or hairy, always bearing some stout setae or bristles on inner surfaces of femora and tibiae. Each tarsungulus with two fine, equal or almost equal setae on inner surface.

Spiracles situated laterally or, in onisciform larvae, frequently above lateral margins, in front of each tergite. Sternopleural sutures usually distinct. Urogomphi usually present. Sternite 10 rarely produced into a pair of fleshy pseudopods. Spiracles circular or oval, without peripheral air-tubes or crenulations, cribriform.

BIOLOGY. Larvae of Lagriinae are usually found amongst leaf litter, especially in forests, in rotten wood, or under the bark of dead trees (unpubl. records; Schiödt 1880; Hayashi 1964). The adults live under bark, under logs, on the ground, or (some Lagriini) on flowers and grass. Both adults and larvae of *Lorelus* live in the stems of dead *Cyathea* fronds (Kaszab 1955, and unpubl. records). Larvae of *Cestrinus punctatissimus* have been found attacking germinating wheat in Victoria, Australia (*see below*).

REMARKS. This subfamily includes the family Lagriidae of authors (catalogued by Borchmann 1910), plus the tenebrionid tribes Goniaderini, Pycnocerini, and most of the Heterotarsini and Adeliini as listed by Gebien (1938–44). *Heterotarsus* is excluded from Lagriinae by its nine-striate elytra, and appears to be related to Opatrini (Koch 1956). Genera to be excluded from Adeliini are listed in Table 7.

Gebien gives no reasons for including Amphidorini in Adeliini, and none are apparent. According to Blaisdell (1939), Amphidorini are closely related to Eleodini.

The New Zealand genus *Mitua*, erroneously placed in Nyctofoilini by Gebien, is shown in cleared preparations to have 10-striate elytra, and the penultimate tarsal segments are weakly lobed. It is closely related to *Mesopatrum* and *Periatrum*. The Australian genera *Cestrinus*, *Achora*, and *Adelodemus*, hitherto referred incorrectly to Opatrini, are Adeliini as defined here.

The Pycnocerini are readily distinguishable from the other Lagriinae both as adults and larvae. Lagriini are easily recognisable as adults, but the larvae can be separated from those of certain Adeliini only by their general hairy appearance. All the remaining Lagriinae except Apocryphini are tentatively included in a single tribe, Adeliini.

KEY TO TRIBES OF LAGRIINAE

ADULTS

1. Penultimate tarsal segment simple, terminal segment arising at its apex. Apex of lacinia with sclerotised, mesally directed tooth..... **Pycnocerini**
— Penultimate tarsal segment lobed below, at least weakly, terminal segment arises before and above its apex (Fig. 41). Apex of lacinia without sclerotised tooth..... 2
 2. Terminal segment of antenna usually elongate and slender, as long as or longer than segments 9 and 10. Front coxae projecting strongly, contiguous or almost contiguous externally. Sides of prothorax rounded..... **Lagriini**
— Terminal segment of antenna not elongate, not as long as segments 9 and 10. Front coxae not as above. Lateral margins of prothorax carinate or explanate, except in *Phobelius* and Apocryphini..... 3
 3. Prothorax and elytra completely rounded off laterally, lacking epipleural carinae. Middle coxae without exposed trochantins..... **Apocryphini**
— Prothorax rarely (subtribe Phobeliina) and elytra never completely rounded off laterally, distinct epipleural carinae present. Middle coxae with exposed trochantins, except in *Lorelus*..... **Adeliini**
- LARVAE (Apocryphini unknown)
1. Antenna without distinct sensorium, end of segment 2 bearing numerous sensilla, giving a sieve-like appearance. Hypopharyngeal sclerome strongly tridentate anteriorly. 'Abdominal glands' present at sides of sternites 2 and 3..... **Pycnocerini**
— Antenna with distinct dome-shaped or sinuous sensorium at apex of segment 2. Hypopharyngeal sclerome irregularly bidentate or truncate anteriorly (e.g., Fig. 65). 'Abdominal glands', if present, situated on pleura..... 2
 2. Body covered with long setae, thus characteristically 'hairy'..... **Lagriini**
— Body not as above, though sometimes covered with short pubescence and a few long setae (e.g., Fig. 62)..... **Adeliini**

Tribe Pycnocerini

Pycnocérides Lacordaire, 1859, Gen. Col. 5: 399.
Chirosclinae Kolbe, 1903, Arch. Naturgesch. (2)1: 161.

This tribe has been monographed by Koch (1954) for adults, and by Skopin (1964a) for larvae. It is divisible into two subtribes, Chirosclina (=Prirosclina Skopin) and Pycnocerina.

Almost all Pycnocerini are confined to tropical Africa, the exceptions being *Pheugonius* and *Aediotorix*, which occur in Indonesia and the Philippines. Their larvae are unknown, but on adult characters they are referable to Chirosclina.

KEY TO SUBTRIBES OF PYCNOCERINI

ADULTS

1. Apices of mandibles bifid. Elytra usually black, very rarely metallic..... **Chirosclina**
— Apices of mandibles truncate. Elytra almost always metallic..... **Pycnocerina**
- LARVAE
1. Tarsungulus without inner tooth. Antennae not as long as head. Metallic reflections absent..... **Chirosclina**
— Tarsungulus with strong tooth near base of inner surface. Antennae longer than head. Usually with metallic reflections..... **Pycnocerina**

Tribe Adeliini

Adéliides Lacordaire, 1859, Gen. Col. 5: 434.
Goniadérides Lacordaire, 1859, *op. cit.*: 390.
Laenina Seidlitz, 1898, Naturg. Ins. Deutschl. 5: 666, 669.
Lupropsini [*sic*] Ardoïn, 1959, Bull. Acad. malgache 35: 59 (= Heterotarsini auct. but not Koch 1956).
Phobeliina Ardoïn, 1961, Bull. Acad. malgache 37: 33.

As noted by Ardoïn (1961), there is no satisfactory basis apparent for separating Lupropini and Goniaderini from Adeliini *sensu stricto* on adult characters. Larvae of the first two groups have their spiracles situated dorsolaterally, as in Pycnocerini, and have characteristic 'abdominal glands' (Skopin 1964a). Until more larvae have been studied, it seems best to follow Ardoïn's (1961) classification, including Lupropina and Goniaderina in Adeliini as subtribes, together with Laenina and Phobeliina.

A few genera which should be included in Ardoïn's Adeliina (e.g., *Coripera*, *Mitua*, certain *Pheloneis* spp.) lack externally visible striae, and may lack striae altogether, although some *Pheloneis* spp. have up to 21 striae on each elytron. No Adeliina have the closely punctate, non-striate elytra characteristic of Lupropina. Adults of *Lorelus* have mesocoxal cavities closed laterally by sterna, and mesocoxae without exposed trochantins. The larval 'abdominal glands' on the sides of abdominal tergites 2 and 3 are very inconspicuous, and all abdominal spiracles are in line. The genus agrees in most adult characters with Lupropina, however.

Adeliina are confined to Australia, New Caledonia, and New Zealand, unless "*Adelium*" *aeneum*, "*A.*" *sulcatulum*, and "*A.*" (*Rues*) *ovipennis* belong to this subtribe. The first two of these species are from Chile, the other from California. As noted by Ardoïn (1961), these American species cannot be included in the genus *Adelium*, but they require further study to determine their correct position in the classification.

The subtribe Laenina comprises the Palaearctic genus *Laena*, and two genera from Malagasy (Ardoïn 1961). Phobeliina includes only the South American *Phobelius*. The Goniaderina correspond to the Goniaderini of Gebien (1938-42), although on larval characters Skopin (1964a) also includes *Anaedus* in this subtribe. Goniaderina *sensu* Ardoïn is exclusively Neotropical in distribution. Members of Lupropina occur in the warmer and moister parts of all the zoogeographical regions.

PUBLISHED DESCRIPTIONS OF LARVAE. *Phymatestes tuberculatus* (Schiodte 1880), *Anaedus brunneus* and *Paratenetus punctatus* (Böving & Craighead 1931), *Luprops sinensis* (Hayashi 1964), *Laena starcki* (Byzova 1958), *Mitua tuberculicostata* (Hudson 1934), *Pheloneis gratiosus* (Hudson 1950).

Böving & Craighead (1931) and Byzova (1958) mistook the dome-shaped sensorium at the apex of antennal segment 2 for a third segment. All larvae of Lagriinae examined by me, including *Laena viennensis*, have two-segmented antennae.

KEY TO KNOWN LARVAE OF ADELIINI

1. Body onisciform, with first pair of abdominal spiracles situated below lateral margin and all others above it. Urogomphi very short or absent. Clearly visible 'abdominal glands' present laterally below lateral margins on abdominal segments 1-3 or 2 and 3..... 2
 - If body onisciform, then all abdominal spiracles situated below lateral margins (Fig. 62). Urogomphi moderate to long. 'Abdominal glands', if present, visible only at high magnifications in cleared preparations..... 4
2. 'Abdominal glands' present on first three abdominal segments, their orifices each covered by a conical group of setae (Schiodte 1880, pl. 14, fig. 10)..... 3
 - 'Abdominal glands' present on abdominal segments 2 and 3 only, visible as oblique projections, orifices non-setose (Hayashi 1964, fig. 44)..... *Luprops*
3. Apex of antennal segment 2 rounded, with a dome-shaped sensorium at apex (Böving & Craighead 1931, pl. 60, fig. A)..... *Anaedus*
 - Antennal segment 2 expanded to apex, then truncate; sensorium sinuous (Schiodte 1880, pl. 14, figs 1-3)..... *Phymatestes*

- | | |
|--|---------------------|
| 4. Sensorium at apex of antennal segment 2 circular or broadly oval in end view..... | 5 |
| —Sensorium at apex of antennal segment 2 a long, narrow strip, sinuous, S- or U-shaped in end view (Fig. 64). (Adeliina)..... | 6 |
| 5. Abdominal segments 2 and 3 with microscopic 'abdominal glands' on pleura. Antennae almost as long as head. Five ocelli visible on each side, grouped in an oblique row of four with one behind. (New Zealand, Pacific Islands)..... | <i>Lorelus</i> |
| —'Abdominal glands' absent. Antennae much shorter than head. Ocelli in two contiguous groups, individual ocelli not distinguishable. (Palaeartic)..... | <i>Laena</i> |
| 6. Body onisciform, with distinct, projecting lateral margins (Fig. 62). (New Zealand)..... | 7 |
| —Body not onisciform, subcylindrical, slightly depressed, without projecting lateral margins..... | 8 |
| 7. Urogomphi contiguous at base, borne on slight projection..... | <i>Periatrum</i> |
| —Urogomphi separated at base, arising directly from tergite 9..... | <i>Pheloneis</i> |
| 8. Antennae, legs, and urogomphi very long and slender: antennae longer than head; urogomphi longer than abdominal tergites 7 + 8 + 9. (Australia)..... | <i>Cardiothorax</i> |
| —Antennae, legs, and urogomphi not long and slender: antennae shorter than head; urogomphi much shorter than abdominal tergites 7 + 8 + 9..... | 9 |
| 9. Ocelli indistinct or absent. (New Zealand)..... | ? <i>Edalus</i> |
| —Ocelli distinct..... | 10 |
| 10. Ocelli arranged in two slightly oblique vertical rows (as in Fig. 62), the first row containing three and the second two ocelli..... | 11 |
| —Anterior row contains four ocelli, behind the second-to-lowest of which is the fifth ocellus. (Australia)..... | 12 |
| 11. Urogomphi contiguous at base, not curved, densely punctate and tomentose..... | <i>Mitua</i> |
| —Urogomphi separated at base, curved, not punctate or tomentose. (Australia)..... | <i>Cestrinus</i> |
| 12. Urogomphi contiguous at base, distinctly curved at apex. Colour cream. (Kiandra, N.S.W., Australia)..... | Genus indet. |
| —Urogomphi separated at base, not or very slightly curved. Colour dark brown or black..... | <i>Adelium</i> |

(I have examined examples of all the above genera except *Anaedus*.)

MATERIAL EXAMINED. Larvae of: *Laena viennensis* Sturm – Lake Bohinj, Slovenia, 4.vii.1960, R. A. Crowson (1 large and many small larvae, also 6 adults); *Adelium arboricola* Carter – Gwydir Highway, N.S.W., Australia, in rain forest litter, 2.xii.1963, B. P. Moore No. 31 (reared; 1 adult and 1 exuvium mounted on card). *Adelium alpicola* Blackburn – Mt. Macedon, Victoria, Australia, in damp moss in forest, 4.i.1959, B.P.M. No. 9 (reared; 1 adult and 1 exuvium mounted on card). *Cardiothorax cordicollis* Macleay – Brisbane, Queensland, Australia, ix.1963, G. Monteith (larva, skin on slide, pupa in alcohol, adult pinned; Dept. of Entomology, Univ. of Queensland). *Cardiothorax macleayi* – Cunningham's Gap, S. Queensland, Australia, under log, 24.iii.1963, C. H. S. Watts (adult in alcohol, pupal exuvia and head of last larval exuvium on slide). *Pheloneis gratosus* Broun (Figs 62–66) – Hawdon Valley, Cass, Canterbury, N.Z., 28.v.1960, P. M. Johns No. 342 [3 adults (1 cleared), 1 cleared larva (H.W. 2.68 mm). Agrees with Hudson's (1950) description, and was collected in the same area as his specimens. This is the largest *Pheloneis* larva examined, and adults of *P. gratosus* are larger than those of any other species of the genus]. *Cestrinus punctatissimus* Pascoe – Euroa, Victoria, Australia, attacking germinating wheat, 28.vii.1962, van Baer [4 larvae (1 on slide), H.W. 0.79, 0.82, 0.86 mm, identified by rearing; Nat. Mus. of Victoria, Melbourne].

Adeliini are so numerous in Australia and New Zealand that association with adults, unsupported by other evidence, does not provide satisfactory identification of larvae. There is an urgent need for more rearings of adeliine larvae in both countries. Only larvae of definite specific identity have been listed above.

Tribe Lagriini

Lagriariae Latreille, 1825; Fam. nat. Regne anim.: 381.

Lagriidae auctorum.

Statirini Leconte, 1862, Class. Col. N. Amer. II: 246.

This tribe is equivalent to the family Lagriidae of Crowson (1955) except "Heterotarsini" (cf. Adeliini), and excluding *Trachelostenus*, which is not a tenebrionid. The adults of Lagriini have been monographed by Borchmann (1937). Only two of his 'subfamilies' fall within Lagriini as defined here, the remainder belonging to Anthicidae (Ictistyginae), Mycteridae (Stilponotinae), Cononotidae (Agnathinae), and possibly Pythidae (Trachelosteninae).

In their strongly projecting front coxae and general 'malacoderm' facies, adult Lagriini are strikingly unlike ordinary Tenebrionidae, but as noted by Crowson (1955), "a series of transitional forms can be found from typical *Lagria* to typical Tenebrionids". Resemblances between Lagriidae and his Adeliinae were noted by Ardoin (1961).

The larvae of Lagriini are closely related to those of Adeliini and Pycnocerini, as noted previously. They are not easily distinguishable from those of certain Adeliini.

Lagriini occur in all the continents and Malagasy, but are absent from New Zealand. This fact and the obviously specialised structure of the adults compared with Adeliini suggest that they evolved their distinctive characters more recently than the latter tribe. Lagriini are especially numerous in the tropics, and are not very well represented in temperate regions.

PUBLISHED DESCRIPTIONS OF LARVAE. See references in Borchmann 1910. Hayashi (1964) has described thoroughly larvae of *Arthromacra viridissima*, *Nemostira rufobrunnea*, and *Lagria nigricollis*.

Tribe Apocryphini

Apocryphides Lacordaire, 1859, Gen. Col. 5: 432.

Adults of *Apocrypha* are small, anthicid-like beetles, with the sides of the prothorax and elytra rounded and without carinae. The elytra in some species have 10 rows of punctures. Intersegmental membranes are exposed between visible abdominal sternites 3-5. The antennae are 11-segmented, with an indistinct, 3-segmented club. The mesocoxae lack exposed trochantins.

The Tasmanian genus *Melytra*, listed by Gebien (1938-42) under Apocryphini, has only the extreme base of the antennal scape concealed from above. It is superficially similar to some Perimylopidae, but the trochantins of the procoxae are concealed, and the latter project only slightly and have concealed lateral extensions. The prosternal intercoxal process is expanded somewhat posteriorly, but lacks the long, curved postcoxal extensions characteristic of Ulodinae and Parahelopinae (Fig. 93). Until its internal structure can be studied, *Melytra* is best retained in Apocryphini, with which it agrees in its 10-striate elytra, exposed intersegmental membranes between abdominal sternites, and absence of lateral carinae on prothorax and elytra.

Subfamily NILIONINAE new status

Nilionidae Champion, 1888, Biol. C. Amer. Col. 4(1): 470.

Leiochrinae Lewis, 1894, Ann. Mag. nat. Hist. (6)13: 390.

ADULTS. Strongly convex, nearly hemispherical, *Coccinella*-like.

Antennae 11-segmented, filiform, weakly perfoliate or bluntly serrate. Antennal insertions covered by small canthi, which usually conceal only base of scape, but project back to and encroach on anterior borders of prominent, reniform eyes. Epistomal suture usually distinct. Labrum transverse, rounded anteriorly, usually with basal membrane exposed. Mandibles each with a single, prominent apical tooth and dorsal and ventral preapical teeth (*Nilio*), or bidentate at apex, with a long dorsal cutting edge (Leiochrini); prostheca with a dense covering of setae (*Nilio*), or a pecten-like row of setae on inner surface (Leiochrini). Lacinia without apical tooth. Terminal segments of palpi fusiform.

Prothorax strongly transverse, lateral margins explanate. Procoxal cavities closed behind externally, each closed internally by a quadrant-shaped plate (Fig. 72). Exposed part of procoxae transversely oval, somewhat projecting. Prosternum in front of coxae short, at most little longer than coxal cavity. Mesocoxae without exposed trochantins, their cavities closed laterally partly by mesepimera. Elytra, if striate, with nine striae and scutellary striole, or at least with sutural striae diverging strongly at base. Epipleura broad, nearly horizontal, complete to apex. Metacoxae transverse, with short internal flanges. Metendosternite with short stalk and slender arms, which bear anterior tendons towards apex (Crowson 1955, fig. 148). Wings with reduced venation in anal region, without subcubital flecks. Front trochanters (Fig. 40) reduced from usual heteromeroid type, middle and rear trochanters also non-heteromeroid in *Nilio*. Femora and tibiae unarmed except for usually very short apical spurs of latter; tibiae more-or-less densely pubescent. Tarsal formula 5-5-4; penultimate and frequently other tarsal segments lobed below, at least weakly and often strongly, clothed below with fairly dense, fine pubescence; claws simple.

Abdomen with exposed intersegmental membranes between visible sternites 3-5. Aedeagus orientated normally. Ovipositor variable, often elongate with long styli, greatly reduced in *Nilio*.

LARVAE (see also Böving & Craighead 1931, pl. 59). Form short, broad, strongly convex, almost onisciform, moderately sclerotised.

Head strongly transverse. Antenna short, with a few setae but not pubescent, two-segmented, segment 2 very short (*Leiochrini*) or elongate (*Nilio*); sensorium a dome-shaped, membranous area at apex of segment 2. Antennal and mandibular bases separated by at least length of antenna (Fig. 78). Ocelli four, situated behind antennae, on a lateral projection in *Leiochrini*. Mandibles short, each with a prominent apical tooth and dorsal and ventral preapical teeth, molar parts with (*Leiochrini*) or without fine, transverse ridges, apex of left mola projecting, that of right receding. Outer surface of mandible rounded, without scrobe or carinae. Palpi short. Maxillary mala broadly rounded at apex, without uncus. Articulating area elongate, membranous. Hypopharynx with sparsely setose lobe projecting in front of sclerome, latter anteriorly tridentate (*Nilio*) or strongly concave (*Leiochrini*), with dorsal surface depressed anteriorly. Gular sutures distinct, gula transverse.

Thoracic nota strongly transverse and convex. Precoxale and postcoxale sclerotised. Coxae widely separated with distinct median sternal plates between. Legs slender, similar; tibiae with some fine bristles on inner surface; tarsunguli each with a pair of fine, equal setae.

Abdominal terga strongly transverse and convex, all spiracles situated above lateral margins; pleural areas membranous, pleurosternal sutures distinct; sterna flat to moderately convex. Urogomphi absent, tergite 9 without ventral surface, sloping downwards to apex, anus subterminal. Sternite 9 nearly semicircular, sternite 10 produced behind a pair of short, blunt, contiguous pseudopods. Tergite 10 membranous, not exposed. Spiracles small, simple, circular, without discernible filter apparatus (at 400× magnification).

PUBLISHED DESCRIPTIONS OF LARVAE. A *Leiochrodes* larva was illustrated by Böving & Craighead (1931, pl. 59), and the larva of *Derispia maculipennis* was described and illustrated by Hayashi (1959). Adults of *Leiochrini* have been monographed by Kaszab in a series of papers; Kaszab (1961) includes a revised key to genera, and references to his earlier papers.

BIOLOGY. Larvae of *Derispia maculipennis* feed on mosses (Hayashi, pers. comm.). Adults of *Leiochrodes suturalis* live on the ground under decaying leaves in eastern Australia (Carter 1926). These and similar habits are probably characteristic of the Leiochrini. The differences in the mouthparts of both adults and larvae (*see* key, *below*) suggest that Leiochrini and Nilionini have substantially different feeding habits.

DISTRIBUTION. Nilionini are confined to tropical America. Leiochrini are numerous in the Oriental region; a few species extend into subtropical eastern Australia, and others into southern Japan. Three species of *Leiochrodes* occur in tropical Africa, and two in Malagasy (Kaszab 1961).

REMARKS. The members of this subfamily are in some respects highly specialised, and in superficial appearance both adults and larvae are unlike ordinary Tenebrionidae. The evidence, however, strongly supports the view that they are modified Tenebrionidae rather than an independent family. In the adult the antennal insertions, abdomen, and aedeagus are all of the tenebrionid type. The non-heteromeroid trochanters of *Nilio* are linked to the heteromeroid form characteristic of most Tenebrionidae by those of Leiochrini, in which tribe only the front trochanters are not heteromeroid (although in the middle and rear trochanters the anterior extensions of the femoral bases do not extend as far around the trochanters as they do in most Tenebrionidae).

In larvae of Nilioninae, the head is unlike that of any other beetle larva known to me, but in all except its obviously specialised features it agrees with heads of more normal Tenebrionidae. The very wide separation between the antennal and mandibular bases is a necessary consequence of broadening the head while retaining the antennae in their most useful (anterolateral) position. Larvae of *Nilio* differ less from those of normal Tenebrionidae in most respects than do larvae of Leiochrini (*see* key, *below*).

A pupal skin of *Nilio lanatus* has lateral, club-like processes, as in the pupa of *Lagria hirta* (Schiödt 1880, pl. 14).

KEY TO TRIBES OF NILIONINAE

ADULTS

1. Anterior trochanters approximately as in Fig. 40, middle and posterior trochanters of heteromeroid type (Fig. 36). Disc of epipharynx with a few fine setae. Ligula transverse, with straight anterior border, bearing fine setae. Mandibular prosthema long and narrow, bearing a pecten-like fringe of stout setae on its inner edge. Tarsal segments often strongly lobed below..... **Leiochrini**
- Trochanters all as in Fig. 40, none of heteromeroid type. Disc of epipharynx densely clothed with stout setae. Ligula elongate, rounded anteriorly, bearing numerous stout setae. Mandibular prosthema short, clothed with a dense mass of short, fine setae on inner surface. Tarsal segments weakly lobed below..... **Nilionini**

LARVAE

1. Body almost glabrous, with some fine, short setae near lateral margins. Antennal segment 2 much shorter than 1, annular. Mandibular mola with fine, transverse ridges. Anterior margin of hypopharyngeal sclerome deeply concave. Side of head with a prominent rounded projection behind antenna bearing ocelli..... **Leiochrini**
- Body densely clothed on upper surface with long, stout, pigmented setae, interspersed with very long, fine, colourless setae; undersurface clothed more sparsely with short, fine, pigmented setae. Antennal segment 2 much longer than 1 (Fig. 78). Mandibular mola without transverse ridges. Anterior margin of hypopharyngeal sclerome tridentate. Side of head without projection behind antenna..... **Nilionini**

MATERIAL EXAMINED. Larvae of: *Derispia maculipennis* (Marseul) — Sarakurayama, Fukuoka-ken, Kyushu, Japan, 16.iv.1961, A. Haga [J. C. Watt Coll. No. 2092; 1 adult, 5 larvae (1 on slide; H.W. 0.85, 1.04, 1.09, 1.12, 1.13 mm); larval food: mosses; Entomology Div., Auckland]. *Nilio lanatus* Germar — "S. Catharina, Nova Teutonia [Brazil], 27. Br.° 52–53. L.°, Plaumann Zucht!" [van Emden Coll. No. El 1875; 2 complete larvae (H.W. 1.51, 1.58 mm), several larval exuviae (1 on slide), 1 pupal skin].

Subfamily PIMELIINAE new sense

Pimeliariae Latreille, [1802], Hist. nat. Crust. Ins. 3: 165.

Tentyrites Solier, 1834, Ann. Soc. ent. Fr. 3: 501.

Asidites Solier, 1834, *op. cit.*: 502.

ADULTS. Antennae not distinctly clubbed. Labrum distinctly, often strongly transverse. Mentum often large, concealing mouthparts. Procoxal cavities closed behind externally. Mesocoxae with or without exposed trochantins, their cavities closed laterally by sterna or partly by mesepimera. Elytra rarely striate; if so, each with 10 striae and scutellary striole. Metendosternite with long, slender arms projecting forwards over mesocoxae, their apices sometimes fused to mesonotum. Wings rarely present, without subcubital flecks. Tarsal segments and claws simple; tarsal formula 5-5-4. Abdominal sternites with intersegmental membranes concealed, except in the Palearctic tribes Pimeliini and Platyopini. Aedeagus inverted (cf. Figs 16, 17).

LARVAE. Antennae (Fig. 81) three-segmented, glabrous except for terminal setae, or with one or two other setae, rarely with a group of long setae on lateral surface of segment, never pubescent. Strip of head capsule between antennal and mandibular bases very narrow, partly concealed by basal membranes. Mandibles (Figs 82, 90, 91) each with anterior part of dorsolateral edge carinate or explanate, posterior part with a membranous elevation bearing numerous setae; mola prominent, strongly sclerotised, without fine, transverse ridges. Hypopharyngeal sclerome with flat or slightly concave dorsal surface and usually concave anterior margin, latter rarely convex (Fig. 79), never distinctly tridentate. Hypopharynx without setose lobes. Gula distinct. Legs (Figs 88, 89) strongly modified for digging. Front legs much stouter than others, with different chaetotaxy. Tarsungulus of each front leg with a strongly sclerotised, asymmetrical, flattened apical lobe, and a weakly sclerotised, short base (Fig. 88), tarsunguli of other legs (Fig. 89) subdivided less distinctly and less modified. Setae of tarsunguli unequal, with one displaced on to inner lateral margin.

Pleurosternal sutures distinct. Abdominal tergite 9 usually curved downwards at least slightly to apex (e.g., Fig. 84), rarely curved upwards to subacuminate apex, true urogomphi absent. Sternite 10 produced into a pair of usually prominent pseudopods, which usually bear small, articulated spines (e.g., Fig. 83).

Spiracular peritreme oval, simple, without peripheral air-tubes or crenulations. Complex filter apparatus present.

PUBLISHED DESCRIPTIONS OF LARVAE. There have been considerable advances in knowledge of larvae of Pimeliinae recently. Marcuzzi & Rampazzo (1960) described several European forms, and the first known Nearctic pimeliine larvae (*Coniontis viatica* and *Coelus ciliatus*). Skopin (1962) gives a detailed account of larvae of Pimeliini and Platyopini and a key to the major groups of "Pedobionta", and also has described fully larvae of *Adesmia* (1960c), the Akidini (1958, 1960b), and the Erodiini (1961). Keleinikova described some larvae of Tentyriini (1959), Pimeliini (1961), and Erodiini (1962). Ghilarov (1964) includes many of the Pimeliinae described above in his key to soil-inhabiting tenebrionid larvae. Schulze (1962) described some South African Adesmiini and Eurychorini.

BIOLOGY. Pimeliinae are characteristic of arid and semi-arid regions. Adult life is usually long, and larval development is rapid, taking place during and immediately following the rainy season if there is one, or following the very infrequent heavy falls of rain in deserts (Pierre 1958). In captivity, adults of *Pimelia cribra* and *Akis acuminata* will oviposit only in a moist substratum, but *Tentyria schauvi* will oviposit in dry sand.

Larvae live in soil, especially in light, sandy soil or sand. They feed usually on dead plant debris, although some species feed on living roots or seeds, and some of these are agricultural pests in semi-arid regions of Africa, the U.S.S.R., and probably elsewhere. In captivity they can be reared on diets normally used for Tenebrionidae of stored products (e.g., wholemeal wheat flour and debittered yeast).

Adult Pimeliinae are frequently diurnal, taking shelter only during the hottest part of the day. The subelytral cavity helps to control water loss from the spiracles (Cloudsley-Thompson 1965).

DISTRIBUTION. Pimeliinae are strongly represented in the drier parts of the Palaearctic, Nearctic, Neotropical, and Ethiopian regions (including Malagasy), but are rare in the Oriental region and entirely absent from Australia and New Zealand.

REMARKS. This very large subfamily includes the subfamilies Tentyriinae and Asidinae of Gebien's (1937-42) catalogue (excluding Zopherini, Usechini, *Cotulades*, and *Docalis* - cf. Zopheridae), plus the tribes Platyopini, Pimeliini, Physogasterini, Praocini, Branchini, Coniontini, and Coelini. It is equivalent to Tentyriinae of Koch (1955) plus Platyopini and Pimeliini, and corresponds to Pedobionta excluding Blapimorpha of Skopin's (1964a) larval classification.

Pimeliini and Platyopini differ in the adult stage from all the other tribes included here in having exposed intersegmental membranes between visible abdominal sternites 3-5. In other adult characters and in larval structure they agree closely with the Tentyriinae of Koch (1955), and the available evidence suggests strongly that they are specialised members of this group, rather than an independent phyletic line arising directly from primitive Tenebrionidae. If the latter alternative were correct, Pimeliini and Platyopini would have to form a separate subfamily, as they could certainly not be included in Tenebrioninae as defined here. The Eocene fossil *Eodromus agilis* may belong to Pimeliinae as recognised here.

Each of the main arid regions of the world except that of Australia has its own endemic fauna of Pimeliinae. Some of the endemic groups are worthy of tribal status (e.g., Neotropical Nycteliini, Nearctic Nyctoporini and Coniontini, Palaearctic Pimeliini, Ethiopian Cryptochilini), but others should be included in Tentyriini *sensu* Koch 1955 (e.g., Triorophini, Thinobatini) or merged with other tribes.

The construction of a satisfactory tribal classification of Pimeliinae is greatly hindered by inadequate knowledge of larvae, which applies even to the Palaearctic fauna, despite the advances of recent years. Adequately determined larvae of Pimeliinae from South America are unknown. It is not difficult to rear large numbers of larvae from eggs laid by captive adults, as has been demonstrated by Skopin, Schulze, and others (*see* Published Descriptions of Larvae, *above*).

The resemblances between larvae of Pimeliinae and those of the more specialised soil-inhabiting Tenebrioninae ("Blapimorpha") are almost certainly due to convergence. Such primitive features of some adult Pimeliinae as 10-striate elytra would preclude the possibility of them having originated from "Blapimorpha", and there is no evidence that "Blapimorpha" could have arisen from Pimeliinae.

The larva of *Nyctoporis* Eschscholtz, described below, is more primitive than any other known larva of the subfamily in its hypopharyngeal sclerome, and the presence of sclerotised masticatory processes on the posterior transverse bar of the epipharynx. The adult of

Nyctoporis is primitive in its relatively small mentum, mesocoxae with exposed trochantins and cavities closed laterally partly by mesepimera, and tarsi clothed below with dense, fine pubescence. The elytra lack distinct striae, but there are 10 rows of punctures between the elytral tubercles. The pupa differs from those of Tenebrioninae and Alleculinae, and resembles those of Diaperinae (Schiödte 1878), in having prominent projections in the pleural region.

Nyctoporis spp.

LARVAE (Figs 79–84, 87–92). Moderately elongate, subcylindrical, slightly depressed, mainly cream. Body lightly sclerotised, head, pronotum, and abdominal tergite 9 moderately sclerotised.

Head broad, somewhat depressed. Antenna about as long as width of labrum, segments 1 and 2 about equal in length (Fig. 81), 3 short, cylindrical, with two short, apical setae. Sensorium semicircular, absent dorsally, broadened ventrally (Fig. 92). Labrum (Fig. 82) with a transverse row of 16–22 articulated spines near anterior margin, and some long, fine setae on anterior margin. Clypeus (Fig. 82) with a blunt, articulated spine and three setae on each side near base. Frons and dorsal surface of epicranium finely and sparsely punctate. Side of head densely covered with long, fine setae. Ocelli arranged in an anterior group of three and a posterior group of two on each side (Fig. 82). Epipharynx as in Fig. 80. Mandibles slightly asymmetrical (Figs 90, 91), molar areas, apical teeth, and cutting edges strongly sclerotised; membranous dorsolateral elevation bearing a brush of moderately long, slender spines, which grade outwards and downwards into setae (Figs 81, 82). Maxillary mala with two rows of stout, curved bristles, and some slender setae on inner surface, narrowly rounded at apex. Hypopharyngeal sclerome as in Fig. 79, dorsal surface slightly concave, anterior margin convex. Ventral side of head as in Fig. 81.

Thoracic nota each bearing some fairly long setae laterally. Ventral areas of prothorax as in Fig. 87. Front coxae contiguous, others almost contiguous. Front legs as in Fig. 88. Middle (Fig. 89) and hind legs similar to each other, much more slender than front legs; tibia of middle legs with three articulated spines on inner surface, hind legs with only two spines there.

Each abdominal tergum with two setae on each side near posterior edge, and some others laterally, especially around spiracles. Sternum 1 with about 30 setae near anterior margin (Fig. 87), sterna 2–5 each with three setae on each side near anterior angle and one posteriorly, sternum 6 with two on each side anteriorly and one posteriorly, 7 with two on each side anteriorly and a row of four posteriorly, 8 as in Fig. 83. Tergite 9 as in Fig. 84, dorsal surface slightly convex, with rows of small, articulated spines near its margin. Sternite 9 transverse (Fig. 83), with a row of three to six articulated spines and a few setae on each side. Sternite 10 produced into a pair of prominent, blunt pseudopods (Fig. 83), each with 15–18 curved, articulated spines on anterior and lateral surfaces and a row of fine setae on inner surface.

Spiracles lateral, oval, with complex filter apparatus composed of numerous fine setae on processes.

KEY TO LARVAE OF *Nyctoporis* EXAMINED

1. Five or six articulated spines on each side of sternite 9 (Fig. 83). Mentum with one pair of setae on disc near base (Fig. 81).....*carinata*
- Three or four articulated spines on each side of sternite 9. Mentum lacking setae on disc near base.....*cristata*

PUPAE (Figs 70, 85, 86). Moderately elongate, somewhat depressed (Fig. 70), cream except for jaws of gin-traps, which are brown, all setae small and fine.

Head strongly deflexed beneath prothorax (Fig. 70), dorsal surface except occiput deeply excavate on each side of a median ridge; a few short setae near borders of clypeus and on outer surfaces of mandibles, latter sclerotised at apices on inner edges.

Pronotum campanuliform, with a deep (*crystata*) or shallow (*carinata*) fovea on each side near centre of disc, and another, fairly shallow depression behind and towards lateral margin on each side (as in adults). Lateral margins with numerous fine, short setae (Fig. 70), and a few setae on submarginal depressions. Meso- and metanota strongly transverse, bearing (like abdominal tergite 1) a short, lateral seta. Elytra (Fig. 70) bluntly acuminate at apex, with shallow, longitudinal depressions. Hind wings shorter than elytra, usually completely obscured by them. Femora with short setae on anterior and dorsal surfaces near 'knees' and on anterodorsal surface of distal half of front femora (Fig. 70).

Abdominal tergites 1-6 with prominent lateral lamellae, between which are gin-traps. Lamellae as in Figs 85 and 86, those of tergites 3 and 4 similar to that of tergite 2 but longer and more prominent, and each with seven lateral setae (eight or nine in *carinata*). Edges of gin-traps sclerotised, with numerous sharp, small teeth. Tergites 7 and 8 with lateral, somewhat flattened lobes; tergite 9 with a pair of slender, slightly curved, weakly sclerotised urogomphi (Fig. 70). Functional spiracles below lamellae on segments 1-6. Distinct projections in pleural region. Sternites 3-8 each with a pair of short setae near posterior margin (Fig. 70); sternite 9 much smaller and narrower than others. Genitalia of usual type; small, rounded papillae in male, conical, projecting papillae in female.

KEY TO PUPAE OF *Nyctoporis* EXAMINED

1. Discal foveae of pronotum deep. Lateral lamellae of abdominal segments with no more than seven lateral setae on each; tubercles from which they arise mostly inconspicuous.....*crystata*
 —Discal foveae of pronotum obsolete. Lateral lamellae of abdominal segments with eight or nine lateral setae on each, tubercles from which they arise mostly prominent.....*carinata*

MATERIAL EXAMINED. *N. carinata* Eschscholtz - Santa Barbara, California (Blaisdell Coll. No. 52; H.W. 2.48, 2.56 mm); same data [No. 38; 1 larval skin in alcohol, 1 incomplete (head and thorax only) on slide]; same data, 30.ix.1934 (No. 78; ♀ pupa) (California Academy of Sciences). *N. cristata* Leconte (labelled "*Nyctoporis galeata*") - Stockton, California (Blaisdell Coll. No. 44; H.W. 1.84, 2.00, 2.12, 2.12, 2.24 mm), plus 2 *Eleodes* larvae; same data (No. 33; H.W. 2.00 mm) plus 2 ♂ pupae (Calif. Academy of Sciences).

Subfamily COSSYPHINAE

Cossyphores Latreille, [1802], Hist. nat. Crust. Ins. 3: 164.

ADULTS. Broadly oblong-oval, strongly depressed.

Antennae 11-segmented, with flattened, 4-segmented club, inserted below small canthi, which extend back to eyes. Labrum elongate, parallel-sided. Epipharynx membranous except for an anterior strip, with dense rows of small setae posteriorly on inner processes of tormae; latter extend straight back from posterior angles of labrum, as in Lagriinae (Fig. 75). Terminal segment of maxillary palp securiform, that of labial palp fusiform. Lacinia without apical tooth.

Lateral and anterior margins of prothorax foliate, anterior foliation semicircular in outline (Fig. 76), completely covering head. Procoxal cavities closed externally by broad postcoxal processes of propleura, which meet in mid-line behind prosternal intercoxal process (Fig. 76). Procoxal cavities each closed internally by a quadrant-shaped plate (Fig. 76). Mesosternum scarcely depressed anteriorly. Mesocoxae without exposed trochantins, their cavities closed laterally by sterna, not contiguous internally. Wings often

reduced, lacking subcubital flecks. Metendosternite with short stalk, without 'laminae' or anterior median process; broad expansions near apices of arms bear anterior tendons. Elytra non-striate, with broad, slightly reflexed lateral foliations extending to apices. All trochanters heteromeroid. Legs unarmed except for small tibial spurs. Tarsi rather sparsely clothed below with short bristles, tarsal segments and tarsal claws simple; tarsal formula 5-5-4.

Abdomen without exposed intersegmental membranes between visible sternites. Aedeagus normally orientated. Ovipositor short, with slender, divided coxites and moderately long styli, without rods.

LARVAE. Unknown.

BIOLOGY. *Cossyphus moniliferus* lives most commonly under stones, often in colonies of several individuals. Its movements are very slow, and although provided with wings it has never been observed to fly (Español 1954). Some of the African species resemble dead leaves, amongst which they are found (P. Blasdale, pers. comm.). The adults are superficially similar to the myrmecophilous Cossyphodinae, but I have seen no suggestion of myrmecophily amongst Cossyphinae in the literature.

DISTRIBUTION. *Endustomus* is confined to tropical Africa. Species of *Cossyphus* occur in southern Europe, Africa, Malagasy, the Oriental region, and Australia. The subfamily is unknown in America, New Zealand, and oceanic islands.

REMARKS. This subfamily is equivalent to the tribe Cossyphini of Gebien's (1938-42) catalogue. The highly specialised insects comprising it were once thought to be related to Helaeini, but there is no sound basis for this belief. Cossyphinae appear to be most closely related to Toxicinae, sharing with that subfamily antennae with a four-segmented, flattened club, abdominal sternites without exposed intersegmental membranes, and a normally orientated aedeagus. The discovery of their larvae will be of great interest.

KEY TO GENERA OF COSSYPHINAE

1. Head concealed below by a foliate process of the anterior margin of the prosternum.....*Endustomus*
—Head not concealed below, anterior margin of prosternum emarginate.....*Cossyphus*

Subfamily COSSYPHODINAE new status

Cossyphodidae Wasmann, 1899, Deutsche ent. Zeitschr. 1899: 161-2.

Cossyphoditinae Basilewsky, 1950, Rev. Zool. Bot. Afr. 43: 187.

Paramelloninae Andreae, 1961, in Hanström, Brinck, and Rudebeck, S. Afr. anim. life 8: 213.

ADULTS. Broadly oval, strongly depressed.

Dorsal surface of head flat, margins produced into broad, foliate expansions, outline semicircular (Fig. 77), mouthparts completely concealed from above. Eyes completely divided, lower parts vestigial, upper parts on dorsal surface of head towards lateral margins, sometimes reduced. Antennae 9- or 11-segmented, geniculate, with distinct club of 1 or 2 segments, scape almost as long as other segments together; when retracted, concealed in antennal pouches (Fig. 77). Labrum slightly transverse. Epipharynx membranous, with a few small bristles on each side near anterior margin. Tormae extending straight back from posterior angles of labrum, without inner processes. Mandibles relatively elongate, apices bidentate, prosthecae broad, molae short but prominent, without fine, transverse ridges; left mandible with long, dorsal cutting edge, right with short cutting edge. Terminal segments of maxillary palpi cylindrical, of labial palpi fusiform. Lacinia not armed.

Lateral margins (but not anterior margin) of prothorax produced as extensive foliations. Procoxal cavities closed behind externally, and internally by a quadrant-shaped plate (as in *Cossyphinae*, Fig. 76). Exposed parts of front coxae almost circular, not projecting. Mesosternum scarcely depressed anteriorly. Mesocoxae without exposed trochantins, their cavities closed laterally by sterna, not quite reached by mesepimera. Elytra not striate, with broad, lateral, foliate epipleural margins extending to apex. Metasternum with curved femoral lines behind mesocoxae, as in *Coccinellidae* (Crowson 1955), without median longitudinal suture. Metepisterna broad. Metacoxae oval, weakly transverse. Metendosternite without stalk, anterior median process, or 'laminae', with long, slender arms. Wings vestigial. All trochanters heteromeroid. Femora with dorsal concavities receiving tibiae when legs folded. Tibial spurs minute. Tarsal segments and claws simple, former clothed below with fairly sparse, fine setae; tarsal formula 5-5-4 or 5-4-4.

Visible abdominal sternites 1 and 2 each with W-shaped lines (not easily seen except in cleared preparations), visible sternite 3 with a pair of parallel longitudinal lines on disc. Intersegmental membranes exposed between visible sternites 3-5. Aedeagus normally orientated.

LARVAE. Unknown.

BIOLOGY. All members of this subfamily live in nests of ants (*Formicidae*).

DISTRIBUTION. Ethiopian region, Canary Islands, Madeira, Cape Verde Islands, St. Helena, India.

REMARKS. *Cossyphodes* was originally regarded as an aberrant member of the *Colydiidae*. Wasmann (1899) correctly withdrew it from the latter family and placed it with *Cossyphodinus*, which has 5-5-4 tarsi, in a new family, *Cossyphodidae*. This was catalogued by Hetschko (1926). Crowson (1955, p. 172) synonymised this family with *Tenebrionidae*, without explanation.

The only characters of *Cossyphodinae* which do not occur in other *Tenebrionidae* are the deep antennal pouches, the femoral lines on the metasternum, and the lines on the abdominal sternites. The latter are not homologous with the femoral and lateral lines of *Biphyllidae* (Crowson 1955, fig. 121), which are parallel to each other rather than W-shaped. These characters do not preclude *Cossyphodinae* from being specialised *Tenebrionidae*.

Andreae (1961) proposed dividing *Cossyphodidae* into two subfamilies. The division appears to be soundly based, if the "subfamilies" are reduced to tribes (*see key, below*).

Cossyphodinae are so specialised that their relationships to other *Tenebrionidae* are not readily apparent. Their resemblance to *Cossyphinae* is probably mainly due to parallelism. The strongly clubbed antennae and the mouthparts suggest affinities with the more primitive subfamilies such as *Toxicinae* and *Phrenapatinae*, but the relationships are not close. The larvae, when discovered, may throw considerable light on the affinities of *Cossyphodinae*.

KEY TO TRIBES OF COSSYPHODINAE

1. Tarsal formula 5-5-4. Antennae nine-segmented. India.....**Paramellonini**
(including *Paramellon* and *Cossyphodinus*)
- Tarsal formula 5-4-4. Antennae 11-segmented. Africa and adjacent Atlantic islands.....**Cossyphodini**
(including *Cossyphodinae* Basilewsky, 1950)

TRIBES AND GENERA OF UNCERTAIN AFFINITY

Tribe **Belopini**

Adults of the Palaearctic genus *Belopus* have 10-striate elytra, an elongate labrum-epipharynx with tormae projecting straight back, and the aedeagus orientated normally. In these respects they agree with Lagriinae, but differ from them in lacking exposed inter-segmental membranes between abdominal sternites. The tarsal segments are simple, but this is true also of Pycnocerini.

A larva attributed to *Belopus procerus* was described by Byzova (1958). This differs from larvae of Lagriinae as defined here in having three-segmented antennae, which are, however, stated to be covered with numerous short setae. Unfortunately the description does not mention the strip of head capsule between the antennal and mandibular bases, or the detailed structure of the spiracles. Identification of the larvae appears to have been based on association with adults, which leaves their identity open to doubt. If these larvae are correctly identified, and agree with Lagriinae in the undescribed characters, then Belopini should be included in Lagriinae. *Belopus* was listed in the Tenebrionini by Gebien (1938-42), but cannot be included in Tenebrioninae as defined here.

Tribe **Rhysopaussini**

This group was originally described as the family Rhysopaussidae, which was later reduced to the rank of a subfamily of Tenebrionidae (Wasmann 1921) and was listed by Gebien (1942-44) as a tribe. In Gebien's catalogue it includes highly specialised termitophilous genera (e.g., *Rhysopaussus*, *Rhysodina*), and others obviously closely related to Amarygmini (e.g., *Gonocnemis*).

Ardoin (1962) removed the following genera from Rhysopaussini of Gebien's "Katalog" to Amarygmini: *Euglyptonotus*, *Gonocnemis*, *Ubangia* (= *Crypsinous*), *Borneogonocnemis*, *Microgonocnemis*, *Lemoultia*, *Paragonocnemis*, *Falsosynopticus*, *Microsynopticus*, *Overlaetia*, and *Gonocnemocistela*. He removed *Synopticus* from Tenebrionidae altogether.

This leaves the Rhysopaussini as a still very diverse assemblage of termitophilous forms, most of which are highly specialised. It seems quite probable that some of these genera are not tenebrionids. Paulian (1947), on the basis of the structure of *Bancous irregularis* Pic, transferred Rhysopaussidae to his Cucujaria. As Ardoin has pointed out, however, it is unjustified to extend a conclusion based on one genus to the whole tribe. Like Ardoin, I have not been able to examine any authentic *Rhysopaussus dohertyi*, so it is not certain whether the name Rhysopaussini can be used in Tenebrionidae, but other supposedly related genera are definitely tenebrionids.

A larva in the British Museum (Natural History) collection is labelled "?*Rhysopaussus dohertii* Wasm., 1962, N. Skopin det."; the collecting data are "Penang, 2000', March 1898, S.B. Flower". This larva is similar to those of known Amarygmini, which are quite common in Malaysia. It seems much more likely that the larva belongs to one of these than to the rare *Rhysopaussus dohertyi*, in the absence of any habitat data.

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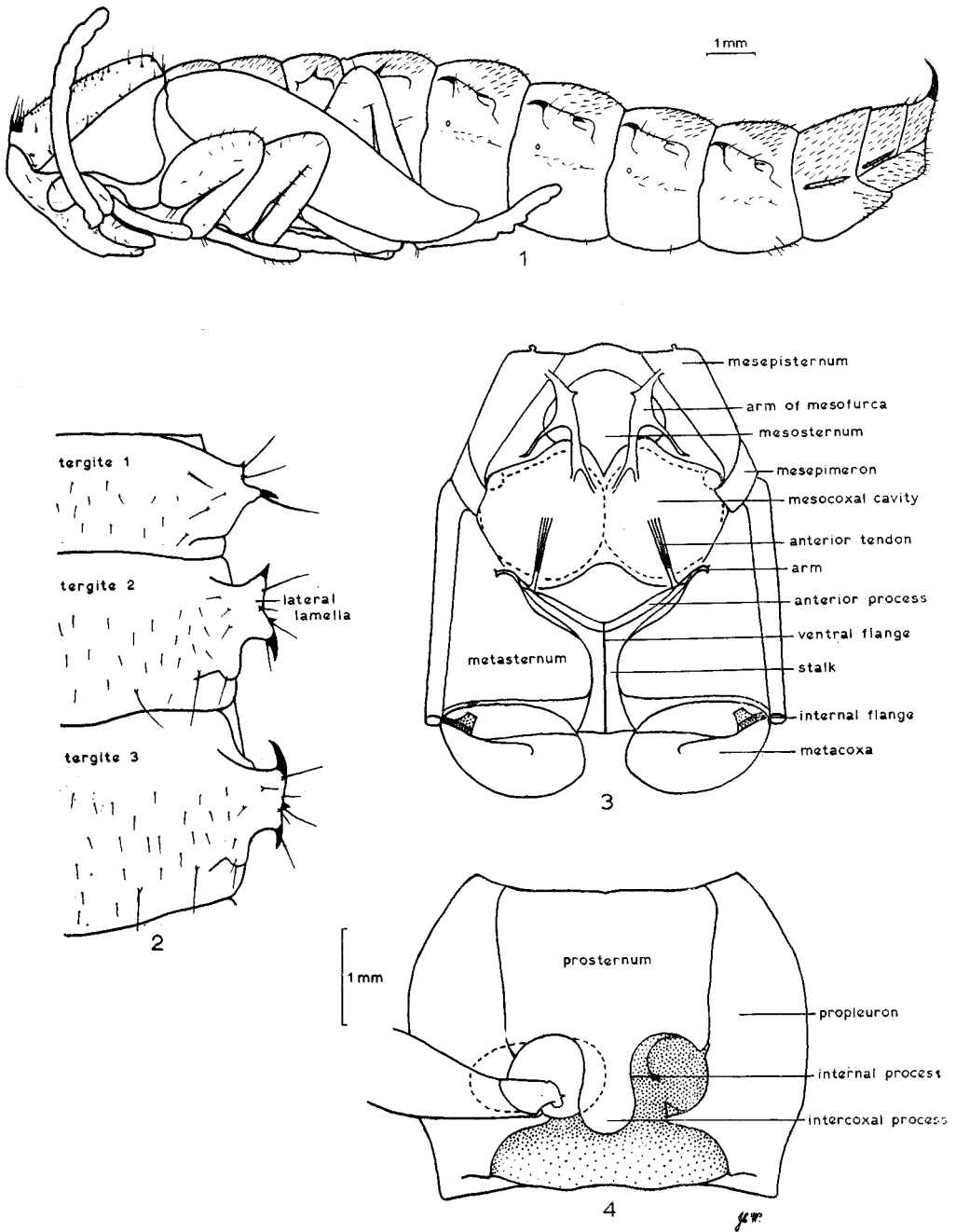
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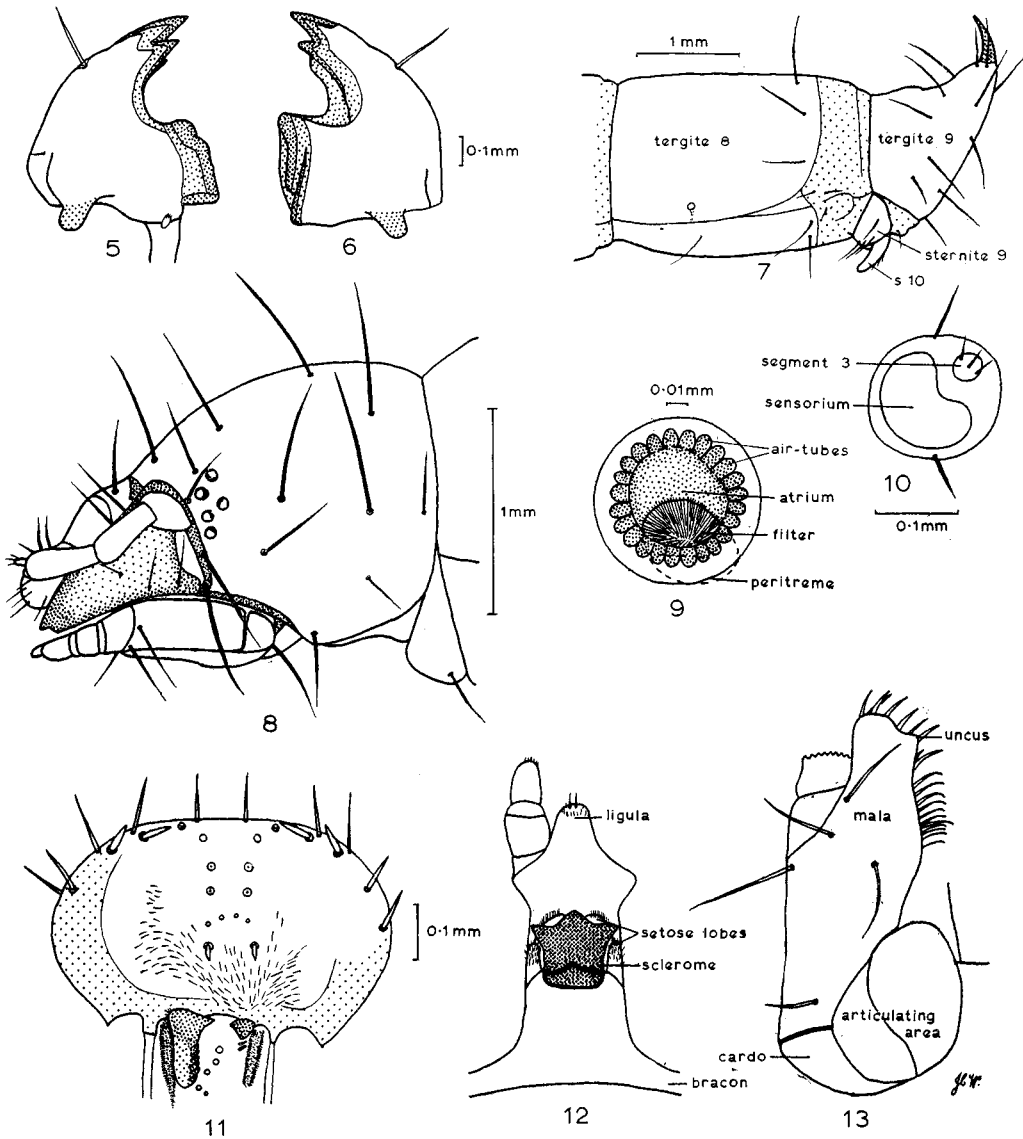
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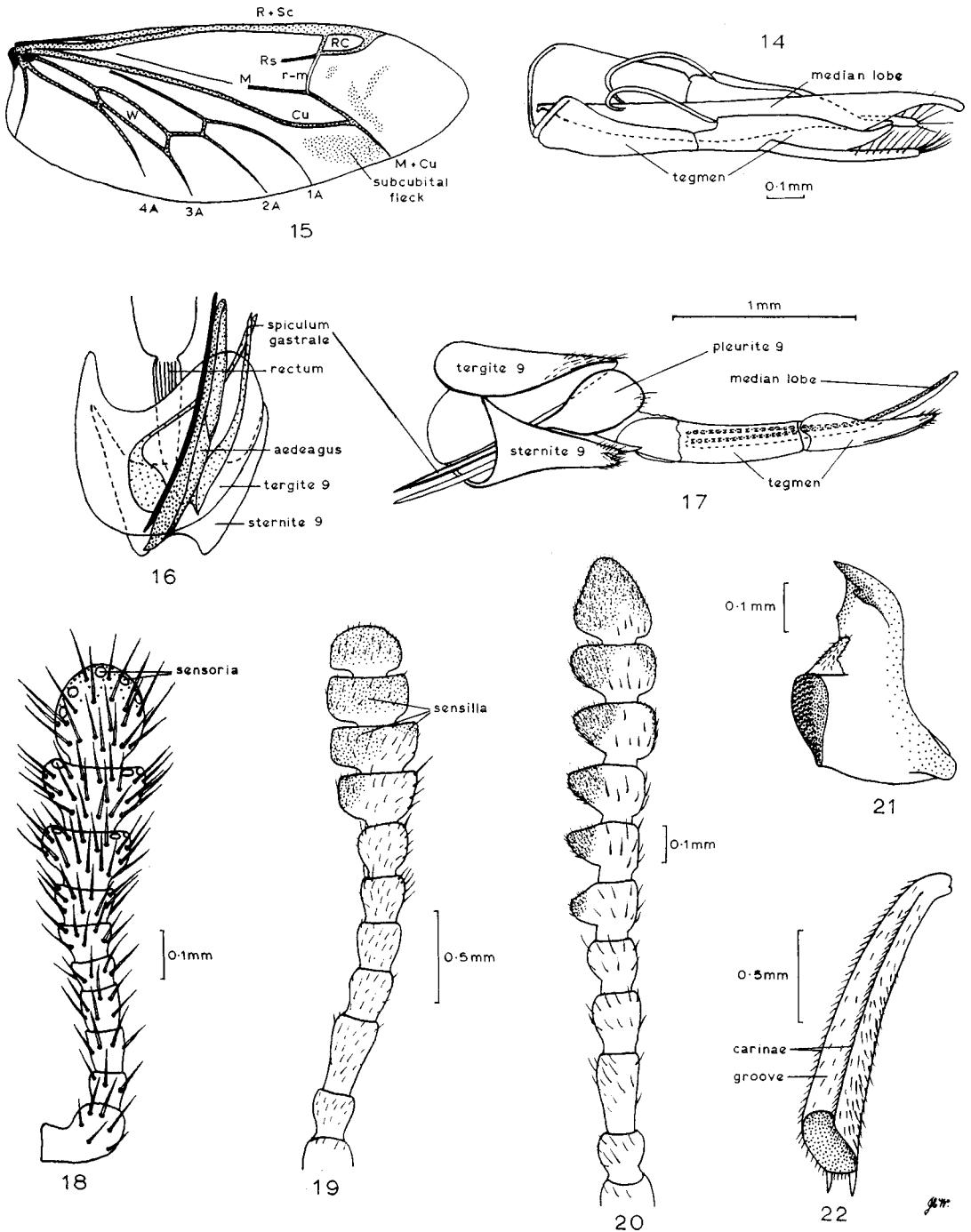
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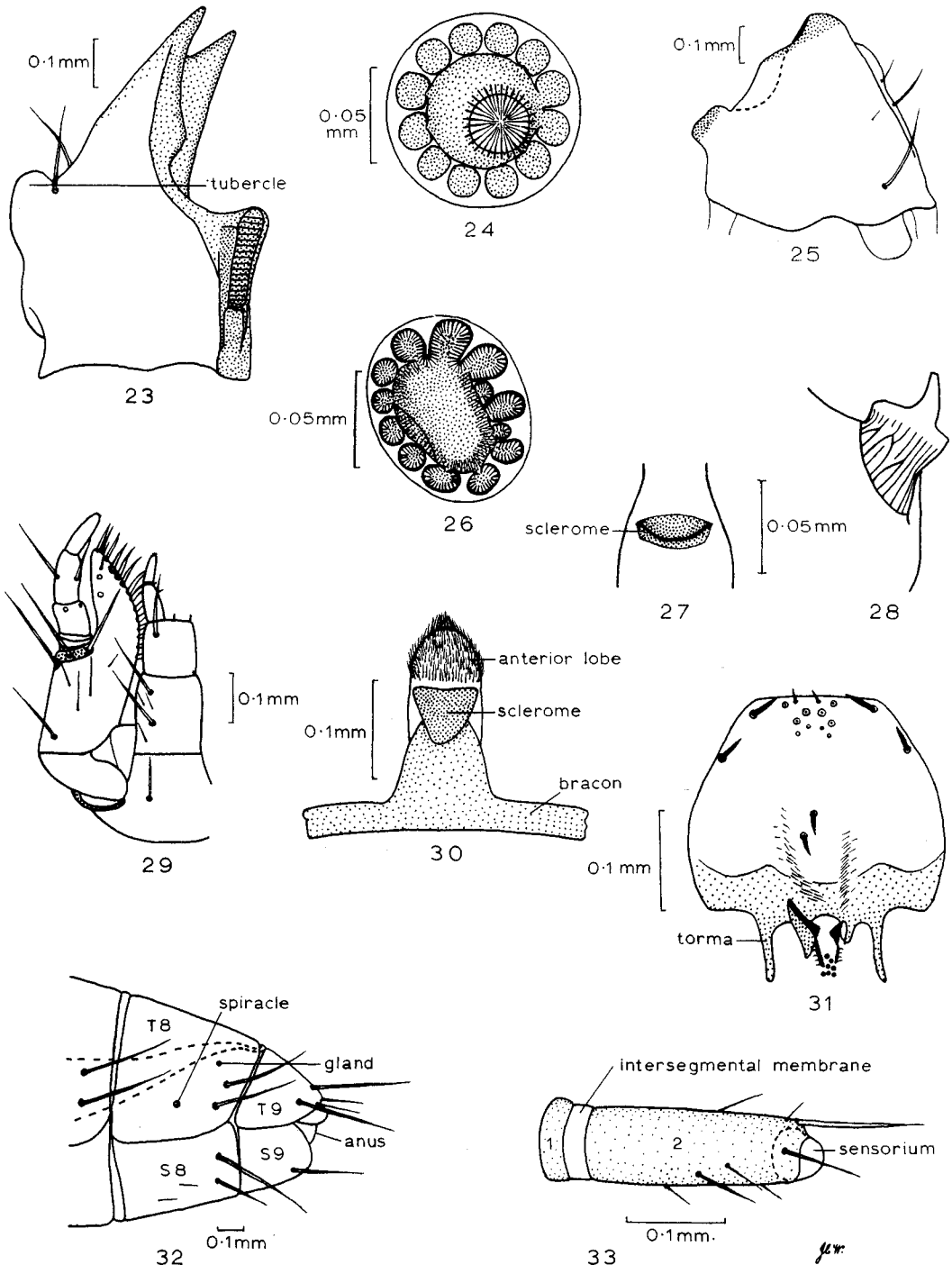
FIGS 1-4—ZOLODININAE, *Zolodinus zealandicus*: (1) pupa, lateral view; (2) pupa, dorsal view of abdominal tergites 1-3; (3) adult, dorsal view of meso- and metathorax after maceration with KOH and removal of tergites; (4) adult, ventral view of prothorax, left coxa removed.



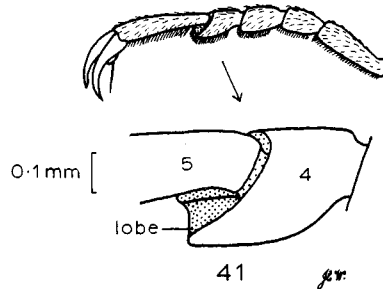
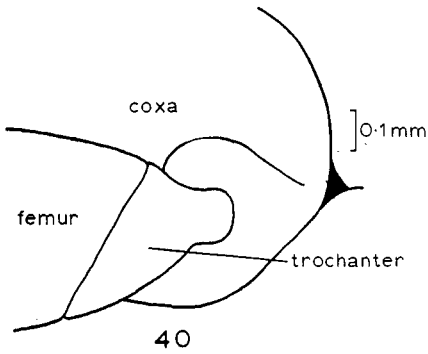
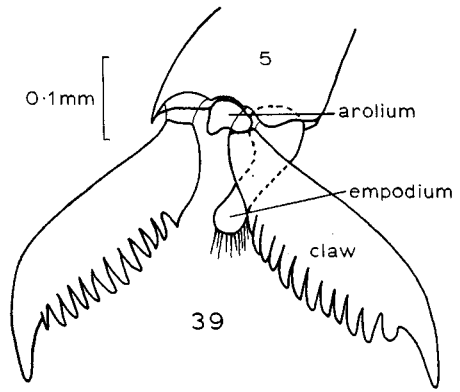
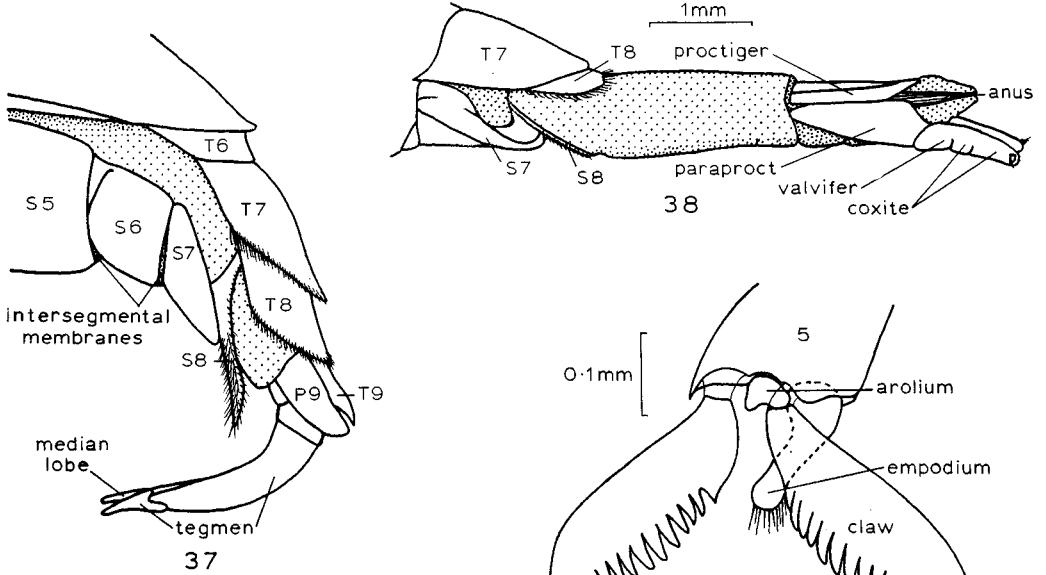
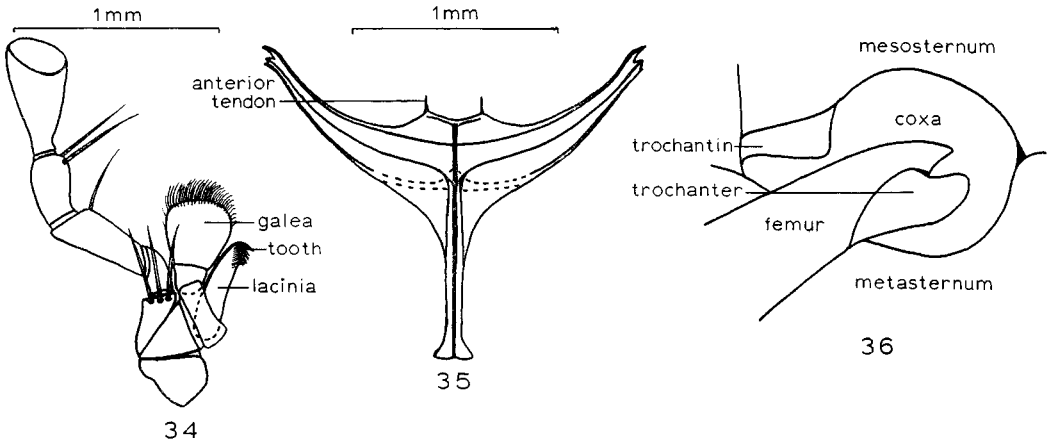
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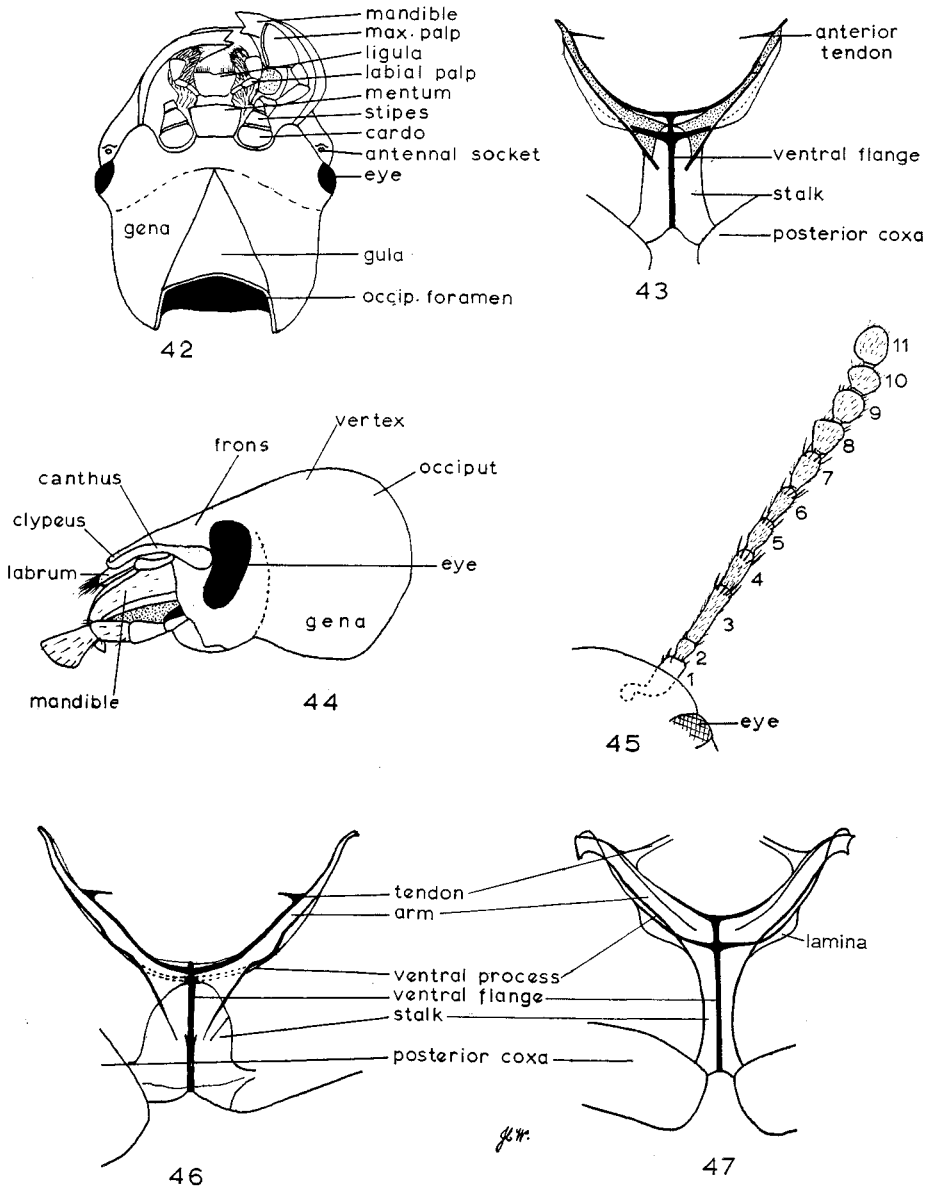
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FIGS. 23-33—TENEBRIONIDAE, larvae: (23) DIAPERINAE, *Diaperis boleti*, left mandible, oblique dorsal view; (24) *Bolitophagus reticulatus*, abdominal spiracle 3; (25) TOXICINAE, *Cryphaeus duellicus*, right mandible, dorsal view; (26) *C. duellicus*, abdominal spiracle 5; (27) *Toxicum* sp. A, hypopharyngeal sclerome, dorsal view; (28) *C. duellicus*, left urogomphus, lateral view; (29-33) GNATHIDIINAE, *Menimus* sp. B—(29) right maxilla and labium, ventral view; (30) hypopharynx, dorsal view; (31) epipharynx; (32) terminal abdominal segments, lateral view (T, tergites; S, sternites); (33) left antenna, dorsal view (apex on right).



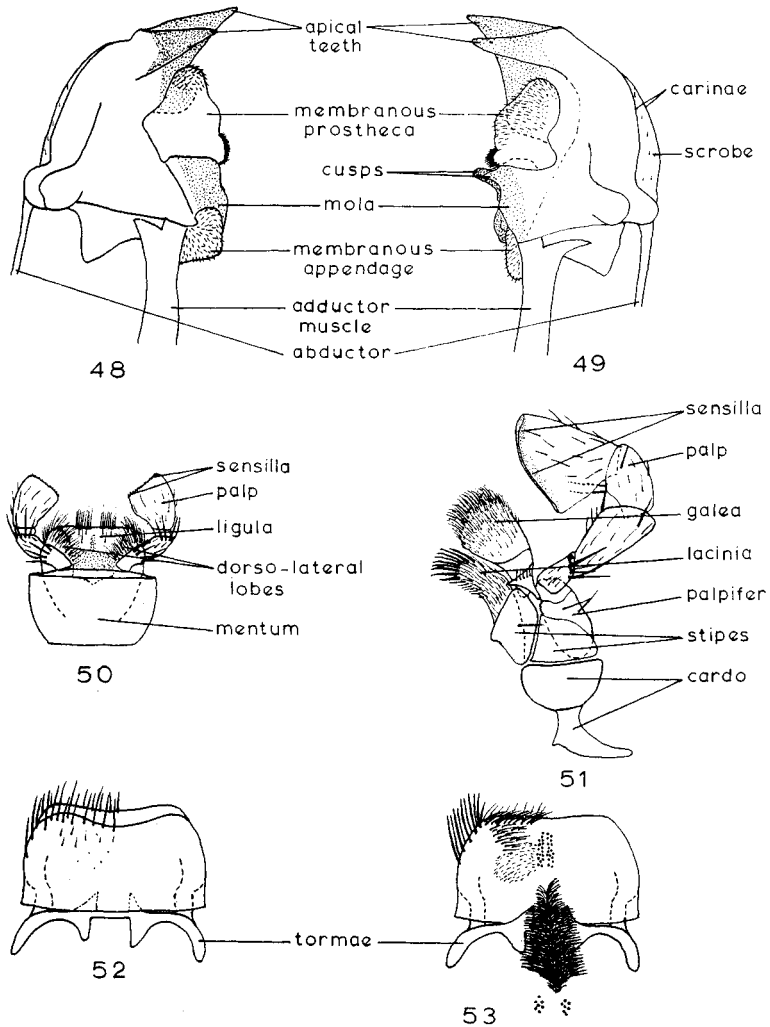
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FIGS 42-47—TENEBRIONINAE, adults: (42) *Mimopeus elongatus*, head, ventral view; (43) *Tenebrio molitor*, metendosternite, dorsal view; (44) *M. elongatus*, head, lateral view (antenna not shown); (45) *M. elongatus*, right antenna, dorsal view; (46) *M. opaculus*, metendosternite, dorsal view; (47) *Uloma tenebrioides*, same.

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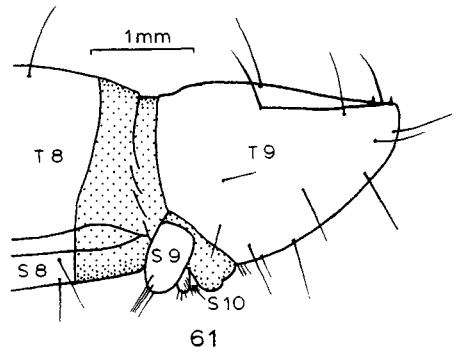
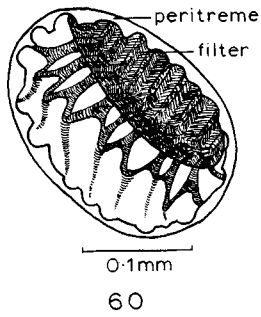
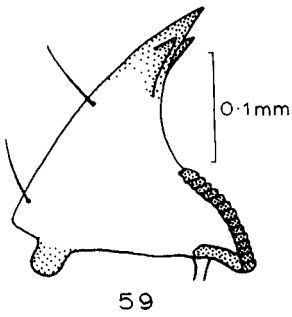
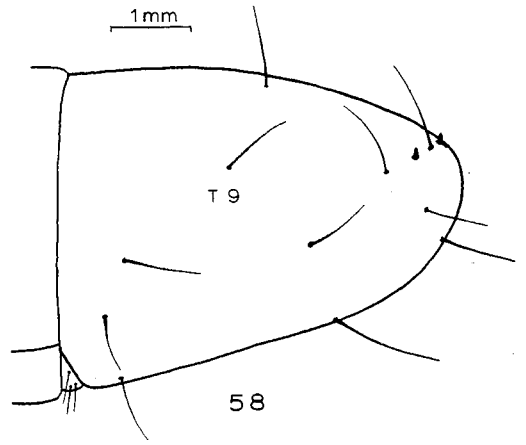
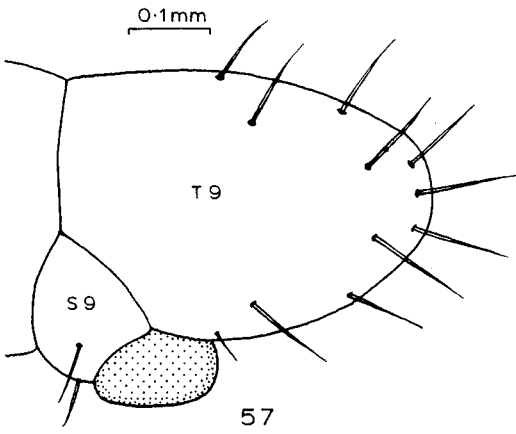
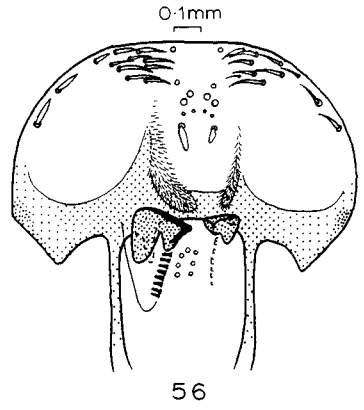
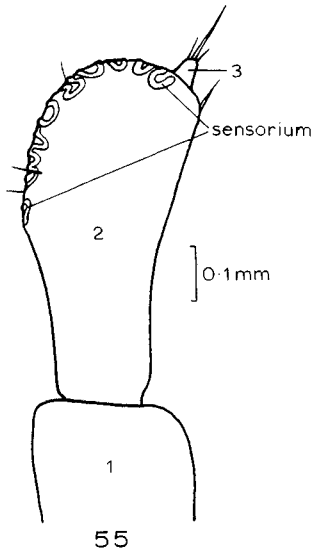
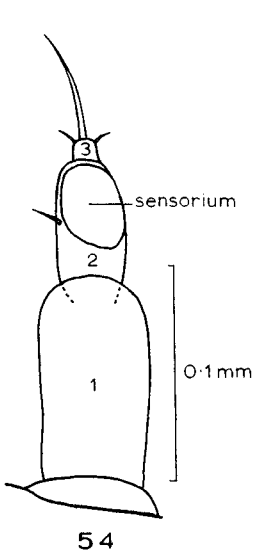
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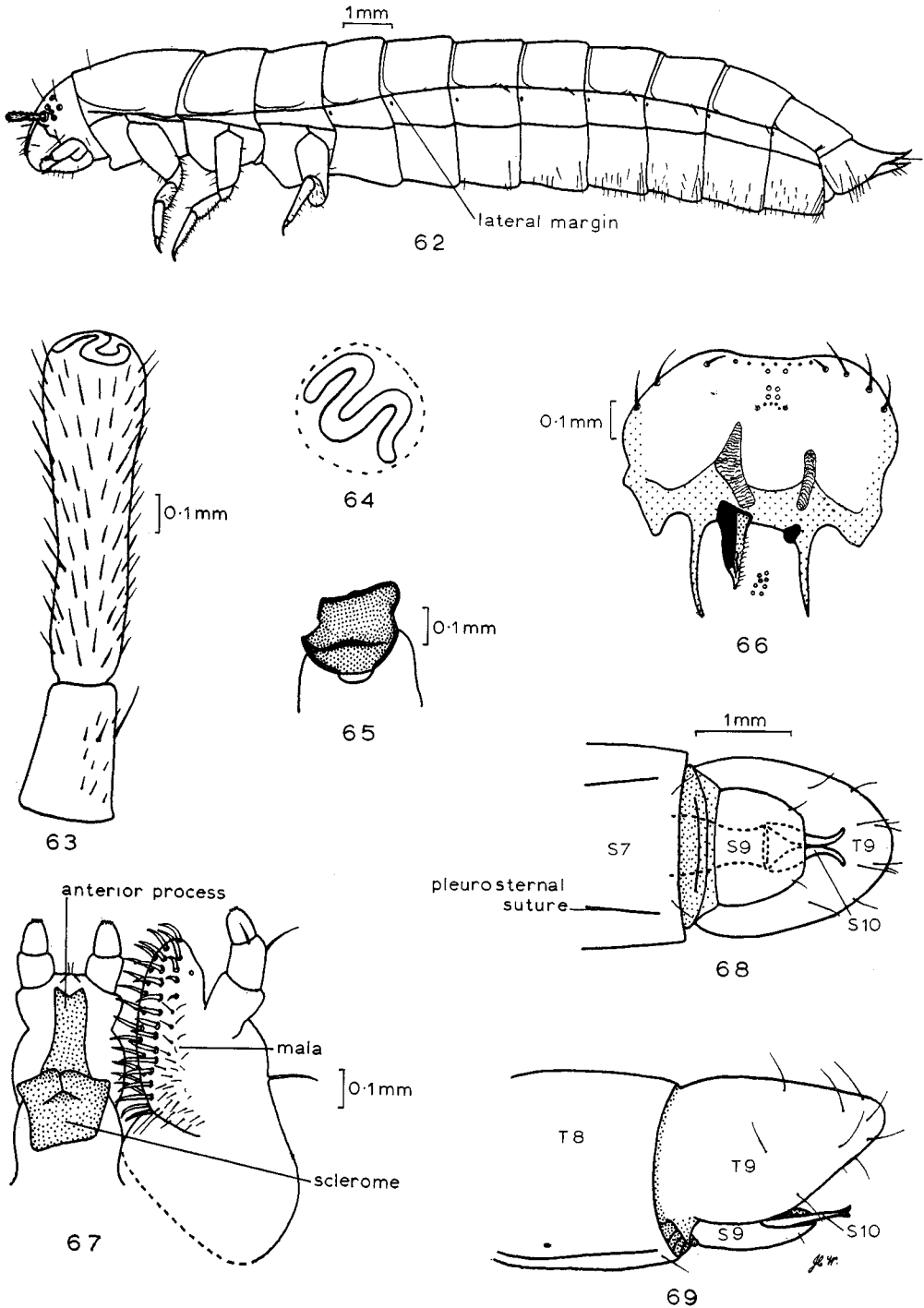


FIGS 48-53—TENEBRIONINAE, *Mimopeus elongatus*, adult, mouthparts, ventral views: (48) right mandible; (49) left mandible; (50) labium, ligula partly retracted; (51) left maxilla; (52) labrum (dorsal view, setae of right half omitted); (53) epipharynx (setae of left half omitted).

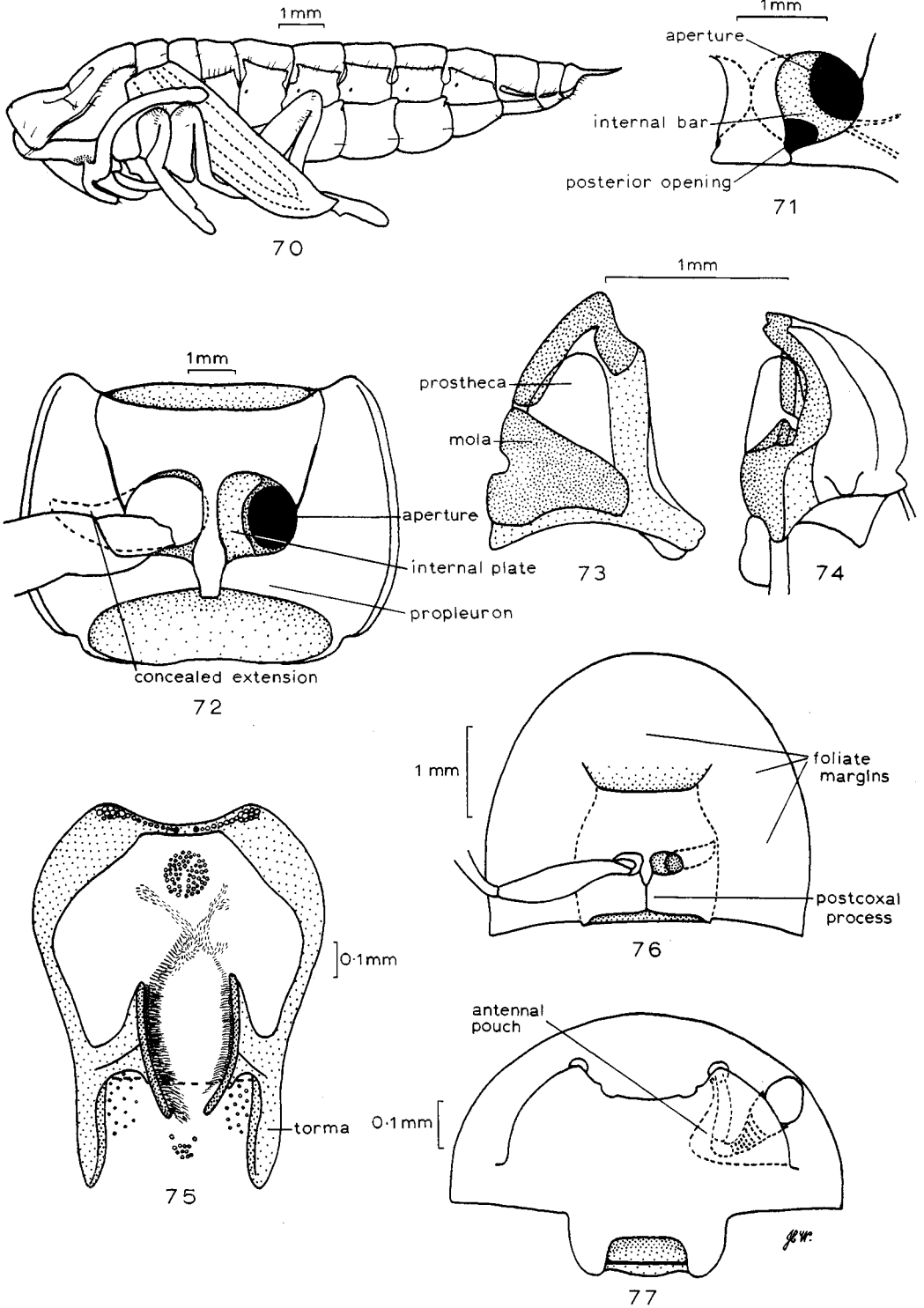
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FIGS 54-61—TENEBRIONIDAE, larvae (T, tergite; S, sternite): (54) PHRENAPATINAE, *Archaeoglenes costipennis*, left antenna, ventral view; (55) TENEBRIONINAE, *Lepispilus sulcicollis*, left antenna, lateral view; (56) *L. sulcicollis*, epipharynx; (57) *A. costipennis*, terminal segments, lateral view (segment 10 unsclerotised); (58) *L. sulcicollis*, terminal segments, lateral view; (59) *A. costipennis*, right mandible, ventral view; (60) *L. sulcicollis*, abdominal spiracle 3; (61) *Mimopeus elongatus*, terminal segments, lateral view.

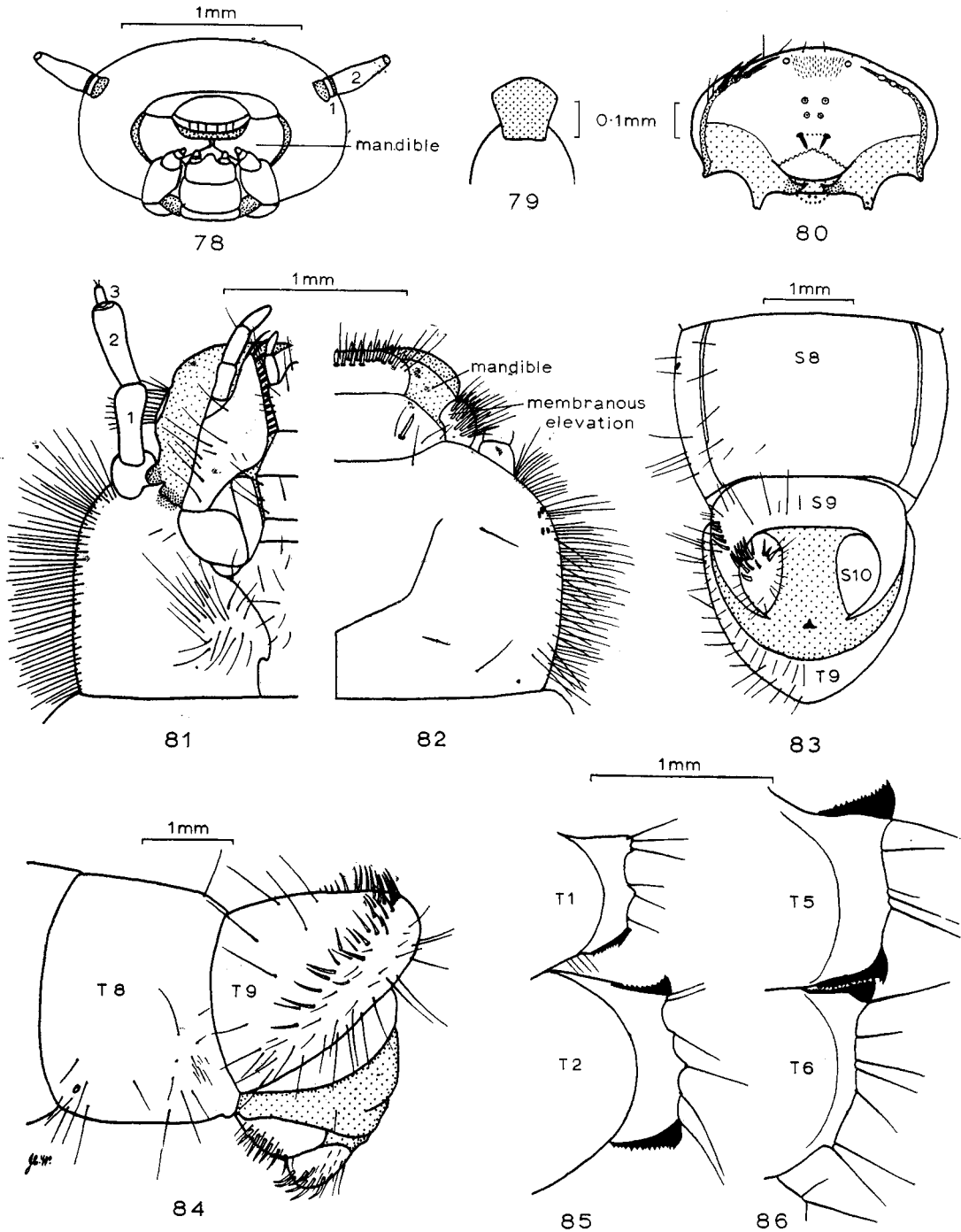




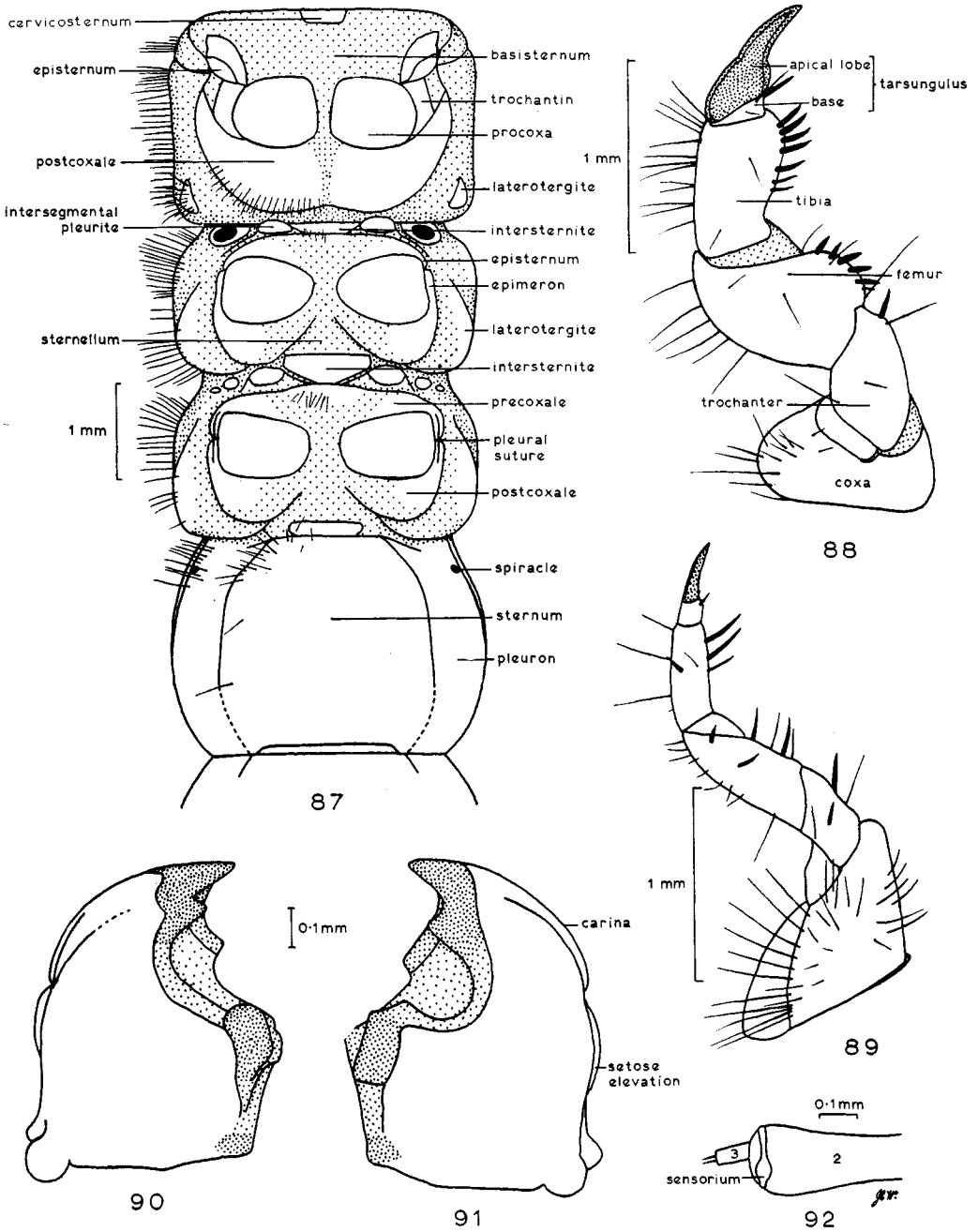
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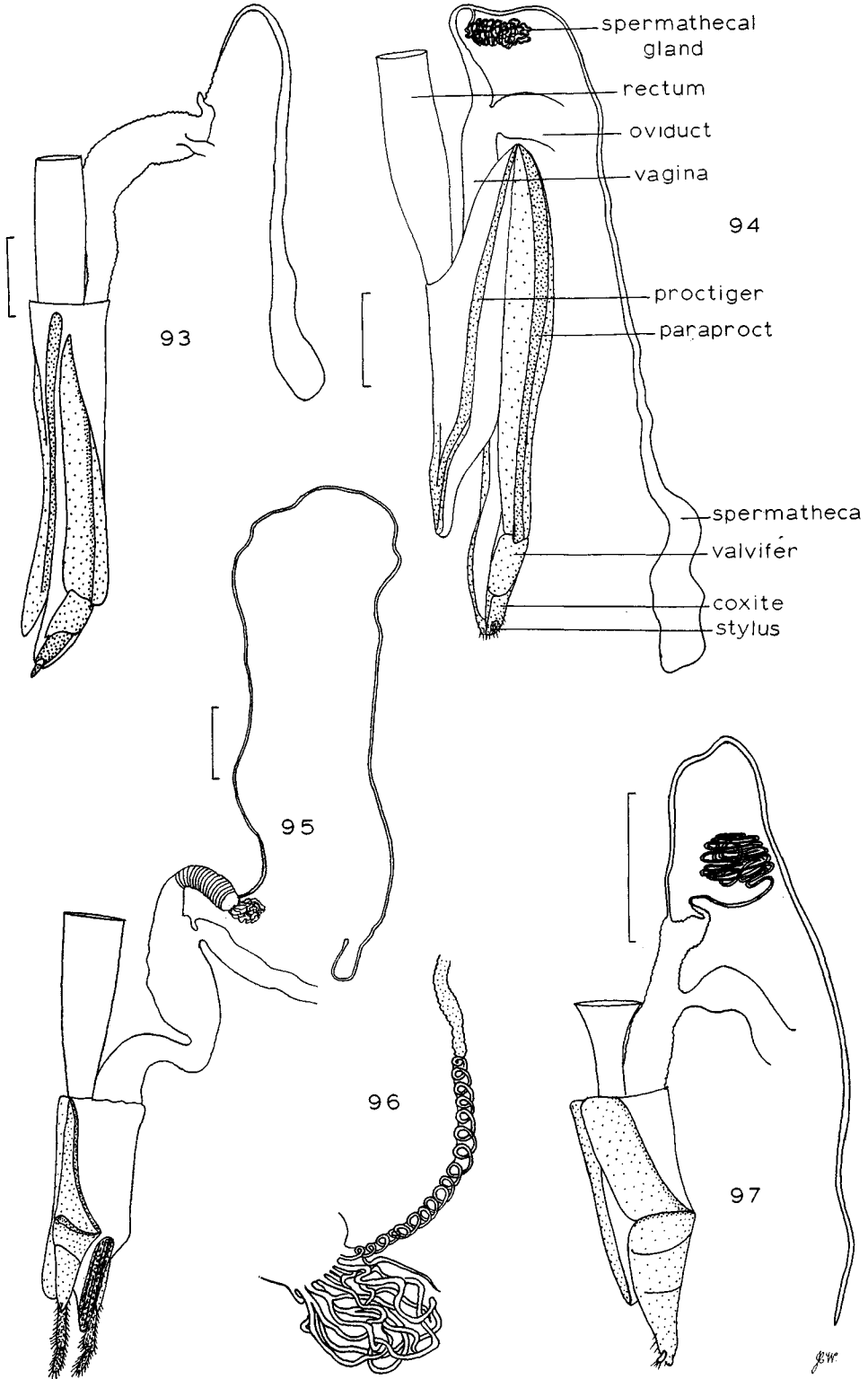
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(Opposite page)

FIGS 93-97—TENEBRIONIDAE, female genitalia (scale lines = 1 mm): (93) PIMELIINAE, *Tentyria schaumii*; (94) ZOLODININAE, *Zolodinus zealandicus*; (95) LAGRIINAE, *Pheloneis indigator*; (96) *P. indigator*, detail of spermathecal gland (8 tubules, 4 branched) and spermathecal duct; (97) TENEBRIONINAE, *Tenebrio molitor* (spermathecal gland has 3 branches).

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