# A review of the classification of Cleroidea (Coleoptera), with descriptions of two new genera of Peltidae and of several new larval types

By R. A. CROWSON
*Zoology Department, University of Glasgow*

## CONTENTS

With 1 plate and 80 Text-figures

## SYNOPSIS

The superfamily Cleroidea is redefined, and a key to the families based on adult and larval characters is given. Each family is discussed and a number of hitherto undescribed larvae are characterised. Three new genera, including one from Baltic Amber, are described.

## I. HISTORY AND CONSTITUTION OF CLEROIDEA

THE superfamily Cleroidea was first established in the larval system of Böving & Craighead (1931), in which forms widely separated in older classifications, the Trogositidae ("Clavicornia") and Cleridae-Melyridae ("Malacodermata"), were brought together. It is rather surprising that similarities between Trogositid and Clerid larvae seem to have been almost entirely overlooked by the earlier coleopterists (*e.g.*, Lacordaire, Perris); the very real similarities between certain adult types of the same two families likewise received very little attention or comment, the first suggestion of a possible connection between them appearing to have been made (very tentatively) by Sharp & Muir as late as 1912. We may see in this an instance of scientific thought blinkered by tradition, the time-honoured categories of Clavicornia and Malacodermata having become so deeply (and probably unconsciously) ingrained in the thoughts of coleopterists that they would not think of comparing a family in one with a family from the other. After Sharp & Muir, the next explicit suggestion of a connection between Cleridae and Trogositidae came in the works of Forbes on wing-venation (1922) and wing-folding (1926). The Cleroidea of Böving & Craighead included, in addition to the families here regarded as Cleroid, the Dermestidae, the Cisidae and (with reservations) the Catogenidae (=Cucujidae-Passandrinae *auctt.*) and Bothrideridae (=Colydiidae-Deretaphrinae and Bothrider-

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inae *auctt.*). Böving & Craighead themselves remarked that the Cleroid features in the larvae of the last two families might be secondary adaptations to a parasitic life, and that their true affinities might lie in the Cucujoidea, with which they are now generally placed. The larvae of Dermestidae have a quite distinct maxillary articulating area and thus would not easily trace to Cleroidea in Böving & Craighead's key to superfamilies, as was pointed out to me by F. van Emden (*in litt.*). Other non-Cleroid features in Dermestidae are the excavate hind coxae and the well-developed spiracles on abdominal segment 8 in the adult, and the maxilla with distinct galea and lacinia and tarsungulus with two setae in the larvae. The Dermestidae have more recently been transferred to an independent superfamily, Dermestoidea (Crowson, 1955).

Most coleopterists other than Böving & Craighead have referred the Cisidae either to Teredilia (=Bostrychoidea; van Emden, 1942) or to Cucujoidea (Crowson, 1955). The wing-venation and folding (Forbes, 1926), and also the aedeagus, in adult Cisidae will immediately separate them from any Cleroidea, and there is nothing distinctively Cleroid about their larvae, *e.g.* the tarsungulus bears two setae, the ocelli do not have the Cleroid arrangement, and the maxillary mala does not bear a pedunculate seta.

In addition to the three main families of Böving & Craighead's Cleroidea, the group will now include three small families, each closely related to one of the large ones—the Phloiophilidae (close to Peltidae), the Chaetosomatidae (close to Cleridae) and the Phycosecidae (close to Melyridae); the last-named family had been referred to Cucujoidea in my previous work (Crowson, 1955). Another family, Helotidae, considered by me in 1955 as possibly related to Cleroidea, has been conclusively established as Cucujoid, following the descriptions of its larvae by Fukuda (1943) and van Emden (1958). In the present work the family Trogositidae, as generally recognised for the last 100 years or more, is divided into two, in the belief that the system of families in Cleroidea is thereby brought into closer conformity with the canons of the phylogenetically based systematics of Hennig (1950).

The place of Cleroidea in the great Polyphagan series named Cucujiformia by me (Crowson, 1955) seems fairly well established, and I see no reason to doubt that the closest affinities of the superfamily are to Lymexyloidea and Cucujoidea; further than this it seems hardly justifiable to go at present. Transitional forms connecting any one of these superfamilies with either of the others are not known to me, but may yet be brought to light; the separate ancestries of all three must date from well back in the Mesozoic era, probably from the Jurassic period.

Interesting analogies and differences may be traced between the larvae (and to some extent the adults) of various Cleroidea and those of some Elateriformia, notably Elateroidea and Cantharoidea. The larvae of Trogossitidae-Trogossitinae are notably similar to those of certain Elateridae, *e.g.* Pyrophorinae and Cryptohypnini (Negastriinae), the similarity extending even to the presence in *Trogossita* (*Temnochila* auctt.) of paired post-gular sensillae (?proprioceptors) in the same positions as in *Hypnoidus* (*Hypolithus* auctt.)—*see* Zacharuk (1962). The differences between Trogossitine larvae and those of any Elateridae are of course numerous and important. The presence in Elaterid larvae of a distinct lacinia and articulated galea, and the absence in them of the normal spiracular closing apparatus, are phylogenetically deep-seated characters that link them with superficially dissimilar types in Dryopoidea and Byrrhoidea; there is every reason to suppose that larval similarities between Elateridae and Trogossitinae result from parallel or convergent evolution. An obvious un-Elaterid-like feature of Trogossitine larvae is the presence in them of a free articulated labrum, where the Elaterids have a rigid toothed nasale. In beetle larvae generally, there seems to be a strong correlation between the presence of such a nasale and the habit of extra-oral digestion—usually but not invariably associated with carnivorous habits. Extra-oral digestion has been reported from a number of species of Elaterid larvae, also from larvae of various Cantharoidea, Carabidae, Dytiscidae, Hydrophilidae, and Staphylinidae-Staphylininae—all of which also appear to lack a peritrophic membrane. I have seen no reports of extra-oral digestion in Cleroid larvae, and the gut-contents of Trogossitine larvae examined by me frequently contain recognisable fragments of food, which are rarely if ever found in larvae of Elateridae. Larval Trogossitinae are probably basically carnivorous, though with evident adaptability to the use of vegetable foods (e.g. *Tenebroides*), and the same is very probably true of Elateridae; from the results of Zacharuk (1963) and others, it appears that practically all species of Elaterid larvae will take animal food if it is available, and that such food tends to speed up development, reduce mortality rates and produce larger adults.

The fundamentally carnivorous nature of Clerid and Cantharoid larvae can hardly be doubted, but there is considerable difference in head-form and mouth-part structure between these groups and Trogossitinae or Elateridae. A certain parallelism can in fact be traced between the relations Trogossitinae-Cleridae on one hand and Elateridae-Cantharoidea on the other, which may prove highly significant when we know more. Analogies between the Cleroid family Melyridae and the Cantharidae are more easily explained as adaptive to very similar habits—adult and larval—in the two groups. In adult Coleoptera generally, "Malacoderm" features are doubtless degenerative rather than primitive, associated with short-lived and free-living adults and often with some form of chemical defence.

## II. Definition and General Features of Cleroidea

### (*a*) *Imagines*

With the general features of Polyphaga-Cucujiformia. Abdominal segment 8 without functional spiracles. Aedeagus sheath-like or Cucujoid, distal prolongation of tegmen usually lying ventrally to median lobe (penis *auctt.*). Hind coxae flat or somewhat projecting, never excavate. Malpighian tubules 4, 5, or 6, cryptonephridic (Stammer, 1934). Met-endosternite of Hylecoetoid type (Crowson, 1938, 1944) or derivable from it, usually with a median projection, anterior tendons always separated. Wings with short radial cell, rarely with more than 4 anal veins in main group. Elytra, if striate, never with a scutellary striole; at least sometimes with all 6 tracheal trunks (*Sc*, *R*, *M*; *Cu*, 1*A*, 2*A*) developed. Ovipositor supported by 4 slender sclerotised rods (baculi of Tanner, 1927). Tarsi nearly always all 5-segmented. Front coxae almost always transverse or projecting and with more or less exposed trochantins. Fore gut never with a markedly sclerotised proventriculus.

### (*b*) *Larvae*

With the general features of Polyphaga-Cucujiformia. Antennae with sensory appendage of segment 2 lying ventrally to segment 3. Labrum free; frontal sutures very rarely of Cucujoid shape, if so a distinct endocarina present (fig. 4). Hypopharyngeal bracon always present. Typically 5 lateral ocelli, arranged in 2 parallel vertical rows, an anterior one of 3 and a posterior one of 2. Maxillary mala undivided, often with a pedunculate seta (*vide infra*) (fig. 38). Mandibles never with a true molar part, usually with characteristic lacinia mandibulae near base of cutting edge (*cf.* fig. 37). Legs well developed and 5-segmented, coxae more or less widely separated; tarsungulus always with a single seta. Dorsal sclerites nearly always present on prothorax and abdominal segment 9, also smaller paired ones on meso- and metathorax, rarely any sclerotisation of abdominal terga 1–8. Abdominal tergite 9 nearly always with rigid corneous urogomphi. First instar, as far as known, without special egg-bursting spines.

*Pupae*, as far as known, without "gin-traps".

Some interesting features are shown by the aedeagus in male Cleroidea. It is usually, and no doubt primitively, inverted in this superfamily, the apex of the tegmen and the distal orifice of the median lobe (penis) lying on the ventral side of the median lobe. This feature, in Coleoptera generally, is associated with a "back to back" position in copulation, whereas when the aedeagus is uninverted the male climbs on the back of the female. In most Cleroidea, the aedeagus maintains the inverted

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orientation both when it is retracted into the abdomen and when functionally extruded, although in some instances the retracted aedeagus lies on one side. There are, however, species of Cleridae (and perhaps of other families) in which the male climbs on to the back of the female in copulation, and, at least in *Necrobia* spp., *Corynetes coeruleus* and *Tillus transversalis* (*cf.* Crovetti, 1962), this is associated with an uninverted aedeagus. A second notable feature of the aedeagus is the "double tegmen" found in Peltidae, Trogossitidae and the Melyrid genus *Acanthocnemus* (*cf.* figs. 12, 70). In these forms there is what appears to be an additional sclerite, situated anteriorly to the distal (ventral) part of the tegmen, and with anterodorsal prolongations extending partly or wholly round the median lobe parallel to the "ring" part of the main tegmen. The only structure I have seen in other Cucujiformia that seems to be at all comparable with this is the so-called "sipho" of the Coccinellidae.

The "pedunculate seta" of the maxillary mala occurs in all Cleroid larvae that I have seen, other than *Phloiophilus* and Peltidae. The only previous authors who seem to have noticed this organ are Vinson (1957) and Fiori (1962); in his excellent and detailed study of larval Malachiinae, the latter author referred to it as "una corta appendice spiniforme (entrambi sempre presente) sorretta da una estroflessione tegumentale cylindriforme". Vinson figured it in the larva of the Melyrid *Pelecophora*, under the name of "lacinia"—this name implies a homology which seems at least doubtful. Among the Cucujoidea, one or more organs of this type occur in the Coccinellidae (and perhaps in other larvae of the Cerylonid sub-group), but they are lacking in those Cucujoid larvae which are otherwise most Cleroid-like in their mouth-parts—Phalacridae, Cucujidae-Laemophloeinae, Nitidulidae, etc. In other superfamilies, pedunculate setae on the maxilla occur very sporadically, for example, in a number of Dryopoidea (in Elmidae-Larini the organ is very similar to that of many Cleroidea), and in Elateridae—in both these groups it is quite independent of the lacinia—and in some Chrysomelidae. All known carnivorous larvae within the superfamily have the pedunculate seta, and all known specifically fungivorous ones (i.e., *Phloiophilus* and Peltinae) lack it; this parallels the condition in the Cerylonid subgroup of Cucujoidea, in which the pedunculate seta is lacking in the fungivorous larvae of Endomychidae but present in the carnivorous Coccinellidae. A major question is whether the ancestral Cleroid larvae were fungivorous like Peltidae and lacked the pedunculate seta, or whether the Peltid-Phloiophilid larval type is secondarily derived from a carnivorous ancestor with the pedunculate seta.

In the mandibles of Cleroid larvae, the presence of the spine-like processes referred to by Böving & Craighead as the lacinia mandibulae is almost as constant a feature as the absence of a true molar part. In larvae of *Phloiophilus* and Peltinae there are normally three stout teeth on the basal part of the cutting edge of the mandible, very similar to the structures seen in the likewise fungivorous larvae of the Cucujoid genus *Tetratoma* (Crowson, 1963). The condition in the Decamerine larva (described below, *cf.* fig. 24), and a comparison of *Tetratoma* with other Heteromera, suggest that the "lacinia mandibulae" may be developed from the front of an original molar part rather than from a true prostheca (which appears to be fundamentally lacking in larval Heteromera). In most Cleroid larvae the lacinia mobilis takes the form of one or more (often three) slender pointed processes, which project somewhat backward. The most similar structures I have seen in other Coleopterous larvae occur in certain Dryopoidea (Elmidae-Larini) and Cucujoidea (Phalacridae).

The presence of dorsal and/or lateral paired glands, of presumably repugnatorial function, on some or all of the trunk segments is a character that recurs in beetle larvae of many unrelated groups, *e.g.* Chrysomeloidea (many Chrysomelinae, certain Galerucinae), Cucujoidea (Coccinellidae, Corylophidae, some Tenebrionidae), many Cantharoidea (Cantharidae, Lycidae, some Lampyridae), certain Elateroidea (Eucnemidae *partim*), a few Dryopoidea (*e.g.* Ptilodactylid genus *Brounia*) and Staphylinoidea. The larger and more specialised glands may be developed from the minute pore-like openings that occur on the trunk of many beetle larvae. Two pairs of such minute openings, close to the posterior transverse row of tergal setae, are particularly widespread in the abdominal terga of Coleopterous larvae and may be found in some Cleroidea (*cf.* fig. 8). The more specialised glands on abdominal segments 1–8 occur, as far as known, in only two Cleroid families, Trogossitidae and Melyridae. Comparable glands on abdominal segment 9 are found in Peltinae (fig. 17), *Phloiophilus* and certain Cleridae (*Metaxina*, fig. 55).

The mode of formation of the adult mid-gut, by which Mansour (1934) showed most of the Cucujiformia he studied to be set apart from other Coleoptera, was recorded by him for only one Cleroid species, *Tenebroides mauretanicus*; he recorded the adult mid-gut in this species as being formed from scattered groups of replacement cells, as in most Polyphaga other than Cucujiformia. This character needs further investigation in Cleroidea and related groups.

It is perhaps worthy of note that, as far as I am aware, stridulatory organs have not been reported to occur in any species of Cleroidea as yet, such organs being quite widespread in the related superfamilies Cucujoidea, Chrysomeloidea and Curculionoidea.

The available information on the chromosomes of Cleroidea is summarised in the works of Smith (1953, 1960) and Virkki (1963). These authors record, for a number of species of Cleridae-Clerinae, eight pairs of autosomes and an x–y sex pair forming a "parachute" figure at meiosis. In a single species of Melyridae-Malachiinae, Smith (1960) records nine pairs of autosomes and an unpaired "X" in the male. These data suggest that the ancestral Cleroidea may have had the standard Coleopteran complement of nine pairs of autosomes and a very unequal X–y sex pair in the male. It will be necessary to study many more species from this point of view before we can judge what value the chromosomes may have in characterising groups within the Cleroidea.

The proventriculus, in both the adult and larval Cleroidea studied by me, appears as a constricted thick-walled region following the more or less capacious crop; it is never markedly sclerotised, but the longitudinal ridges bear a setose armature. In the terminology of Reichenbach-Klinke (1952), it is of the "heteronomous" type, with four stronger ridges alternating with four weaker ones.

## III. A Note on the Tarsungulus and Its Setae in Polyphagan Larvae

The last segment of the legs in normal Polyphagan larvae is usually claw-like in appearance and function; it has by many been homologised with one or both of the claws that terminate the leg in Adephagan and Archostematan larvae. At the other end of the larval leg, the homology of the three basal segments as coxa, trochanter and femur has not been seriously questioned in recent times; between the femur and the claw(s) the Adephagan larva normally has two segments where in Polyphaga there is never more than one. Jeannel (1949) considers the segment following the femur in Adephagan larvae (he calls it the medius and homologises it with the carpopodite of higher Crustacea though not apparently with any segment in the legs of other insects) to have disappeared without any trace in larvae of Polyphaga. Most other authorities are agreed that it is the Adephagan tarsus (the segment preceding the claws) that has disappeared as a separate segment in the larval leg of Polyphaga. It seems to me that there are four logically possible explanations of the Polyphagan condition—(1) that the tarsus has disappeared in the way that Jeannel suggested for his "medius", (2) that the tarsus has fused with the tibia, (3) that the tarsus has fused with the claws and (4) that, after the loss of the original claws, the tarsus in Polyphaga has taken on the function and form of a claw.

I have not encountered any serious advocacy of the first of these theories, but there have been many upholders of the second and the third; use of the term "tibiotarsus" for the penultimate segment of the larval leg implies acceptance of the second, and those who call the claw in Polyphagan larvae a "tarsungulus" are upholding the third. The fourth theory, while appearing *a priori* hardly less likely than the others, has not to my knowledge been advocated in print. Whatever the actual course of evolution of the Polyphagan larval leg, the crucial changes will have occurred at least as far back as the Triassic period, and intermediate stages are unlikely to have survived to the present day; it is not very likely that fossils showing them will be found, so that choice between the four theories will probably depend on subjective estimates of the relative likelihood of particular types of evolutionary change. In adopting the third theory and the term tarsungulus I have followed Böving & Craighead.

The paired claws of typical Caraboidea larvae bear a single seta each, variously placed; where, as in Clivinini, Broscini, Bembidiini, *etc.*, there is a single claw bearing two setae, it is likely that it represents a fusion of two; in other Carabid groups the claws may become very unequal but it seems that this development rarely leads to one claw disappearing altogether.

The larval claw in Polyphaga usually, and no doubt primitively, bears two setae, variously placed but usually towards the middle of the tarsungulus, whereas the paired setae of the claw in Broscini, *etc.*, are usually very near its base; likewise the unguitractor tendon usually attaches somewhere near the middle of the Polyphagan tarsungulus, whereas in Broscini, *etc.*, it ends almost at the extreme base of the claw. There are a few larval Polyphaga in which the tarsungulus bears more than two setae, for example, in *Dascillus* and various Lymexylidae. This condition seems to me unlikely to be primitive, but if it were it would provide an additional argument in favour of the tarsungular theory.

In addition to Cleroidea, within which it appears to be universal, a tarsungulus bearing only one seta occurs in certain Cucujoidea and appears to be general in Dryopoidea. Such larvae as I have examined of Elateroidea and Cantharoidea all possess two tarsungular setae, as does an undetermined Callirhipid larva from Borneo. This might be taken as evidence against the theory, put forward by Böving & Craighead (1931) and myself (1955, 1960), that all these forms are ultimately derivable from Dryopoid ancestors. It may be, however, that Dollo's Law is not strictly applicable here—as it cannot be if the plurisetose tarsungulus of *Dascillus* and Lymexylidae is derivable from the ordinary bisetose Polyphagan type.

## IV. THE FOSSIL HISTORY OF CLEROIDEA

For the purposes of phylogenetic classification, direct information about the Cleroidea of the past is greatly to be desired. In fact, a considerable number of Tertiary fossils have been attributed to families of this group, many of them no doubt correctly. However, it is one thing for a fossil to display a recognisably Trogositid or Clerid facies and quite another for us to be able to discern in it features that are significant in relation to the phylogeny of these families. From a study of the figures and descriptions of the described fossil Trogositids and Clerids, the only conclusion that seems to me to be justifiable is that both these families were in existence in the Eocene period, which one would have been justified in assuming from the "classificatory perspective" of the existing forms. There is one type of fossil, however, from which much more detailed conclusions could and should have been drawn—the inclusions in the Baltic amber and other Lower Tertiary fossil resins. Such amber fossils frequently permit the study of almost all the external characters that museum systematists habitually use for the classification of modern beetles. It is most unfortunate, and not to the credit of German entomology, that the large collections of amber beetles that were accumulated by various private collectors were hardly ever the subject of proper specialist study. The usual practice seems to have been for the collector to submit his beetles *en masse* to some German coleopterist of his acquaintance, who proceeded to write determination labels for the specimens; the collector might himself publish a list of such names in some local natural history journal. Even such an eminent coleopterist as Edmund Reitter, who should surely have known better, lent himself to this sort of practice. As a result, apart from Wasmann's unsatisfactory study of the Paussidae, Schedl's careful study of the Scolytidae, and Uhmann's description of two species of Chrysomelidae-Hispinae, practically none of the Baltic amber beetles have ever been properly described or classified. In the course of the second World War, many important amber collections seem to have been lost, perhaps irretrievably. In the small part of the Klebs collection now preserved in the British Museum, I was able to find two fossil Cleridae, one of them described later in this work.

It is to be hoped that amber fossils will in future receive the most careful study by world specialists in their respective groups; where the Baltic amber is concerned, any specimens containing insects that appear to be identical with modern (and especially, modern European) species should be most critically investigated with a view to the possibilities of faking in one way or another. There is, fortunately, little likelihood of faking where most of the non-European ambers are concerned, these not having been the basis of anything like the highly skilled and lucrative trade that Baltic amber supported—the main difficulty with these is likely to be false attribution of specimens, trying to "pass off" copal as Burmese amber, and so on.

## V. KEY TO FAMILIES OF CLEROIDEA: ADULTS AND LARVAE

1 ADULT: mandibles with a distinct molar part (figs. 10, 27) or lacinia mobilis (fig. 9). Lacinia nearly always with a hooked spine at the apex (fig. 11); if with spine on the inner face only, mandibular mola asperate. Front coxae not or slightly projecting, strongly transverse. Gular sutures usually widely separated posteriorly. Antennae with not more than 8 segments before the 1–3-segmented club. Tarsi filiform, apical segment usually as long as preceding 4 together, a conspicuous bisetose empodium between the claws. LARVA: mandibles with a 3-toothed structure (fig. 2) in basal part of cutting edge. Maxillae with transverse cardo, much shorter than stipes, and some trace of an articulating area (fig. 15); mala without pedunculate seta. Head with distinct endocarina, no median epicranial suture. A ventral pigment spot often present in addition to the usual 5 ocelli (fig. 3) . . . . . . . . 2

– ADULT: mandibles without a definite molar part or lacinia mobilis. Lacinia never with a terminal hooked spine, rarely with a spine on inner face. LARVA: mandibles with lacinia mobilis composed of 1–3 elongate articulated processes (figs. 37, 47, 67). If cardo transverse, much shorter than stipes and with a perceptible articulating area, head without endocarina and with a distinct median epicranial suture; mala with a pedunculate seta (fig. 38) . . . . . . . . . . . 3

2 ADULT: mandibles with lacinia mobilis (fig. 9) but no molar part. Front coxae distinctly projecting. No spines (other than apical) on any of the tibiae. Tegmen of aedeagus in one piece. LARVA: frontal sutures of markedly Cucujoid form (fig. 4) . . . (1) PHLOIOPHILIDAE

– ADULT: mandibles with distinct molar part. Front coxae not at all projecting. Usually at least front and middle tibiae with very short spines on outer face. Tegmen of aedeagus in two pieces (fig. 12). LARVA: frontal sutures not so shaped . . . . . . . (2) PELTIDAE

3 ADULT: mandibles with a single apical tooth and another behind it on cutting edge (fig. 47), basal part of cutting edge very rarely denticulate.

If tarsi filiform, usually gular sutures more or less confluent or antennae clubbed. If prothorax with distinct side edges, antennae nearly always clubbed. LARVA: maxillae never with any trace of articulating area; if cardo transverse, stipes not or little longer than it. Endocarina nearly always distinct, median epicranial suture rarely present 4

– ADULT: mandibles normally with a pair of apical teeth, one above the other, the ventral one sometimes reduced or absent, in which case the base of the cutting edge is more or less denticulate (fig. 78). Tarsi nearly always filiform; tibiae rarely with very short spines along their outer faces; antennae very rarely clubbed. Prothorax nearly always with distinct side margins. LARVA: maxillae with some trace of an articulating area, cardo transverse, stipes moderately elongate, mentum never very elongate. Endocarina absent, median epicranial suture present . . . . . . . . . . . . . . . . . . 6

4 ADULT: front coxae not at all projecting. Tarsi filiform. Tibiae usually with very short spines along their outer edges. General facies more or less "Clavicorn". LARVA: ventral mouth-parts retracted, stipes and mentum very long, or dorsal sclerite of abdominal segment 9 divided transversely into two parts. Mandibles with two apical teeth (fig. 37). Abdominal segments 1–8 with dorsolateral glands (fig. 40) (3) TROGOSSITIDAE

– ADULT: front coxae distinctly or strongly projecting. If tarsi filiform and tibiae with very short spines along their outer edges, antennae not or scarcely clubbed. General facies more or less "Malacoderm". LARVA: ventral mouth-parts protracted, stipes never very long, dorsal sclerite of abdominal segment 9 never divided transversely. Mandibles (fig. 47) with only one apical tooth. Abdominal segments 1–8 without dorsolateral glands . . . . . . . . . . . . . . . . . 5

5 ADULT: all tarsi filiform. At least front and middle tibiae with short stout spines on their outer faces. Front coxae only slightly projecting. Gular sutures almost confluent. Antennae filiform, or with last 3 segments very slightly thickened, prothorax with distinct side edges. LARVA: hypostomal rods (fig. 49) extending to hind margin of head capsule . . . . . . . . . . . . (4) CHAETOSOMATIDAE

– ADULT: at least front tarsi nearly always with two or more dilated segments; if not, front coxae strongly projecting and gular sutures well separated. Tibiae never with short stout spines along outer face. If antennae filiform, prothorax usually without distinct side edges. LARVA: hypostomal rods never extending to hind margins of head capsule (5) CLERIDAE

6 ADULT: antennae 10-segmented, with strong 1-segmented club. Front coxae small, slightly transverse, not projecting, their cavities almost or quite closed behind. General facies "Clavicorn". LARVA: head with 6 ocelli on each side, the ventral one corresponding in position to the pigment spot of *Phloiophilus*. Epicranial suture very short. Abdominal segments (fig. 69) with dorsal sclerites but without evident glandular openings . . . . . . . . . . . . (6) PHYCOSECIDAE

– ADULT: antennae usually filiform or serrate, rarely with a loose weak club. Front coxae large, strongly projecting. General facies "Malacoderm". LARVA: head with not more than 5 ocelli on each side. Epicranial suture usually longer. Abdominal segments, if with dorsal sclerites, also with distinct glandular openings on them (fig. 75) (7) MELYRIDAE

## VI. Family 1. PHLOIOPHILIDAE

Of the genera listed under this name by Pic (1926), *Xerasia* Lewis appears, from my examination of the single adult in the British Museum, to be allied to *Byturus* (Cucujoidea); according to the imaginal characters used in my key, *Acanthocnemus* Perris is Melyrid, though its larva is still undescribed. There remains only *Phloiophilus* Westw. (*Phloeophilus* auctt., an emendation which appears to be invalid under the current rules), with its single European species *P. edwardsi* Steph.

I had already noted a remarkable similarity in adult structure between *Phloiophilus* and a primitive Peltid type collected by me in New Zealand, *Protopeltis* (*Grynoma* Broun) *viridescens* (Broun), before I succeeded in finding the *Phloiophilus* larva, which proved to exhibit an equally marked affinity to that of *Protopeltis*. The question had immediately to be faced—might not these two genera be placed in the same family? The most important larval difference I have noted between these genera is the different form of the frontal sutures; the lack of a mandibular mola in the adult distinguishes *Phloiophilus* not only from *Protopeltis* but from all known Peltidae, and its non-spinose tibiae are unmatched in Peltinae (though paralleled in some of the otherwise very dissimilar Egoliinae). Moreover, I have seen no Peltid with the undivided tegmen or distinctly projecting front coxae of *Phloiophilus*.

The tracheation of the elytra is unusual in *Phloiophilus;* there are 5 distinct tracheal trunks, 3 in the anterior group and only 2 in the posterior group, the missing one being the second of the group, interpreted by me (Crowson, 1955) as 1A.

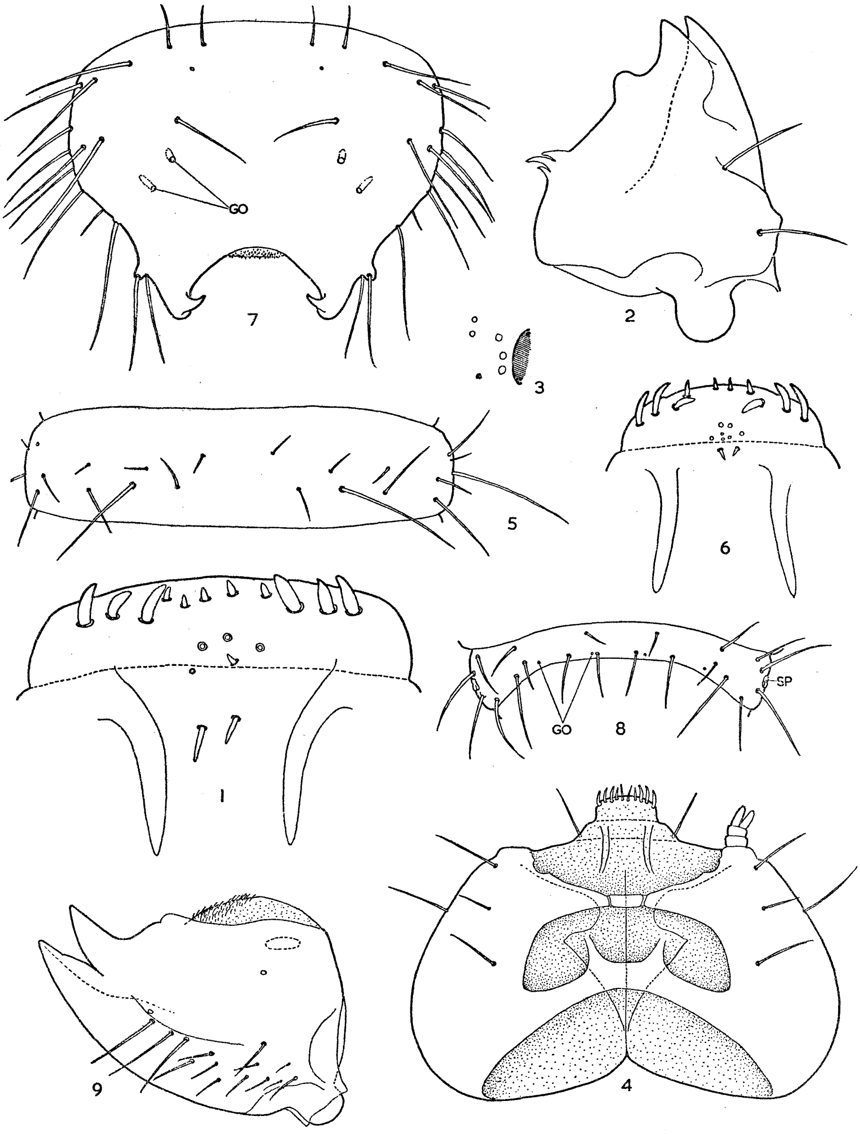
The habits of *Phloiophilus*, which are described in Crowson (1964), and of *Protopeltis* appear to be very similar, and it may be that part of the similarity between them consists in characters that are not truly primitive but result from parallel adaptation. On this hypothesis, *Protopeltis* may be phylogenetically closer to other Peltinae than to *Phloiophilus*, and the latter might even be more closely allied to the ancestors of Melyridae. If, as this theory implies, the ancestral Cleroids did not have habits like those of *Phloiophilus*, the question arises—how did they live? On present knowledge, the most plausible answer is that they were carnivorous, at least in the larval stage.

Distributionally, this family is unique—no other Coleopterous group of comparable status is represented by a single species that is confined to Europe. It is, of course, still possible that Phloiophilidae may yet be discovered in other parts of the world.

### *Description of the larva of* Phloiophilus edwardsi

*General form.*—Rather short and broad, somewhat flattened, with relatively short legs; movements very slow; predominant colour whitish, head capsule and ninth abdominal tergite brownish-testaceous, pronotum rather lighter testaceous. Length of largest specimens about 4·5 mm., width of head capsule about 0·8 mm.

*Head.*—Head capsule strongly transverse, strongly rounded at sides, much narrower in front than behind; endocarina well marked, frontal sutures (fig. 4) of markedly Cucujoid form, median epicranial suture extremely short; halves of head capsule not nearly meeting below, hypostomal rods distinct, slightly divergent; hypopharyngeal bracon broad and strong, median part delimited by distinct sutures (fig. 4); ocelli characteristically arranged, 5 on each side, bearing distinct lenses; also a pigment-spot without a distinct lens, situated more ventrally (fig. 3); labrum free, small, transverse, front margin evenly rounded, epipharynx with characteristically arranged sensillae (fig. 6) and widely separated epipharyngeal rods. Antennae (fig. 4) 3-segmented, the 2 basal segments broader than long, apical segment elongate, segment 2 bearing a conical sensory appendage ventrally to segment 3. Mandibles (fig. 2) without a molar part, characteristically shaped, with an apical ventral and a slightly pre-apical dorsal tooth, also a blunt pre-apical process of the cutting edge; a 3-toothed non-articulate retinaculum-like structure on basal part of cutting edge, in the position of the usual Cleroid lacinia mandibulae. Maxillae with a transverse cardo and well marked articulating area, stipes elongate and bearing an apically blunt mala; mala without a pedunculate seta, with irregularly arranged large spines from apex down most of inner edge, near the middle of which are 2 tooth-like processes; palpi short, with 3 distinct segments arising from a distinct palpiger, segments 1–2 very transverse, 3 nearly twice as long as wide and slightly narrowed to its apex. Labium with broad obtuse ligula, insertions of palpi widely separated, prementum very transverse, narrowed to base, mentum less transverse, somewhat widened to base; palpi 2-segmented, segment 1 transverse, 2 elongate; prementum, mentum and postmentum each with a pair of long ventral setae.



FIGS. 1–9.—Phloiophilidae and *Thymalus*. (1) *Thymalus limbatus* F., larva, epipharynx. (2–8) *Phloiophilus edwardsi* Steph. larva: (2) right mandible, dorsal view; (3) ocelli of right side, antennal socket cross-hatched, pigment spot dotted; (4) head capsule, ventral view, mouthparts removed; (5) metanotum, to show chaetotaxy; (6) epipharynx; (7) abdominal segment 9, dorsal view; (8) abdominal segment 8, dorsal view; (9) *P. edwardsi* adult, left mandible, dorsal view.

*Thorax*.—Prothorax with large weakly sclerotised tergite, divided by a pale median line, bearing 4 pairs of large setae along front margin and 3 pairs along hind margin; prosternum with a weak transverse central sclerotisation bearing a pair of setae; front coxae moderately widely separated. Meso- and metathorax without evident tergal sclerotisations, with dorsal setae characteristically arranged (fig. 5); sterna each with a distinct transverse sclerotisation bearing a pair of setae; hind coxae appreciably more widely separated than the front pair.

*Abdomen*.—Segments 1–8 without tergal sclerites and without distinct ampullae, with regularly arranged setae (fig. 8) but no dorsal glands. Segment 9 (fig. 7) with well marked characteristically shaped dorsal sclerite, produced posteriorly into a pair of urogomphi with upturned hook-like apices, ventral surface membranous and bearing the short pygopod-like tenth segment; dorsal surface with 2 pairs of narrow tubular ducts (fig. 7, *GO*), probably the openings of glands. Spiracles moderate sized, bicameral, with well developed, lateral paired air tubes, which are directed nearly dorsally in front spiracle, nearly posteriorly in remaining ones. Anterior spiracle situated anterolaterally in the mesothorax, the others dorsolaterally in abdominal segments 1–8, slightly before middle of each segment. Legs, with coxae rather strongly sclerotised and pigmented in front, with a strong pre-apical seta and 2–3 along apical margin anteriorly; trochanters moderate sized, about as wide as long, each with 2 strong setae on ventral edge and 1 or 2 each on anterior and posterior faces; femora about twice as long as their maximum width, each with about 4 setae on its ventral side; tibiae slightly longer than femora, at least two and a half times as long as their maximum width, each with an anterodorsal and a posterodorsal seta near middle and slightly more distal anteroventral and posteroventral ones, also 2–3 dorsal apical ones; tarsungulus claw-like and with one strong ventral seta.

### *Analogies between* Phloiophilus *and the Cucujoid genus* Tetratoma

Considerable similarities exist, in both adult and larval stages, between *P. edwardsi* and species of *Tetratoma*, especially *T. ancora* F.; *Tetratoma baudueri* Perris was even redescribed from North Africa as *Phloeophilus flavopictus* Fairm. Here, as in *Protopeltis*, we might attribute the similarities to homology, *i.e.* to inheritance from a common ancestor, or to analogy, *i.e.* to parallel or convergent adaptation. It can hardly be doubted that the relationship of *Phloiophilus* to *Tetratoma* is much more distant than that to *Protopeltis*, so that analogy rather than homology is *a priori* more likely in this instance. From my own investigations, it appears that *Tetratoma ancora* has the same host-fungus as *Phloiophilus* but a different seasonal life-cycle, whereas *T. desmaresti* Latr. has the same life-cycle as *Phloiophilus* but a different (though supposedly related) host fungus.

The larvae of *Tetratoma ancora* resemble those of *Phloiophilus* in the general form of the body and of the head capsule, the antennae, the mandibles, epipharynx, maxillae, and to some extent the ocelli, also in the form and orientation of the spiracles; these larvae are unlike *Phloiophilus* in (1) the presence of a short but distinct epicranial suture and absence of an endocarina, (2) the distinctly sclerotised tergites of all the thoracic and abdominal segments (including the tenth), (3) the bisetose tarsungulus. Despite some similarities in habits, *Tetratoma* adults are notably unlike *Phloiophilus* in (1) the heteromerous tarsi, (2) the met-endosternite, (3) the basically pseudotrilobe aedeagus, (4) the subcubital fleck of the wings. In most respects in which they differ, *Tetratoma* resembles other Cucujoidea (*e.g.* Byturidae, Mycetophagidae, *etc.*) and *Phloiophilus* resembles other Cleroidea. The fact that the presumably convergent similarities between *Phloiophilus* and *Tetratoma* are particularly manifest in the shape of the head-capsule and the structure of the mouthparts, while differences appear in the dorsal sutures of the head, presents some parallel with the *Phloiophilus-Protopeltis* relation, and strengthens the supposition that there too similarities may be in part convergent.

## VII. Family 2. PELTIDAE

The heterogeneity of the old family Trogositidae (Ostomidae, Ostomatidae, Peltidae, Temnochilidae *auctt.*) has been noted by many authors; Thomson (1859) even divided it into two, his Peltidae and Trogositidae. The division adopted in the present study is rather different from Thomson's in that Egoliinae, which all previous authors have associated with Trogositinae, are part of my Peltidae, whereas the forms allied to *Lophocateres*, hitherto associated with Ostominae, are part of my Trogossitidae. The importance of the characters of the mouth-part, on which the separation of adult Peltidae from Trogossitidae chiefly depends, was correctly appreciated by Erichson (1844), but unfortunately later systematists did not follow him in this. Coleopterists of the early nineteenth century, beginning with Latreille, had attached great classificatory importance to the mouth-parts, but by the time of Lacordaire's great work the tide of fashion was beginning to run against this attitude; later workers on Trogositidae such as Sharp, Reitter and Leveillé, generally gave only perfunctory attention (if any) to the mandibles and maxillae when describing new genera, *etc.*, in the family. Erichson himself was guilty of failing to notice significant features of the mouth-parts in Egoliinae, and Reitter made confusion worse confounded by associating *Nemosoma* with that group, as well as by transferring *Calitys* to Trogositinae.

Peltidae, rather than Ostomidae (or the supposedly more correct form Ostomatidae) is here adopted as the name of the family in an attempt at compliance with the current rules of zoological nomenclature. Peltides of Latreille (1807) seems to be the oldest available suprageneric group name here; Reitter's Ostomini of 1882 was presumably proposed on the assumption that *Peltis* Kugel. of 1792 was a junior synonym of *Ostoma* Laich. (1781). According to our present rules, the name of a family-group taxon need not be changed if its type generic name is found to be a junior synonym. In fact *Peltis* Kugel. and *Ostoma* Laich. are not "objective" synonyms, nor have they usually been treated as "subjective" synonyms in twentieth-century works on Trogositidae. Des Gozis (1886) pointed out that the type of *Peltis* Kugel., by monotypy, was *grossa* L., while designating *ferruginea* L. as the type of *Ostoma* Laich. On the assumption that *Peltis* Kugel. was an invalid junior homonym of *Peltis* Geoffroy (1764), Des Gozis proposed a new name, *Zimioma*, to replace the former; most subsequent authors have maintained *Zimioma* Des Gozis as a full genus. It has recently been ruled (Opinion 228) by the International Commission on Zoological Nomenclature that Geoffroy's work of 1764 was invalid because not strictly binomial, in that the species names in it were French in form; *Peltis* Geoffr. will thus have no status in nomenclature and will not invalidate *Peltis* Kugel. Des Gozis' name is thus superfluous, and *Peltis* can be restored as a good generic name and as the type of the family name Peltidae; there would be no need to change the family name even if *Peltis* were later reduced to a subgenus of *Ostoma*. If it were ever discovered that *Peltis* Geoffr. had been validated before 1792, *e.g.* by republication in strict binomial form, this would of course invalidate *Peltis* Kugel. and necessitate a change in the name of the family—presumably to Ostomatidae or Zimiomidae.

The Peltid larvae available for study represent two of the three subfamilies into which the group may be divided on adult characters; until larvae of Egoliinae are discovered, the characterisation and constitution of the family must be regarded as tentative. On present knowledge, the Peltidae would appear to be directly related on the one hand to *Phloiophilus* by way of forms like *Protopeltis*, and on the other hand (perhaps rather less closely) to Trogossitidae by way of Egoliinae. It is possible, however, that the larva of *Acanthocnemus*, when discovered, may reveal a more or less direct link between the Peltidae and Melyridae. If, as seems possible, the Peltidae include the most primitive of the Cleroidea, we might look in this family for significant resemblances to other, related superfamilies. The most obvious comparison is with the Cucujoid Clavicornia, in one or other family of which almost all the features, adult and larval, of Peltidae may be duplicated; if the remaining Cleroidea did not exist, probably very few coleopterists would ever question the inclusion of Peltidae in Cucujoidea.

### *Key to Subfamilies of Adult Peltidae*

1 Molar part of mandibles closely tuberculate (fig. 21). Lacinia without an apical hook but with a spine on its inner edge (fig. 20). Tarsal claws often split or toothed. Tentorium (fig. 19) characteristic. Habits more or less floricolous . . . . . . . . . . . . . . . DECAMERINAE

– Molar part of mandibles never tuberculate. Lacinia (fig. 11) with a large curved apical hook. Tentorium (*cf.* fig. 13) usually not as in Decamerinae. Habits not floricolous . . . . . . . . . . . 2

2 Middle coxal cavities not nearly closed outwardly by the sterna. Antennae 11-segmented with more or less symmetrical club. General form broad, ovate or rectangular, never cylindrical. Habits fungivorous PELTINAE

– Middle coxal cavities quite or almost closed outwardly by the sterna. Antennae with not more than 10 segments, club somewhat asymmetrical. General form relatively elongate, more or less cylindrical. Habits probably at least partially carnivorous . . . . . EGOLIINAE

The Peltinae seem to be mainly Holarctic; one or two African species have been attributed to *Calitys* Thoms., but the essential characters of the mouth-parts of the group have still to be verified in these. The only definitely Peltine and non-Holarctic form studied by me is a new genus from New Zealand, described below. Most of the tropical forms hitherto placed in Ostominae appear to belong in Trogossitidae-Lophocaterinae. The degree of habitus similarity that may exist between certain Peltinae and Lophocaterinae is exemplified in Broun's New Zealand genus *Grynoma*, which is typically Lophocaterine as far as most of its species are concerned, but also included two species of *Protopeltis* (gen. nov.) that are unquestionably Peltinae. The species of the group seem to be almost entirely fungivorous; gut-contents were visible in preparations of adults and larvae of a number of species studied by me, but in none of them were any fragments of insects visible.

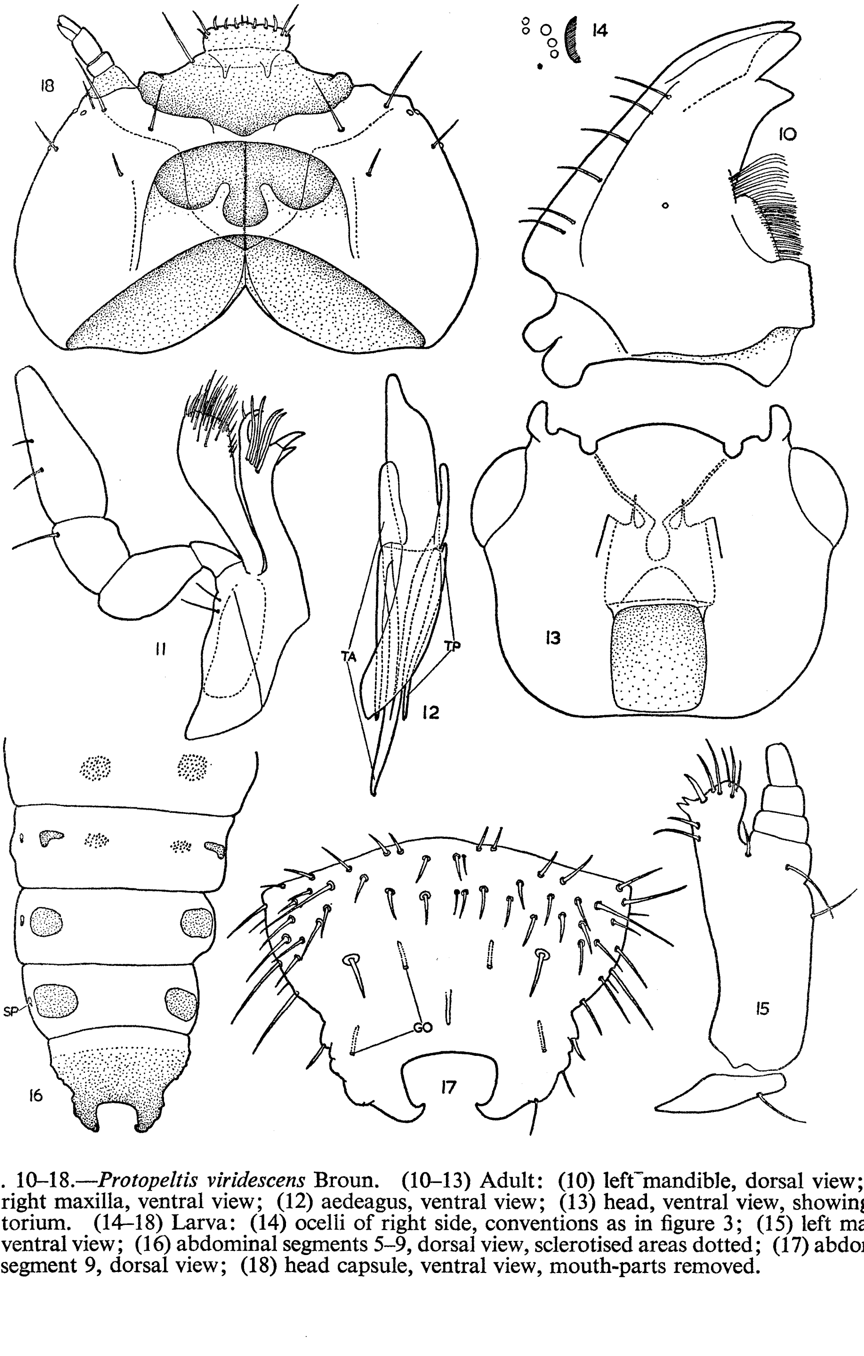
## ***Protopeltis*** gen. n.

*Adult*

*General form.*—Short rectangular-ovate, dorsal surface moderately convex; somewhat resembling *Phloiophilus* but relatively broader and more markedly explanate at the sides.

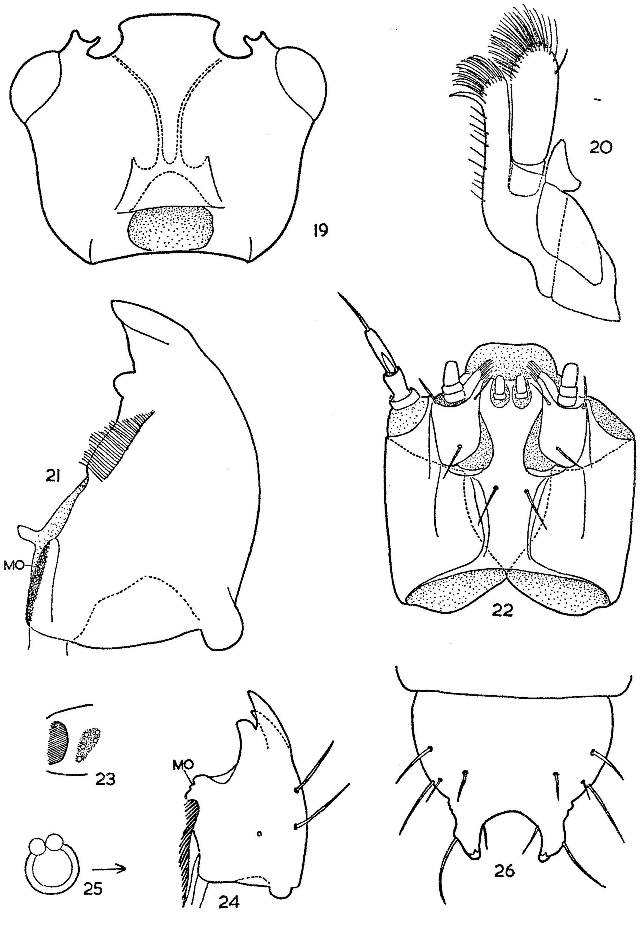
*Head.*—Much narrower than the prothorax with entire, moderately convex eyes, separated dorsally by at least 3 times their longitudinal diameter. Frontoclypeal groove not distinct. Labrum about twice as wide as its median length, front margin evenly rounded. Gular sutures widely separated, tentorium as figured (fig. 13). Antennae 11-segmented, with a broad almost symmetrical 3-segmented club, segments 9 and 10 strongly transverse, 11 slightly so, segment 8 similar in shape to 9 but less than half its width, preceding segments progressively longer and narrower until the third, which is at least twice as long as wide, segments 2 and 1 about as long as 3 but progressively wider than it. Mandibles (fig. 10) characteristic, Cucujoid-like. Maxillae (fig. 11) with elongate galea and lacinia, latter bearing 2 strong hooked processes at apex; palpi with apical segment elongate and more or less conically pointed, the preceding one about as wide as base of apical one and about as long as wide, antepenultimate segment somewhat elongate and strongly curved, preceded by a small palpiger-like segment. Mentum with broad posteriorly concave base and sides strongly converging in front, prementum bearing a moderately broad entire setose ligula, bases of palpi close together; apical segment of palpi broadly ovate, pre-apical one similar to antepenultimate segment of maxillary palpi, preceded by a small palpiger-like sclerite.

*Thorax.*—Prothorax strongly transverse, its sides rounded and strongly narrowed in front, widely explanate with crenulate edges. Front coxal cavities rather widely open behind, prosternal process between them narrow and acuminate, prosternum in front of coxae about as wide as coxae. Mesosternum quite flat, with no trace of impressions for front coxae, intercoxal process narrow like that of prosternum; middle coxae with trochantins partially exposed. Metasternum trapezoidal, base about twice as wide as median length, hind coxae closely approximate in the middle and extending laterally to meet elytral epipleura; met-episternum narrowed almost to a point posteriorly; met-endosternite similar to that of *Phloiophilus* (Crowson, 1944). Elytra with no trace of striae or rows of punctures, bearing relatively large deep punctures and stiff projecting setae, outer edges somewhat explanate and finely crenulate, epipleura of moderate width, sharply bordered almost to extreme apex of elytron. Scutellum very transverse. Wings with distinct radial cell, vein *M* not or scarcely distinguishable on the basal side of the *r-m* cross-vein; apparently 4 anal veins but feebly pigmented and difficult to see, without a closed anal cell. Legs with femora rather thick, middle pair considerably inflated in middle; front and middle tibiae with sharp serrated outer edges and rows of very short spines along outer and inner edges, hind tibiae with outer edge not markedly keeled, bearing normal setae. Tarsi with 2 basal segments partially connate, and thus apparently 4-segmented, apical segment at least as long as preceding 4 together, bearing large simple claws and a bisetose empodium.



FIGS. 10–18.—*Protopeltis viridescens* Broun. (10–13) Adult: (10) left mandible, dorsal view; (11) right maxilla, ventral view; (12) aedeagus, ventral view; (13) head, ventral view, showing tentorium. (14–18) Larva: (14) ocelli of right side, conventions as in figure 3; (15) left maxilla, ventral view; (16) abdominal segments 5–9, dorsal view, sclerotised areas dotted; (17) abdominal segment 9, dorsal view; (18) head capsule, ventral view, mouth-parts removed.

*Abdomen.*—With 5 visible sternites of approximately equal length, each of them with a raised basal ridge, which bends round at the sides to continue along the side margin. Aedeagus (fig. 12) with tegmen in 2 main parts, (morphologically) dorsal part lying below median lobe and entirely membranous.



Figs. 19–26.—Peltidae-Decamerinae. (19) *Decamerus haemorrhoidalis* Sol., adult: ventral view of head, mouth-parts removed, showing tentorium. (20) *D. haemorrhoidalis*, adult: right maxilla, cardo removed, dorsal view. (21) *Antixoon cribripenne* Gorh., adult: left mandible, dorsal view. (22–26) Decamerine larva: (22) ventral view of head, mandibles removed; (23) ocelli of left side, antennal socket shaded; (24) left mandible, ventral view; (25) abdominal spiracle of right side, lateral view; (26) abdominal segment 9, dorsal view.

Type species *Grynoma viridescens* Broun.

The genus includes two described species, both from New Zealand, which are evidently very nearly allied and perhaps of doubtfully specific rank; the specimens I have seen may be distinguished as follows:

Size larger, antennal club broader and entirely dark . . . **pulchella** (Broun)
Size smaller; antennal club less transverse, basal segment more or less pale **viridescens** (Broun)

### *Description of the larva of* Protopeltis viridescens (Broun)

With the general characters of Polyphaga-Cleroidea and of the family Peltidae.

*Head.*—With frontal sutures markedly sinuate (fig. 18) and slightly suggestive of the Cucujoid shape seen in *Phloiophilus*; endocarina long and strong; hypostomal rods not very strong, somewhat diverging posteriorly; 5 well marked lateral ocelli with the usual Cleroid arrangement (fig. 14), plus a weak pigment spot situated more ventrally; front margin of labrum slightly trilobed. Antennae with segment 1 short, about twice as wide as long, 2 slightly narrower than 1 and at least as long as wide, segment 3 not quite as long as 2, about 3 times as long as wide, inserted on dorsal part of apex of 2, sensory appendage of segment 2 rounded-conical, not quite as long as segment 3 and ventral to it. Mandibles with 2 apical teeth, and a third slightly pre-apical tooth on dorsal side, with a tridentate retinaculum-like structure near base of cutting edge, much as in *Phloiophilus*. Maxillae (fig. 15) with cardo very transverse, stipes (excluding mala) at least twice as long as wide, apex of mala rounded and bearing 5–6 stout nearly straight spines, its inner edge with a bidentate projection behind which are 2 or 3 stout spines; palpi with 3 distinct segments, born on a short palpiger, segment 1 about two and a half times as wide as long, 2 about as long as 1, not quite twice as wide as long, segment 3 distinctly longer than 1 and 2, at least one and a half times as long as wide, cylindrical. Labium with prementum wider than long, somewhat angularly produced between bases of palpi; palpi 2-segmented, segment 2 slightly longer than 1, cylindrical and distinctly elongate, 1 slightly transverse.

*Thorax.*—Prothorax with extensive well marked tergal sclerotisation, divided by a pale median line, prosternum with a rather ill-defined somewhat elongate sclerotisation. Meso- and metathorax: terga with a small lateral sclerotisation on each side; meso- and metasterna each with a median pair of setae but no marked sclerotisations.

*Abdomen.*—Terga of segments 1–6 each with a pair of paramedian finely spinulose areas; fifth tergum with a pair of small sclerotisations at its lateral edges, similar but progressively larger sclerotisations at sides of terga 6–8 (fig. 16). Entire dorsal part of tergite 9 strongly sclerotised and pigmented, basal part (fig. 17) coarsely rugose and bearing strong setae, which are short on discal part but become longer at the sides, lateral discal area bearing a pair of specialised seta-like structures; 2 pairs of slender sclerotised ducts opening on tergum, 1 pair discal and the other on bases of urogomphi; urogomphi very stout, apices acute, upturned and somewhat incurved, their outer basal parts bearing stout setae. Legs of moderate length, tarsungulus bearing a single ventral spine, tibiae with a pair of setae on ventral side beyond middle, femora with several scattered slender setae, anterior face of coxae with 3–4 rather short spines. Spiracles bicameral, their lateral air-tubes directed posteriorly on abdominal segments, nearly dorsally on front spiracle, openings of lateral air-tubes complex, almost cribriform. All spiracles similar in size, thoracic pair situated near anterior margin of mesothorax.

*Size.*—Length up to about 5 mm., maximum width of head capsule about 0·7 mm.

An adult and several larvae of this species were collected by me at "The Devil's Punchbowl", Arthur's Pass, Canterbury, New Zealand, on 9th January, 1957, the habitat being recorded in my notebook as "fungusy bark of dead *Nothofagus*". The adult proved to have abundant fungal material in its gut contents, with hyphae showing clamp-connections and abundant large dark-coloured spines, identified by the mycologist, Dr. A. S. Hutchinson, as "probably *Hymenochaete* sp."

The mandibles of the adult *Protopeltis* (fig. 10), with their strongly protuberant molar part and well-developed prostheca, are the most Cucujoid-like that I have seen in Cleroidea. This may well be a primitive feature, and indeed it is difficult to indicate any feature of *Protopeltis*, adult or larval, that is clearly derivative in relation to the conditions in other Cleroidea. The spinose tibiae of the adults might be derivative in relation to the simple ones of *Phloiophilus*, but as it would appear that the non-spinose tibiae of Cleridae may be derived from spinose ones in *Chaetosoma*-like ancestors, there is no evident reason why a similar explanation should not apply to *Phloiophilus*. At least in Cleroidea, spinose tibiae appear as a regular correlative of a "Clavicorn" habitus—if the ancestral Cleroid had the spines, presumably it had the habitus of the Clavicorn adult as well. The theory that the ancestral Cleroids were more or less similar in characters (and presumably in habits) to *Protopeltis* meets with difficulties, however, as we shall see when we come to consider Melyridae.

Of the forms studied by me, the Decamerinae include four genera, all American—*Ostomodes* Reitt. (=*Eronyxa* Reitt.) with one or two species from California and adjacent areas, *Antixoon* Gorh. with a single Central American species, *Decamerus* Solier (=*Peltostoma* Reitt.) with one Chilean species, and *Diontolobus* Solier (=*Diodontolobus* Lac., *Micropeltis* Reitt.) with several species from Chile. These genera may be distinguished as follows:

1 Tarsal claws simple. Head with well-marked grooves in front of eyes, in which basal segments of retracted antennae are received. Antennae 11-segmented with symmetrical 3-segmented club. Length more than 3·5 mm. Front coxal cavities open behind . . . ***Ostomodes*** Reitter

– Tarsal claws toothed or split. Head without distinct preocular grooves. Antennal club more or less asymmetrical. Length rarely more than 3·5 mm. . . . . . . . . . . . . . . . . . 2

2 Front coxal cavities usually not fully closed behind. Tarsal claws with a tooth near middle. *Chile* . . . . . . . . . . . . . . 3

– Front coxal cavities completely closed behind. Tarsal claws split, the inner tooth practically as long as the outer one. *Central America* ***Antixoon*** Gorham

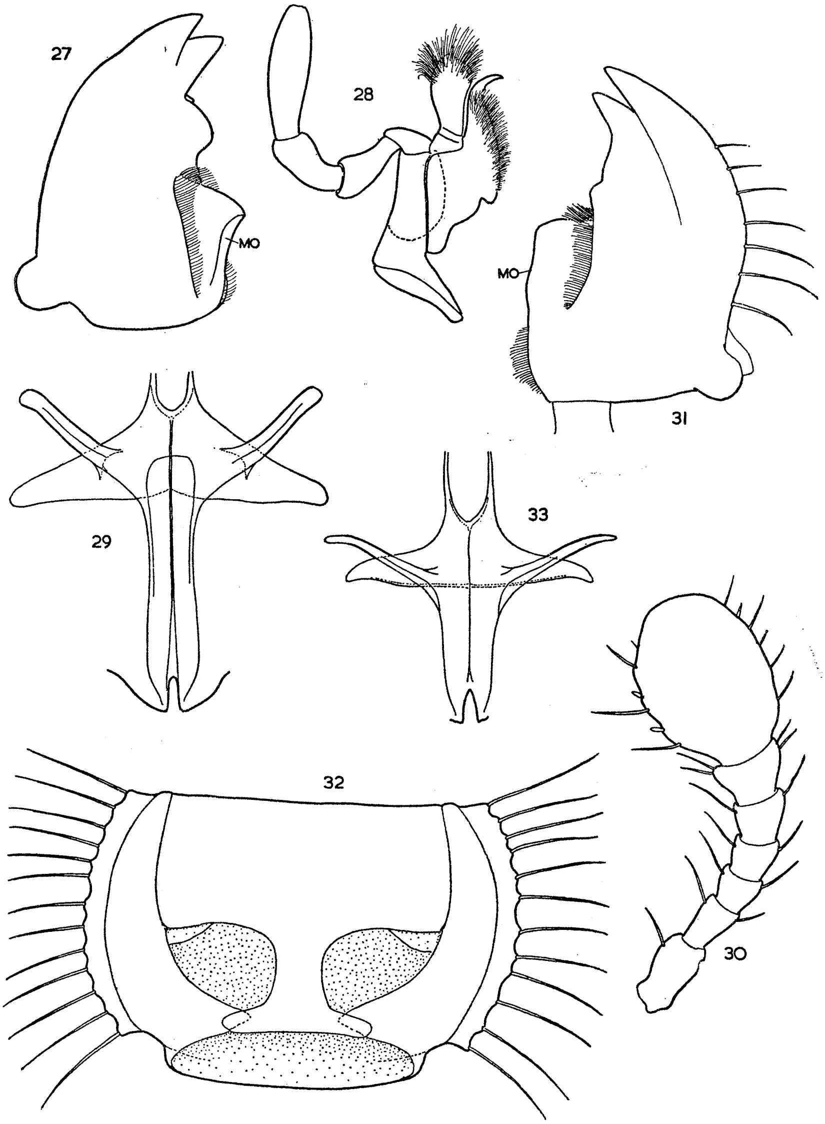
3 Antennae 11-segmented. Side margins of prothorax very broadly explanate . . . . . . . . . . . . . . . . ***Diontolobus*** Solier

– Antennae 10-segmented. Side margins of prothorax only very narrowly explanate . . . . . . . . . . . . . . ***Decamerus*** Solier

A single larva, extracted from a soil sample from La Parva, Chile, on 26th October, 1962, by Dr. F. di Castri, who kindly made it available for me to study, is very probably assignable to Decamerinae. It is a very small form, barely 3 mm. long when fully extended, relatively slender compared with other Peltid larvae and somewhat resembling larvae of Anthicidae or Melyridae-Malachiinae in appearance. In general form of the head capsule and mouth-parts, it seems to be more similar to *Calitys* than to other described Peltid larvae, though the form of the ninth abdominal segment is more suggestive of *Protopeltis*. In the form of the mandibles (fig. 24) and apex of the maxillary mala (fig. 22) it is, however, very distinct. The spiracles (fig. 25) are unusual in having the paired lateral air-tubes directed nearly dorsally. Five ocelli, arranged as usual, are represented by pigment spots without very evident lenses (fig. 23), but I could see no sign of an additional, ventral pigment spot such as occurs in many Peltid larvae. There were no evident tergal sclerites on any of the thoracic segments. The tarsunguli are unisetose. This combination of characters is clearly Cleroid rather than Cucujoid; the bicameral spiracles, endocarina and lack of a median epicranial suture, and also the somewhat Cucujoid form of the frontal sutures, rule out any close connection with Melyridae, the only possible affinity seeming to be to Peltidae. The only known Chilean Peltidae are the Decamerinae, to which group the small size of this larva is appropriate. Numerous adult Decamerinae, collected at the same time and place as this larva, and submitted for determination by Dr. di Castri, proved to be of species of *Diontolobus*, to which genus the larva is therefore provisionally ascribed.

The mandibles and maxillae of this *Diontolobus* larva are unique among the known types of Cleroidea—the mala bears neither the teeth of the fungivorous type nor the pedunculate seta of the carnivores—and suggest a type of food and feeding very unusual in Cleroidea. The closest analogies to the mouth-parts of the *Diontolobus* larva that I have seen are perhaps in the Cucujoid Anthicidae, whose larvae are likewise usually ground-living—probably feeding on miscellaneous detrital materials. Dr. di Castri informs me that many of the accompanying adult *Diontolobus* were found on or about lichens, growing abundantly on the ground among the bushes of the "highland steppe" vegetation of the La Parva area; lichens, indeed are a possible food for the larva.

The adults of Decamerinae are also very unlike other Peltidae in their habits. I am informed by Hugh B. Leech (*in litt.*) that *Ostomodes* adults in California frequent the flowers of *Ceanothus* bushes; he also reports having reared an adult of this genus from a dead *Ceanothus* stem. According to G. Kuschel (*in litt.*), adults of *Diontolobus* and *Decamerus* are common in spring on flowers of various bushes, in more or less open country; the gut-contents of a specimen of *Diontolobus punctipennis* Solier studied by me included numerous pollen grains. The original series of *Antixoon cribripenne* Gorh. were likewise recorded as having been collected in the flowers of bushes in more or less open country, a circumstance which probably influenced Gorham's placing of the genus in Melyridae (though he also suggested a



Figs. 27–33.—Peltidae-Egoliinae, adults. (27–29) *Acalanthis* 4-*signatus* Er.: (27) right mandible, ventral view; (28) right maxilla, ventral view; (29) met-endosternite, dorsal view. (30–33) *Necrobiopsis tasmanicus* Crows.: (30) antenna; (31) left mandible, ventral view; (32) prothorax, ventral view, legs removed; (33) met-endosternite, dorsal view.

resemblance to *Phloiophilus*). It is, on the available evidence, a tenable theory that the Decamerinae represent a specialised (and relatively recent, as suggested by their geographical distribution) offshoot from some small primitive Peltine ancestor (perhaps something like *Protopeltis*), their peculiarities, adult and larval, being in the main caenogenetic. On the other hand, it is also conceivable that they are a relict group and among the most primitive of Recent Cleroidea.

The Egoliinae can be assigned with far more confidence to the relict category. Erichson originally based the group on two genera described by himself, *Egolia* with a single Tasmanian species and *Acalanthis* with two or three species from Chile; Reitter and Leveillé wrongly associated these with *Nemosoma* and its allies to form their subfamily Nemosomatinae—an error caused by inadequate attention to the structure of the mouth-parts. I am now able to add a third genus of Egoliinae, based on an apparently undescribed species from Tasmania:

### *Necrobiopsis* gen. n.

With the general features of Polyphaga-Cleroidea.

*General form* rather less elongate and less cylindrical than in *Egolia* or *Acalanthis*, resembling certain Cleridae-Corynetinae (e.g. *Necrobia* spp.).

*Head.*—Eyes entire, pubescent, moderate-sized, protuberant, their ommatidia of normal size. Antennae with a large scape, followed by 6 moniliform segments, which become progressively shorter and broader (fig. 30), ending in a compact terminal club in which 3 or 4 segments are suggested by surface grooves only. Mandibles with a distinct non-asperate molar part (fig. 31), along the anterior and dorsal edges of which are bands of setae, apex of cutting edge 2-toothed. Maxillae rather similar to those of *Acalanthis* (*cf.* fig. 28), lacinia with a large curved apical hook; palpi with segment 1 very small, segment 4 largest and distinctly tapered to its apex. Labium with small coriaceous slightly bilobed ligula, mentum about twice as wide as long, its front margin emarginate; palpi with last segment largest and tapered to the apex. Head capsule with sides straight and distinctly convergent behind eyes; gular sutures strongly convergent in front, tentorium rather similar to that of *Decamerus* (*cf.* fig. 19); frontoclypeal suture not distinct; labium somewhat transverse, front margin very slightly emarginate.

*Thorax.*—Prothorax with well-marked sharp denticulate side edges (fig. 32), broadest in front of middle and strongly contracted to a basal collar, which is much narrower than elytra at shoulders. Prosternal process relatively broad between the front coxae, its apex strongly produced on each side to meet propleural process and thus close coxal cavities behind; prosternum in front of coxae as wide as width of coxae. Mesothorax with relatively broad and flat sternum, coxal cavities narrowly separated in middle and almost completely closed outwardly by meso- and metasterna. Elytra with 10 regular rows of deep large punctures separated by interstices, the alternate ones of which are raised, no scutellary striole, outer edge only narrowly explanate, basal margin bordered. Scutellum moderate sized, nearly semicircular in outline. Metathorax with sternum markedly narrowed in front, longitudinal suture extending about one-third length of sternum. Hind coxae narrowly separated in middle, extending laterally almost to meet epipleura. Wings with 4 anal veins in main group, no closed anal cell. Met-endosternite as figured (fig. 33). Legs of moderate length. Femora rather thick, those of middle and hind legs scarcely extending beyond outer edges of elytra. All tibiae simple and more or less cylindrical, outer edge not evidently keeled or denticulate; 2 normal tibial spurs. Tarsi with segment 1 very small, difficult to see on front leg, 5 as long as preceding 4 together; with large simple claws and a bisetose empodium; no trace of ventral lobes on any tarsal segments.

*Abdomen.*—With 5 free ventral segments, with a very slight progressive decrease in length posteriorly, the first with an acute intercoxal process, sternites distinctly bordered at sides. Aedeagus not observed. Ovipositor of normal Cleroid type, with moderately long baculi and cylindrical styli about 3 times as long as their apical width, each with a long apical seta.

Type species *Necrobiopsis tasmanicus.*

### *Necrobiopsis tasmanicus* sp. n.

General colour of derm shining dark piceous.

Vertex of head very densely and somewhat rugosely punctured, with large often irregularly-shaped punctures. Pronotum sculptured similarly to upper surface of head, with indistinct impressions of which a median one just before the middle is the most evident; side margins with about 13 setiferous teeth. Elytra with rather irregular depressions, including 3 or 4 along the course of striae 1–2 and 2 or 3 along striae 3–4; reflexed margins continued to apical angles, striae distinct almost to apex, each with about 32 punctures.

Length about 3·5 mm., maximum width of pronotum about 1 mm., length of elytron along suture 2·3 mm.

Holotype ♂ and 2 ♀ paratypes, TASMANIA: Hobart (*G. C. Champion*); in British Museum collections.

The generic name was suggested by the general appearance of the insects, which were found among undetermined Corynetinae in the British Museum collection. A microscopic preparation was made of one of the paratypes, a female, but unfortunately it showed no gut-contents; the mouth-parts do not differ notably from those of *Acalanthis.*

The geographical distribution of Egoliinae is sufficient by itself to establish them as an old, relict group; it would not surprise me if representatives were eventually discovered in other isolated parts of the world (*e.g.* Madagascar) and in the fauna of the Cretaceous or early Tertiary fossil resins of the northern hemisphere. In general facies, adult Egoliinae have more in common with Trogossitidae-Trogossitinae or even with certain Cleridae than they have with other Peltidae—an effect which is accentuated by the Clerid-like elytral patterns of *Acalanthis* and *Egolia.* The development of a Clerid-like facies is probably associated with carnivorous habits, as in *Laricobius* among Derondontidae (to which group Peltidae present certain analogies); it is noteworthy that the gut-contents of a specimen of *Acalanthis quadrisignatus* Er. studied by me included evident fragments of insect cuticle. The absence, presumably through loss, of the tibial spines in adult *Egolia* and *Necrobiopsis* is hardly matched in other Peltidae or Trogossitidae and offers a further parallel to Cleridae. The closure of the middle coxal cavities by the sterna appears to be peculiar to the Egoliinae among Cleroidea, though it is the rule in Curculionoidea and occurs in many Cucujoidea as well as in certain Chrysomeloidea. This is presumably a derivative feature, which may make for a stronger articulation of the middle coxae but can hardly be directly related to carnivorous habits.

### *Key to Larvae of Peltidae*

1 Sides of head, behind antennae, distinctly contracted to base, head (including labrum) at least as long as its maximum width; frontal sutures of markedly Cucujoid shape (fig. 22); mandibles with a mola-like process near base of cutting edge (fig. 24); spiracles with lateral air-tubes directed dorsally. (*Diontolobus* larva, *Chile*) . . . DECAMERINAE

– Sides of head, behind antennae, distinctly widened to base (fig. 13), head not nearly as long as its maximum width; frontal sutures of less markedly Cucujoid form; mandibles often with a group of 3 curved teeth near base of cutting edge but without a mola-like process; spiracles with lateral air-tubes directed more or less posterodorsally . . . PELTINAE

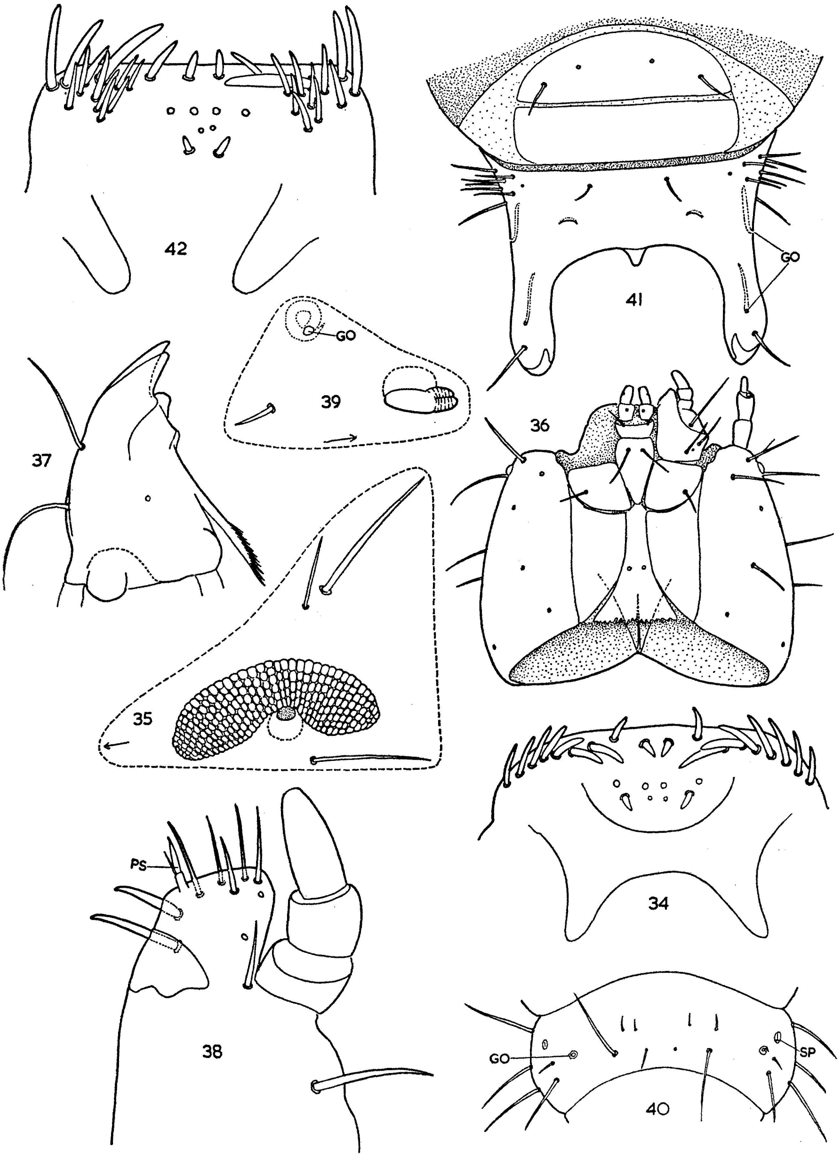
2 Tergal sclerotisations of prothorax and abdominal segment 9 very weak, hardly perceptible; ocelli not distinct; frontal sutures nearly straight and diverging at an acute angle; dorsal ambulatory ampullae present on abdominal segments; mandibles apparently without teeth in basal part of cutting edge (Peltini) . . . . . . . . . . . . 3

– Tergal sclerotisations of prothorax and abdominal segment 9 well marked and pigmented; ocelli well developed; frontal sutures more or less strongly sinuate or angled; abdominal segments without ambulatory ampullae; mandibles normally with a group of 3 curved teeth near base of cutting edge . . . . . . . . . . . . . . . 4

3 Mentum transverse; bearing about 15 short setae; general form shorter and broader, about 4·5–5 times as long as wide . . . . ***Peltis*** Kugel.

– Mentum more or less elongate, bearing 4 long setae; general form more elongate, about 6 times as long as wide . . . . . . . ***Ostoma*** Laich.

4 Abdominal segments 6–8 (fig. 16) with distinct sclerotisations at the lateral ends of the tergites; ninth abdominal tergite with 2 pairs of long tubular glands opening on it (fig. 17); *New Zealand* ***Protopeltis*** Crows.



FIGS. 34–42.—Trogossitidae, larvae. (34, 35) *Grynoma varians* Broun: (34) epipharynx; (35) abdominal spiracle of left side, lateral view. (36–41) *Promanus depressus* Sharp: (36) ventral view of head, mandibles and part of right maxilla removed; (37) right mandible, ventral view; (38) apex of right maxilla, ventral view; (39) abdominal spiracle of right side, lateral view; (40) abdominal segment 8, dorsal view; (41) abdominal segment 9, dorsal view. (42) *Tenebroides mauretanicus* L., epipharynx.

– Abdominal segments 6–8 without distinct tergal sclerotisations; abdominal tergite 9 not bearing openings of long tubular ducts . . . . . . 5

5 Head with sides very strongly diverging behind antennae (as in fig. 13); ventral mouth-parts strongly retracted, hypostomal rods very short behind cardines, no very evident exposed gular region; antennal segment 2 transverse; dorsal sclerite of abdominal segment 9 not ovate and not bordered . . . . . . . . . . . . . . ***Thymalus*** Latr.

– Head with sides much less strongly diverging posteriorly; ventral mouth-parts somewhat protracted, hypostomal rods relatively long behind them and with an evident exposed gular region; abdominal segment 9 with its dorsal sclerite ovate and strongly bordered . . . . ***Calitys*** Thoms.

### *A Note on Fossil Peltidae*

Both Tertiary and Mesozoic fossils have been attributed by various authors to this group, but comparatively few of them seem to show features that are at all convincingly diagnostic of the family, or even of Cleroidea. Klebs (1910) listed four specimens among his collection of Baltic Amber Coleoptera that had been determined by Reitter as belonging to the modern genera *Calitys*, *Grynocharis*, *Lophocateres* and *Ostoma*. As Reitter had published special works on the classification of Trogositidae, there might be reason to expect his determinations in this family to be more reliable than those in Melyridae and Cleridae (*q.v.*). It is very odd, and in conflict with our other knowledge of the early Tertiary faunas and floras of Europe, that three out of four of Klebs' specimens were attributed to genera whose modern species are not only European, but northern rather than southern European at that—though Reitter had indeed referred two African species to *Calitys*.

## VIII. Family 3. TROGOSSITIDAE (Trogositidae, Temnochilidae, Ostomidae, Ostomatidae, auctt. partim)

After the separation of the forms here included in Peltidae, the residue of Trogositidae will comprise only the Trogositinae (including *Nemosoma*) and the forms allied to *Lophocateres*. The determination of the correct appelation of this family according to the latest International Rules of Zoological Nomenclature is not altogether easy. The oldest supra-generic name available here seems to be Trogossitites of Castelnau (1840) rather than Trogositinae of Erichson (1844); according to our current rules the valid name of the family should thus be Trogossitidae, based on the "nominal type genus" *Trogossita*, rather than Trogositidae based on *Trogosita*. The name *Trogossita* is due to Olivier, who included two species under it, *coerulea* L. and *mauritanica* L. (Olivier, 1790); *Trogosita* was first published by Fabricius (1792), presumably as a deliberate emendation of *Trogossita*. Such emendations, based mainly on linguistic considerations, were frequently made before 1850, and most of them, like this of Fabricius, immediately won general acceptance; our latest rules make nearly all of them invalid and thus involve the resurrection of a large number of long forgotten misprints and misspellings. The phrase "nominal type genus" means in effect, whatever actual genus is found to be the legal bearer of the name, which in turn has to be decided by the "principle of typification". We shall need to establish, as has apparently not been done hitherto, a species as type of *Trogossita*. The choice lies between the two species originally included by Olivier, both of which have already been established as types of other generic names; under present rules, a species which is the type of one generic name is not thereby precluded from being made the type of another. As the single originally included species, *mauritanica* is the type "by monotypy" of *Tenebroides* Pill. et Mitt. (1783), and *coerulea* is for the same reason the type of *Temnochila* Erichs. (1844). The last mentioned name itself appeared as a linguistic, hence presumably invalid, emendation of *Temnoscheila*

Westwood (1835). According to Lacordaire (1854), Olivier based the characterisation of his genus mainly on *coerulea* L., though the formation of its name makes evident reference to the grain-damaging propensities of *mauritanica*; *coerulea* was also the first species listed by Fabricius under *Trogosita*. With *mauritanica* as type, *Trogossita* would be a junior "objective" synonym of *Tenebroides*; according to current rules this would not preclude us from basing the family name on *Trogossita*. The ruling that the name of a family-group taxon need not be changed if its "nominal type genus" is found to be a junior synonym is, however, a reversal of the decision of a previous generation of the International Commission, and we can hardly feel confident that it will not itself be reversed by a future one. In order to avoid the consequent danger of having to call the family Tenebroididae, I hereby cite *coerulea* L. as the type of *Trogossita* Oliv. (and of *Trogosita* F.). *Trogossita* will thence, as senior objective synonym, replace *Temnochila* Erichs. (and *Temnoscheila* Westw.) as the name for the genus that will become the type of the family.

The basic features of Trogossitidae that distinguish them from Peltidae particularly concern the mouth-parts—adult mandibles without a definite molar part and lacinia without an apical hook, larval mandibles with a different "lacinia mandibulae" and maxillary mala with a pedunculate seta. These features are common to all Cleroidea, except Phloiophilidae and Peltidae, and would seem to be strongly correlated with carnivorous habits. If the ancestral Cleroids had habits, and mouth-parts, similar to those of Peltidae, then presumably the carnivorous habits and corresponding adaptations of the mouth-parts are derivative in this superfamily. It will follow in turn either that the Melyridae are more closely related to Trogossitidae than are the Peltidae, or that the carnivorous adaptations developed on at least two independent lines, the Trogossitid-Chaetosomatid-Clerid and the Phycosecid-Melyrid. The contrary hypothesis, that carnivorous habits, and mouth-parts resembling those of Melyridae, are primitive, seems almost equally plausible; there may be a case for a third, that the Decamerine larva represents the most primitive among known types in the superfamily—this hypothesis will be considered further when we deal with Melyridae.

In both larval and adult stages, the Trogossitidae studied by me fall into two clear-cut groups, between which I know of no transitional forms; they may be distinguished as follows:

ADULT: front coxal cavities open behind; lacinia well developed, extending at least to middle of galea. LARVA: head with paragular sclerites not bounded by membranous sutures (fig. 36), cardo almost as large as stipes; normally two ocelli on each side; ninth abdominal tergite (fig. 41) divided into two by a transverse suture, with a small median denticle between the urogomphi . . . . . . . . LOPHOCATERINAE

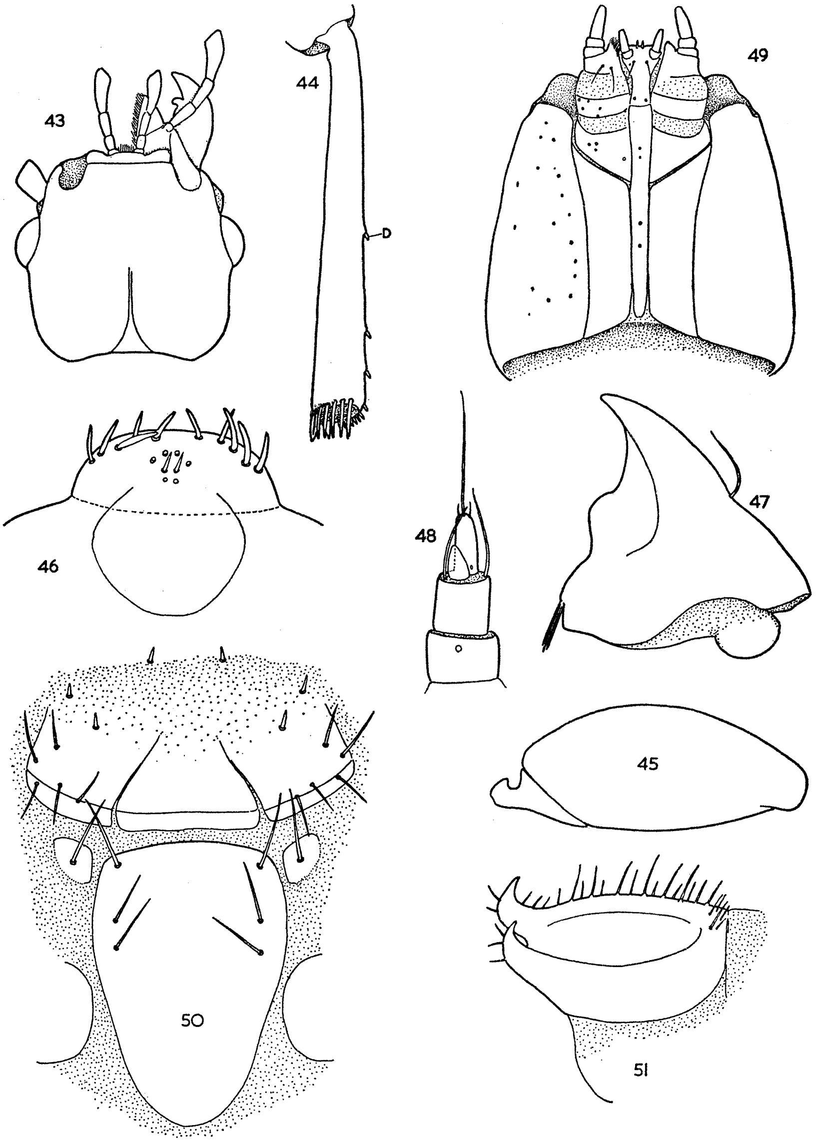
ADULT: front coxal cavities closed behind; lacinia small or vestigial, not reaching middle of galea. LARVA: paragular sclerites bounded by membranous sutures; head with 5 ocelli on each side; ninth abdominal tergite never divided transversely . . . . . TROGOSSITINAE

As far as I am aware, all known Lophocaterinae have in the adult a form more or less broad and like that of Peltinae. The feeding habits in the group are probably somewhat mixed; *Lophocateres pusillus* Klug. is well known to occur in various types of stored cereal products, *etc.*, and is supposed to be at least partially herbivorous in both larval and adult stages. The gut-contents of an adult and a larva of the New Zealand *Promanus depressus* Sharp examined by me were composed largely of insect fragments; in the gut of a male of *Grynoma varians* Broun, I found only detrital material and vegetable fibres, but the fore gut of a larva of the same species contained recognisable insect fragments as well as detrital material.

Adults and larvae of the three Lophocaterine genera that occur, or are likely to be introduced, in New Zealand may be distinguished as follows:

1 ADULT: antennae 11-segmented; elytra without erect setae, usually almost glabrous. LARVA: spiracles with lateral air-tubes directed anteriorly . . . . . . . . . . . . . . . ***Promanus*** Sharp

– ADULT: antennae 10-segmented; elytra with erect setae. LARVA: spiracles with lateral air tubes directed dorsally, or with large, complex and cribriform plate replacing them . . . . . . . . . . . . . 2



FIGS. 43–51.—Chaetosomatidae. (43) *Chaetosoma scaritides* Westw., adult: ventral view of head, mandible and maxilla removed on right side. (44–45) *C. scaritides*, adult: (44) middle tibia; (45) hind trochanter and femur. (46–51) *C. scaritides*, larva: (46) epipharynx; (47) right mandible, dorsal view; (48) antenna; (49) ventral view of head, mandibles removed (sockets of setae shown on right side only); (50) setae and sclerites in prosternal area; (51) abdominal segment 9, dorsolateral view.

2 ADULT: prothorax broadest in front of base; maxillary palpi with apical segment somewhat securiform; elytra not ribbed; margins of front not raised. LARVA: spiracles with a large and complex cribriform plate (fig. 35) replacing the lateral air tubes . . . . ***Grynoma*** Broun

– ADULT: prothorax broadest at base; apical segment of maxillary palpi not at all securiform; elytra with interstices markedly ribbed; margins of front strongly raised between antennae and eyes. LARVA: spiracles with normal bicameral lateral air tubes . . . . ***Lophocateres*** Olliff

The Trogossitinae, represented in New Zealand only by *Leperina* spp. and the introduced *Tenebroides*, show considerable diversity in adult form, from forms such as *Acrops*, like the Peltinae, at one end to the elongate cylindrical *Nemosoma* at the other extreme. Most species of the group are no doubt mainly carnivorous, both as adults and in the larval stage, but the ability of *Tenebroides mauritanicus* L. to live largely on vegetable foods is probably not unique in the subfamily. The larvae of a considerable number of species in this subfamily have been described; those I have studied may be distinguished as follows:

1 Urogomphi, in dorsal view, widely separated, the space between them nearly or quite twice their apparent length. Sclerotised part of ninth abdominal tergite with no distinct raised anterior marginal line. Prosternal sclerite very elongate, at least 3 times as long as its maximum width. Epicranial halves, behind the junction of the frontal sutures, parallel and almost meeting along a line as long as antennal segment 2 2

– Urogomphi, in dorsal view, separated by little more than their apparent length. Sclerotised part of ninth abdominal tergite with a raised anterior marginal line. Prosternal sclerite less than 3 times as long as its maximum width. Inner margins of epicranial halves, behind junction of the frontal sutures, immediately divergent . . . . . . . 3

2 Antennal segment 2 not more than one and a half times as long as wide; larvae small, very elongate, each of the two halves of the pronotal sclerite longer than maximum width . . . . . . . . . . ***Nemosoma*** Latr.

– Antennal segment 2 more than twice as long as wide; larvae larger, less elongate, each of the pronotal halves as wide as long ***Trogossita*** Oliv. (*Temnochila* Er. *et al.*)

3 Disc of ninth abdominal tergite depressed, with a distinct raised margin at sides as well as basally; mesonotal sclerites separated by a distance equal to their width; antennal segment 2 less than twice as long as wide; stipes hardly more than twice as long as wide . . . . ***Phanodesta*** Reitt.

– Disc of abdominal tergite 9 without raised side margins; mesonotal sclerites separated by less than their own width; antennal segment 2 more than twice as long as wide, stipes about 3 times as long as wide 4

4 Urogomphi, in dorsal view, appearing nearly parallel-sided for most of their length, the space between them more or less rectangular ***Tenebroides*** Pill. et Mitt.

– Urogomphi, in dorsal view, more markedly contracted from the base, the space between them appearing more or less semicircular. . ***Leperina*** Er.

To judge from the figures of Böving & Craighead (1931), larvae of *Corticotomus* and *Airora* would probably trace to couplet 2 in the above key, and from the description and figure of Gardner (1931), *Melambia* would probably be traced to couplet 4. It is fairly evident that the apparent relationships of the larvae do not coincide with the previously accepted classifications of the adults, in which *Nemosoma* has usually been isolated in a group apart from the rest, *Trogossita* placed near *Tene-*

*broides*, and *Phanodesta* associated with *Leperina* in a third group. It would, however, be possible, by using characters other than those previously stressed, to classify the adults in a way more consonant with the larval characters—for example the median clypeal groove associates *Nemosoma* with *Trogossita*, and the relatively broad epipleura link *Tenebroides* with *Leperina*.

Observations on the gut-contents of Trogossitinae studied by me are these:

*Acrops dohrni* Reitt.: male, Malaya—dense material including insect fragments but apparently at least partially fungal.

*Phanodesta* sp.: larva, Chile, under bark of dead *Araucaria*—numerous insect fragments in gut.

*Leperina* sp.: male, Whangarei, New Zealand—fore and hind gut with numerous insect fragments, apparently of a larva of *Trogoderma* sp.

*Leperina* sp.: 2 females, Whangarei, New Zealand—hind gut of both with masses of detrital and fungal material.

*Tenebroides mauritanicus* L.[1]: male, France (wild caught)—numerous insect fragments; larva, France (wild caught)—insect fragments and detrital material in fore gut.

*T. mauritanicus* L.: larva, Glasgow (from warehouse)—fine granular matter (?flour).

*Trogossita* (=*Temnochila*) *planicollis* Lev.: female, Mexico—numerous insect fragments.

## IX. Family 4. CHAETOSOMATIDAE

According to the characters given in the key above (p. 282), only the genera *Chaetosoma* Westw. and *Chaetosomodes* Broun belong in this group. In a previous work (Crowson, 1955) I had tentatively included also *Metaxina* Broun, but further study of the characters of the adult and of its supposed larva have led me to consider this genus as more closely allied to Thaneroclerinae; in the present work it is considered under Cleridae. The adult *Chaetosoma* might be considered as an aberrant Trogositid, but with the inclusion of this genus in Trogossitidae the larval separation between that family and Cleridae would become very difficult; conversely the *Chaetosoma* larva could well be treated as a primitive type of Cleridae, but the inclusion of the genus in Cleridae would make the characterisation of that family on adult characters very difficult. It appears that an independent family Chaetosomatidae is justifiable both phylogenetically and practically.

As one of the taxonomically highest-ranking endemic groups among New Zealand Coleoptera, Chaetosomatidae could claim a certain distinction—they are moderate-sized and relatively conspicuous insects, discovered comparatively early in New Zealand and, if they occurred in other parts of the world, would be unlikely to have remained undiscovered until now. Presumably they are to be regarded as relict survivors of an old, probably Mesozoic, group and almost comparable with the celebrated reptile *Sphenodon*; so far, nothing like them has been recorded from the extensive beetle fauna of the early Tertiary ambers of the northern hemisphere. Chaetosomatids doubtless preserve many of the features of a group ancestral to Cleridae, and themselves presumably come from some Trogossitid-like stock.

*Chaetosoma* Westw. (1851) has unquestioned priority over *Chaetosoma* Claparède (1863), a genus of Nematoda; Claparède's name will have to be replaced, presumably by *Tristichochaeta* Panceri. The name Chaetosomatidae, introduced by Steiner in 1916 for a family of Nematoda, long before I employed it in Coleoptera, will likewise have to be replaced in nematology.

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[1] Probably equivalent to *T. fusca* Goeze.

The two genera of Chaetosomatidae are undoubtedly very closely allied, and have presumably diverged since New Zealand became isolated; they may be distinguished as follows:

Antennae distinctly thickened towards the apex, segment 10 transverse; elytra without a tooth at the humeral angle, with no trace of a basal margin; spines on front and middle tibiae few and inconspicuous **Chaetosomodes** Broun

Antennae not thickened apically, segment 10 elongate; elytra with a blunt tooth at the humeral angle, marking the end of a partial basal border; spines of front and middle tibiae more numerous and conspicuous (fig. 44) . . . . . . . . . . . . **Chaetosoma** Westw.

### *Description of the Mature Larva of* Chaetosoma scaritides *Westw.*

With the general features of Coleoptera-Polyphaga and of Cleroidea.

*General form.*—Clerid-like, elongate and slender and only slightly depressed; soft parts of body varying from cream to a deep pink in colour, presumably at different stages within an instar, ninth abdominal tergite and pronotal sclerite more or less dark brown, meso- and metanotal sclerites paler brown.

*Head.*—Head capsule (fig. 49) distinctly longer than its maximum width, broadest near the base, sides slightly rounded and distinctly contracted in front; median epicranial suture short but distinct, frontal sutures somewhat curved, convex inwardly, endocarina well marked in basal half of frons; hypostomal rods complete, extending from outer posterior angles of cardines to occipital foramen, the slightly curved but nearly parallel ventral edges of head capsule separated by a long narrow median sclerite as in Cleridae; labium small, very transverse, front margin convex; epipharyngeal rods fused into a transversely-cordate sclerite (fig. 46). Antennae (fig. 48) 3-segmented, segment 1 very transverse, 2 approximately quadrate, 3 much narrower than 2, and about twice as long as wide, with a long stout apical seta, apex of segment 2 bearing 2 strong setae and a conical sensory appendage ventrally to segment 3. Mandibles (fig. 47) stout, triangular, apices unidentate, a blunt projection in the middle of the cutting edge, lacinia mandibulae composed of a pair of long articulated spines; outer face with a single long seta. Maxillae as in normal Cleridae, with large transverse cardo bearing a large seta near its inner border and 2–3 smaller ones on its disc, sclerotised part of stipes shorter and more transverse than the cardo, bearing a large discal and a lateral seta, the 3-segmented palpi born on a distinct palpiger with a strong seta at its inner basal ventral angle; palpal segments successively narrower, 1 very transverse, 2 less so, 3 about twice as long as wide and tapered towards apex; mala with moderately dense vestiture of stout curved setae, the pedunculate seta situated near inner margin of dorsal face, not far from its apex. Labium without palpigers, prementum transverse trapezoidal, considerably narrowed to its base and partly divided by a pale median line, bearing a pair of long setae ventrally, apex without a definite ligula but bearing a para-median pair of setae; mentum rectangular, transverse, bearing a pair of strong setae, preceded by a long narrow sclerite extending to the occipital foramen.

*Thorax.*—Prothorax with notal sclerotisation well marked, dark brown and nearly semicircular with a fine pale median line, bearing a few relatively long fine setae; prosternum with a large longitudinal-oval pale brown median sclerotisation with a pair of setae close to its front margin and a pair near middle of each side edge; a very transverse ovate sclerotisation lying in front of this is divided into 3 by 2 paramedian longitudinal pale bands and is darker and more strongly sclerotised along posterior margin (fig. 50). Meso- and metathorax with paired notal sclerotisations, separated by a little less than their width in the mesothorax, a little more than their width in the metathorax; median sternal sclerotisation elongate and narrow in mesothorax, very narrow in metathorax. Legs well sclerotised and pigmented; tibiae with 2 strong setae on anterior face, 2 on posterior face, 2 on outer edge, and 2 strong dorsal apical spines.

*Abdomen.*—Segments 1–8 without distinct dorsal or ventral ampullae, without tergal sclerites, setal vestiture rather sparse and of moderate length. Segment 9 (fig. 51) with a dark strongly sclerotised notum, which is rather deeply hollowed on its disc and produced into a pair of parallel upturned urogomphi posteriorly, excavate part practically glabrous, its raised margins and outer face, also bases of urogomphi, bearing rather long setae arising from distinct tubercles. Spiracles of abdomen situated along a mid-lateral line, distinctly before middle of their respective segments, annuliform, thoracic spiracles situated rather more ventrally, in front part of the mesothorax, with distinct small posterodorsal bicameral air tubes.

Larvae were found, together with pupae and cast larval skins, in burrows probably of the Cossonine *Xenocnema spinipes*, in a dead standing Kauri trunk (*Agathis* *australis*) in Waipoua Kauri Forest, Northland New Zealand on 8th October, 1956; adults of *Chaetosoma scaritides* were subsequently obtained from the pupae. Similar larvae were later collected at various localities in New Zealand, mainly in wood of dead Podocarpaceae, but on at least one occasion in a dead *Nothofagus* trunk.

To the characterisation of Chaetosomatidae in the key, the following imaginal characters may be added:

Aedeagus (*see* Sharp & Muir, 1912) of normal inverted Cleroid type, tegmen in one piece; wings with anal region reduced, with only 3 evident veins and no anal cell; front coxal cavities fairly widely open behind; eyes relatively small, entire; head capsule nearly quadrate and parallel-sided, gular sutures confluent and extending to about middle of ventral side of head capsule, mentum very transverse and born on a very broad peduncle (fig. 43), antennal insertions lateral, directly in front of eyes; dorsal surface with vestiture of long erect setae.

I have not seen recognisable gut contents in the adult or larval *Chaetosoma* studied by me, but the mouth-parts and mode of occurrence strongly indicate predaceous habits similar to those of typical Cleridae.

## X. Family 5. CLERIDAE

Of the many problems presented by New Zealand's endemic Cleroidea, that of the relationships of the genus *Metaxina* Broun is certainly among the most interesting. First described as a Clerid, the genus was retained in that family in Corporaal's revised catalogue (1950)—unfortunately Corporaal himself seems never to have studied the genus, or at least never to have published any observations on its characters and relationships. Wolcott (1944), in his generic review of the subfamily Phyllobaeninae, included and redefined the genus *Metaxina*, with the remark "This is truly an anomalous genus, but this being an insular insect, and obviously a highly adaptive form, the singularity of its aspect need cause no great doubt as to the propriety of including this genus in the present subfamily". In a previous work (Crowson, 1955) I transferred the genus, somewhat tentatively, to the new family Chaetosomatidae. The resemblances in adult structure between *Metaxina* and *Chaetosoma* are in fact considerable, but there are also differences between the two genera which may be of more significance than I had formerly supposed. Firstly, the front coxae are more definitely projecting, in the Clerid fashion, in *Metaxina*. Secondly, while the gular sutures of *Chaetosoma* (and *Chaetosomodes*) are practically confluent for most of their length (*cf.* fig. 43), those of *Metaxina* (similarly to *Zenodosus*, fig. 56), though strongly convergent, could hardly be called confluent. Thirdly, the labium in *Metaxina*, as in normal Cleridae, has a much narrower base than in *Chaetosoma*. Fourthly, the tibiae in *Metaxina* have no trace of denticles along their outer edges (*cf.* fig. 44). In all these respects *Metaxina* resembles various Cleridae more than it does *Chaetosoma*. Of the established groups of Cleridae, it is Thaneroclerinae rather than Phyllobaeninae which most resemble *Metaxina*. Only in Thaneroclerinae do we find the gular sutures (fig. 56), middle and hind tarsi, and trochanters, formed essentially as in *Metaxina*—and it may be noted that the pronotal puncturation in this genus approaches the distinctive Thaneroclerine type too.

Though I failed to find adult *Metaxina* during my New Zealand collecting, one larva collected in the Lewis Pass of the South Island, at an altitude of nearly 3000 feet, might well be of this genus. This larva was found by scraping moss, lichens and loose bark of living *Nothofagus* trunks—a mode of collecting that sometimes yields Melyrid larvae but never those of normal Cleridae or Chaetosomatidae. It may be noted that the adult *Metaxina* shows considerable resemblance in its habitus to various Melyridae, and especially to the Mascarene species of *Pelecophora*. Although possessing the fundamental characters of Thaneroclerinae, the larva from the Lewis Pass resembles those of Haplocneminae in general form and vestiture and in the structure of the ninth abdominal segment. The characters of this larva are sufficiently interesting, and the likelihood of its being a larva of *Metaxina* is sufficiently great, to justify publication of a detailed account of it. If it is not the larva of *Metaxina*, it must presumably represent some hitherto undescribed endemic Thaneroclerine type; the beetle fauna of the area in which it was collected is unfortunately not so well known that this possibility can be discounted.

The close affinity of Cleridae to Chaetosomatidae, and their connection through that group to the Peltid-Trogositid stock, can hardly be doubted; in spite of the traditional association of Cleridae with Melyridae, a direct link between these families seems very improbable—for all their common "Malacoderm" features, they can only be connected through the "Clavicorn" Peltidae-Trogositidae.

The Cleridae are a moderately large family, with some diversity of habits and a great range of body form; some of the genera show aberrant features, making difficulties at times in their recognition as Cleridae by formal keys and definitions. In several groups, the lobing of the tarsal segments becomes very weak or even practically absent, as in *Dieropsis* Gahan (which is remarkable also for the dipteron-like partition of its eyes), *Odontophlogistus* Elston (with elongated mouth-parts), and a few others.

The predominant habitat of Clerid larvae is dead wood, and the predominant food consists of the larvae of other lignicolous Coleoptera, Scolytidae, Bostrychidae, Anobiidae, Buprestidae and Cerambycidae being the families mainly attacked. Among the Thaneroclerinae, as among the Phyllobaeninae, there is a tendency towards more free-living larval habits, as in many Melyridae. In *Orthopleura* Spin. and some allied genera, the characters of the larvae (and such scanty information as is available on their habits) suggest a trend to something like ecto-parasitism on larger wood-boring larvae, *e.g.* Buprestidae and Cerambycidae; Böving & Champlain (1920) quote an observation of an *Orthopleura* larva, newly hatched, attached to a larva of the large Buprestid *Chrysobothris*. *Orthopleura* larvae are eyeless, with the head and ninth abdominal tergite much less sclerotised than in normal Cleridae, and the head capsule appreciably deflexed instead of strongly prognathous as is normal in this family. Among Corynetinae, species of *Necrobia* and probably of some allied genera (e.g. *Necrobinus* and *Opetiopalpus*) are liable to develop on dead fatty animal matter (or even sometimes on oily plant substances) as well as, or instead of, on larvae of other insects.

Despite their "Malacoderm" facies and frequently bright colours, adult Cleridae are by no means always floricolous, but some of them do show modifications of the mouth-parts that are probably adaptive to feeding in flowers, for example the Australian forms allied to *Eleale* Newm. and the Chilean *Calendyma* Lac. In many species, *e.g.* the European *Thanasimus* spp., the adults are active predators, often attacking the adults of the species on whose larvae they preyed in their own larval stage.

The Cleridae are a cosmopolitan group, but are more numerous in warmer climates and very poorly represented on oceanic or isolated islands; thus the Seychelles and Canary groups of islands have each only a single recorded endemic Clerid species, while Hawaii and Juan Fernandez have none at all; only four of the eight subfamilies are represented in the endemic fauna of New Zealand. The fossil record of the group is not as yet very informative. The Baltic Amber fauna, of early Oligocene (or possibly late Eocene) age, provides the most valuable evidence so far available concerning the Cleridae (and many other groups) of the geological past. Edmund Reitter saw and "named" a considerable number of Cleridae in the amber collections of Klebs and other German collections. An indication of the standard of Reitter's treatment of this material is furnished by his determination of a specimen in the Klebs collection as "bei *Tillus* und *Trichodes*"—which is rather comparable to describing a fossil of Carnivora as "near *Canis* and *Felis*". The type of *Prospinoza baltica*, described below, was from the Klebs collection and was presumably seen by Reitter, but it is difficult to tell which of the Reitter determinations listed by Klebs (1910) might have corresponded to this specimen. It is indeed astonishing that in a country that had made such great contributions to modern evolutionary zoology, and in which systematic entomology had been carried to such high levels, uniquely valuable evidence concerning early Tertiary Coleoptera could have been treated so superficially and casually. Not a single proper description or figure of a Baltic Amber Clerid seems to have been published before the present work.

Fossils attributable with reasonable probability to Cleridae have been described from several Tertiary horizons, *e.g.* the Lower Oligocene *Thanasimus ostenderus* Theob. from Kleinkembs (though this might just possibly be akin to Egoliinae rather than *Thanasimus*) and species of *Enoclerus* (Wickham, 1914) from the Florissant Lake beds (now generally regarded as Oligocene rather than Miocene). I have not seen figures, descriptions or specimens of Mesozoic fossils that could be assigned with any conviction to Cleridae, though the family is likely to go back at least to the Cretaceous era.

Information about the internal anatomy of Cleridae is somewhat scanty. Stammer (1934) reported that the apices of the Malpighian tubules of a species of *Clerus* examined by him were joined together in two groups of three, one on each side, before becoming attached to the hind gut; in *Tenebroides*, as in *Dasytes* and *Haplocnemus*, he described the apices of the tubules as remaining separate right up to their insertion on the rectum. Further investigation of this character may establish whether it is one by which the family Cleridae may be distinguished from other Cleroidea.

We have a fairly generally accepted classification of adult Cleridae; this can be expressed in the form of an analytical key, by means of which the large majority of species of the family can be attributed without much difficulty to one or other of a series of subfamilies. Unfortunately, it is not yet evident that the same system can readily be applied to Clerid larvae; the number of Clerid larvae so far described is not large enough to provide a satisfactory basis for a classification of the larvae of the group, but it is sufficient to cast doubts on the naturalness of the established system of the adults. Many more larvae will need to be studied before this question can be settled. Fortunately, it is not as a rule very difficult to associate Clerid larvae with the corresponding adults; pupation normally occurs in or close to the larval habitat, and if a pupa is found there will be a cast larval skin in its immediate vicinity. The larval skin can be softened and extended, and will serve as a basis for recognition of other field-collected larvae, while the adult can be reared from the pupa.

In the present work I shall not attempt to construct a key to subfamilies of Clerid larvae, but will give a key for the discrimination of the main larval types collected by me in New Zealand, and reference to the characters of the known larvae will be made in discussing particular subfamilies.

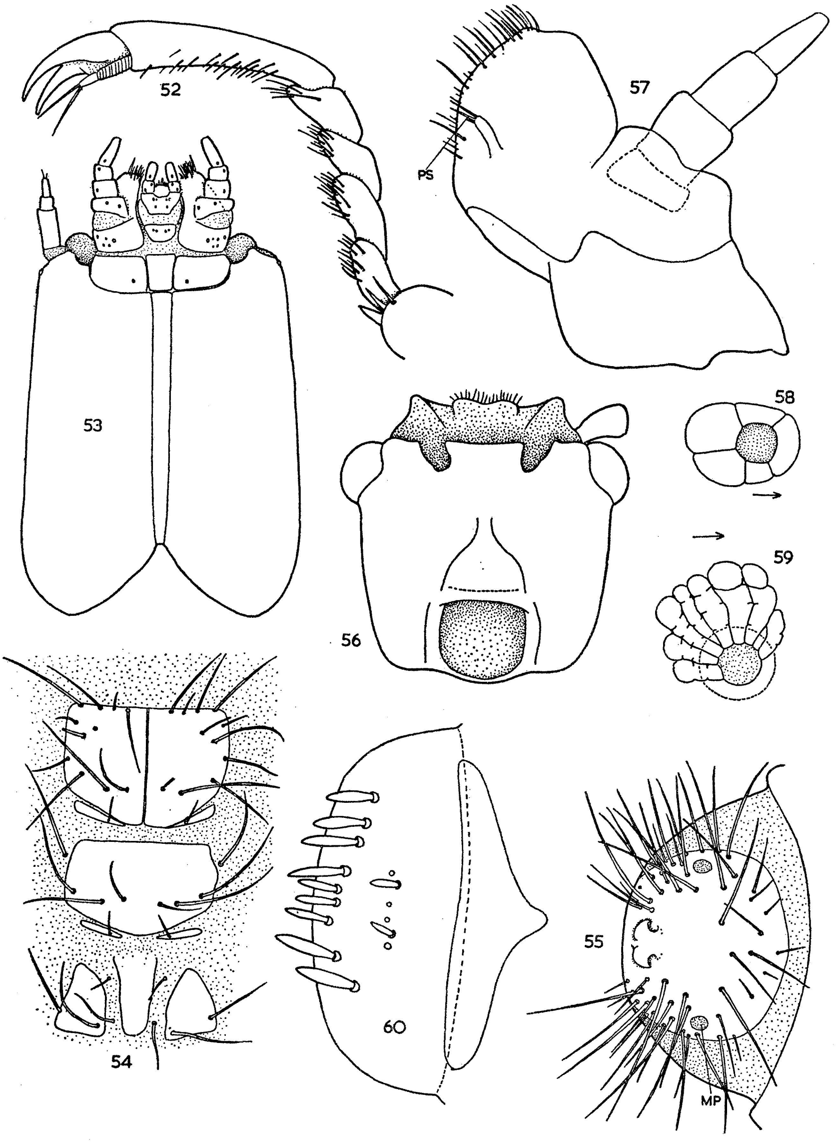
I have very recently been able to examine several specimens of Cleridae from the Scheele collection of Amber inclusions, by the courtesy of Dr. E. Voigt of the Geologisches Staatsinstitut, Hamburg. From a preliminary study, there would appear to be three species represented, all of Clerinae; none of them are at all similar to modern European or North American forms, but there are similarities among them to certain Australian genera. I hope to be able to describe these species in a future publication.

### *Key to Subfamilies of Adult Cleridae*

1 Tarsi, at least in middle and hind legs, with segments only very slightly lobed below, segment 1 smallest, 4 similar in size and shape to 3, a well-marked bisetose empodium between the simple claws. Gular sutures (fig. 56) short, convergent and approximated anteriorly. Pronotum with characteristic large, somewhat elongate punctures. Hind tro-

chanters scarcely protuberant, their lower edges nearly continuing line of lower edge of femur (as in fig. 45) . . . . . (1) THANEROCLERINAE

– Tarsi nearly always with at least segment 3 markedly lobed below, never with a prominent bisetose empodium. If gular sutures short, convergent and strongly approximated in front, tarsal segment 4 much smaller than 3. Pronotum without elongate punctures. Hind trochanters usually with their lower edges protuberant and not nearly continuing line of lower edge of femur (fig. 62) . . . . . . . . 2



FIGS. 52–60.—Cleridae. (52) *Metaxina ornata* Broun, adult: middle tarsus, posteroventral view. (53–55) *M. ornata* larva: (53) head, ventral view, mandibles removed (setal sockets indicated on mouth-parts only); (54) dorsal sclerites and setae of thorax; (55) abdominal segment 9, dorsal view. (56) *Zenodosus sanguineus* Say, adult: head, ventral view, mouth-parts removed. (57) *Tillus elongatus* L., larva: right maxilla, dorsal view of apex. (58) *Paupris aptera* Sharp, larva: third abdominal spiracle of right side. (59) *Balcus* sp. (?) larva: second abdominal spiracle of right side. (60) *Opilo mollis* L., larva: epipharynx.

2 Front coxal cavities more or less broadly closed behind. Antennae rarely with a distinct club. Claws usually with a blunt basal tooth and a sharp one between it and the apex. Tarsomere 4 not or scarcely smaller than 3, 1 usually nearly as long as 2. Tibiae never with ridges along anterior or posterior faces . . . . . . . . . . . (2) TILLINAE

– Front coxal cavities open, or narrowly closed, behind. Antennae usually with a more or less distinct club. Claws not so constructed. Usually either tarsomere 4 much smaller than 3 or 1 much smaller than 2 . . 3

3 Tarsomere 4 approximately similar in size and shape to 3. Prothorax rarely with distinct side edges. Front coxal cavities nearly always open behind . . . . . . . . . . . . . . . . . . . . . . 4

– Tarsomere 4 much smaller than 3 not (or weakly) lobed below . . . 5

4 Eyes not or very weakly emarginate. Antennae very short, clubbed. Tarsomere 1 usually at least half as long as 2, distinctly visible from above. Tibiae never ridged . . . . . . . . (3) PHYLLOBAENINAE

– Eyes usually strongly emarginate. Antennae usually much longer than width of head. Tarsomere 1 usually less than half as long as 2, often scarcely visible from above. Tibiae usually with ridges along anterior and posterior faces . . . . . . . . . . . . (4) CLERINAE

5 Eyes emarginate on their inner edges. Front tibiae spinulose along distal part of outer edge. Pronotum with a discal and a lateral pair of long sensory setae, with more or less distinct side edges. *New World* (5) EPIPHLOEINAE

– Eyes with emargination, if present, anterior. Front tibiae not spinulose. Pronotum without such specialised sensory setae . . . . . . 6

6 Antennae usually serrate or with terminal segments very elongate and forming a loose club. Tarsal claws often toothed at base. Prothorax with well marked side edges. Gular sutures strongly convergent. Aedeagus of normal inverted Clerid type . . . . . (6) ENOPLIINAE

– Antennae with a normal short club, or filiform. If tarsal claws toothed at base, gular sutures not or scarcely convergent . . . . . . . 7

7 Prothorax with side edges absent or incomplete. Eyes deeply emarginate. Tarsal claws not toothed at base. Gular sutures strongly convergent. Aedeagus inverted. General form elongate . . . (7) TARSOSTENINAE

– Prothorax with complete side edges. Eye emargination never very sharp or deep. Tarsal claws often toothed at base. Gular sutures not strongly convergent. Aedeagus not inverted. General form usually relatively broad . . . . . . . . . . . . (8) CORYNETINAE

## *Key to Genera of Adult New Zealand Cleridae*

1 Tarsi with no segments markedly lobed below, segment 1 smallest (fig. 52); prothorax with distinct side edges; antennae filiform with 3 apical segments slightly enlarged . . . . . . . . . ***Metaxina*** Broun

– Tarsi with at least segment 3 strongly lobed below, 4 smallest, or antennae clubbed; prothorax usually without distinct side edges. . . . . 2

2 Tarsomere 4 lobed below and not or scarcely smaller than 3; prothorax with no trace of side edges . . . . . . . . . . . . . . . 3

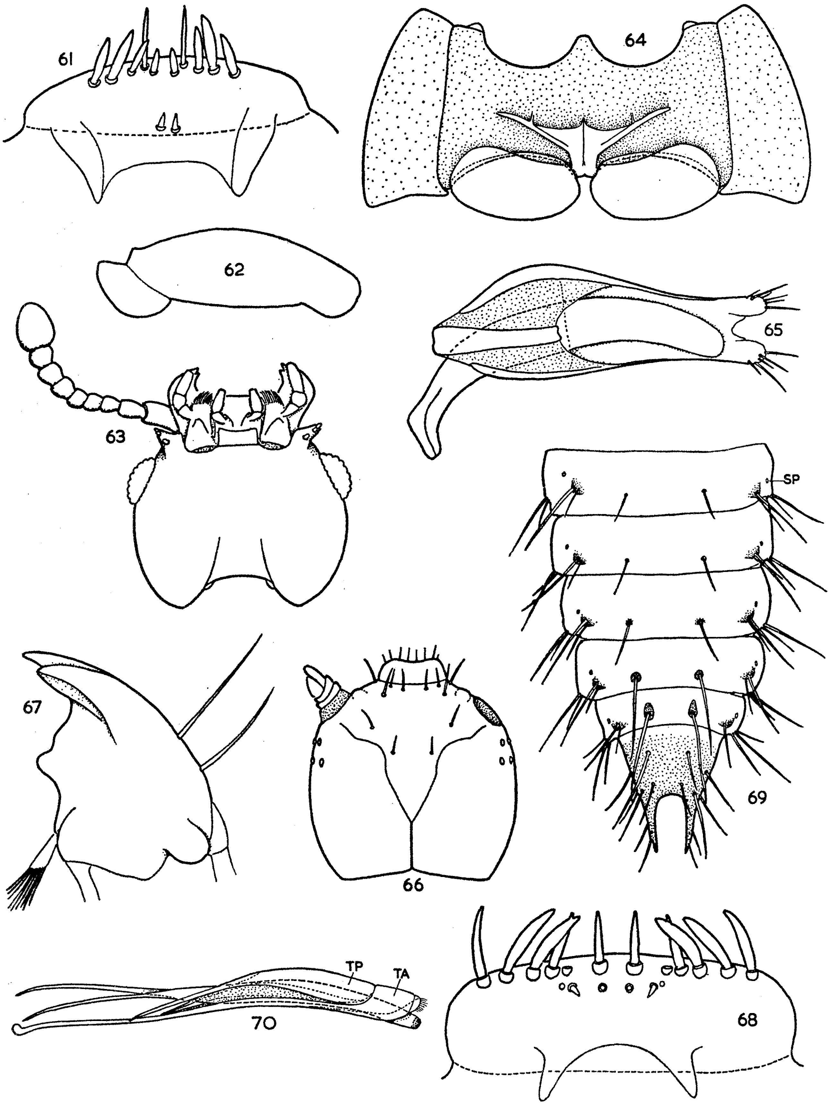
– Tarsomere 4 much smaller than 3, not or scarcely lobed below; prothorax with at least partial side edges . . . . . . . . . . . . . 5

3 Tarsomere 1 much smaller than 2, hardly visible from above; antennae much longer than width of head capsule; eyes strongly emarginate; last segment of maxillary palpi strongly securiform . . . ***Balcus*** Sharp

– Tarsomere 1 nearly as large as 2, easily visible from above; antennae not longer than width of head capsule; eyes scarcely emarginate; last segment of maxillary palpi not securiform (Phyllobaeninae) . . . . 4

4 Antennal club 2-segmented; head rather strongly constricted at base, eyes strongly protuberant; species winged . . . . . ***Parmius*** Sharp

– Antennal club 3-segmented; head less strongly constricted at base, eyes less protuberant; species wingless, ground-living . . ***Paupris*** Sharp



Figs. 61–70.—Cleridae, Phycosecidae, *Acanthocnemus*. (61) *Orthopleura* (or gen. aff.) sp., larva: epipharynx. (62) *Necrobinus defunctorum* Waltl, adult: hind trochanter and femur. (63) *Phycosecis limbata* F., adult: head, ventral view. (64–65) *P. limbata*, adult: (64) metasternum and endosternite, dorsal view; (65) aedeagus, dorsal view. (66–69) *P. limbata*, larva: (66) head capsule, dorsal view; (67) left mandible, ventral view; (68) epipharynx; (69) abdominal segments 4–9, dorsal view (sclerotised areas dotted). (70) *Acanthocnemus nigricans* Hope, adult: aedeagus, right side view.

5 Three apical antennal segments very large, together about as long as entire flagellum; prothorax much narrower than elytra, its sides angled near middle; last segment of maxillary palpi strongly securiform ***Phymatophoea*** Pascoe

– Three apical antennal segments forming a short broad club, much shorter than the flagellum; prothorax almost as broad as elytra, its side margins complete and not angled near middle; apical segments of palpi not securiform (introduced species, in carrion *etc.*) . . . . ***Necrobia*** Ol.

### *Key to Available Larvae of New Zealand Cleridae*

1 Head with a well developed median epicranial suture and no endocarina. Abdominal tergite 9 characteristic (fig. 55). Abdominal segments without ampullae, with vestiture of long projecting setae; thorax with characteristic notal sclerotisations (fig. 54) . . . . ?***Metaxina*** Broun

– Head never with distinct median epicranial suture. Abdominal tergite 9 and thoracic tergites not so constructed . . . . . . . . . 2

2 Frontal sutures well separated at hind border of head, endocarina indistinct. Abdominal segments without distinct ampullae, with vestiture of long projecting bristly setae . . . . . . . . . . . . 3

– Frontal sutures meeting at or before hind margin of head capsule . . 4

3 Urogomphi moderately long, pointed at apex. Larvae not living in leaf-litter layer; spiracles simple . . . . . . . . . ***Parmius*** Sharp

– Urogomphi very short, blunt at apex. Larvae living in leaf-litter layer of forests; spiracles (fig. 58) characteristic . . . . . . ***Paupris*** Sharp

4 Head with only 2 ocelli on each side; larvae living in carrion, stored products etc. . . . . . . . . . . . . . . . . ***Necrobia*** Ol.

– Head with 4–5 ocelli on each side; larvae not living in carrion or stored products . . . . . . . . . . . . . . . . . . . . 5

5 Abdominal segments 2–7 with distinct paired dorsal ampullae; spiracles normal, with small paired lateral air-tubes; urogomphi parallel; setae of abdominal vestiture rather short and sparse . . . ***Phymatophoea*** Pascoe

– Abdominal segments without distinct ampullae; spiracles with complex multicameral lateral air-tubes (fig. 59); urogomphi diverging, resembling those of *Opilo mollis*; setal vestiture of abdomen relatively long and conspicuous (very small larva from leaf-litter, possibly first instar of *Balcus* sp.)

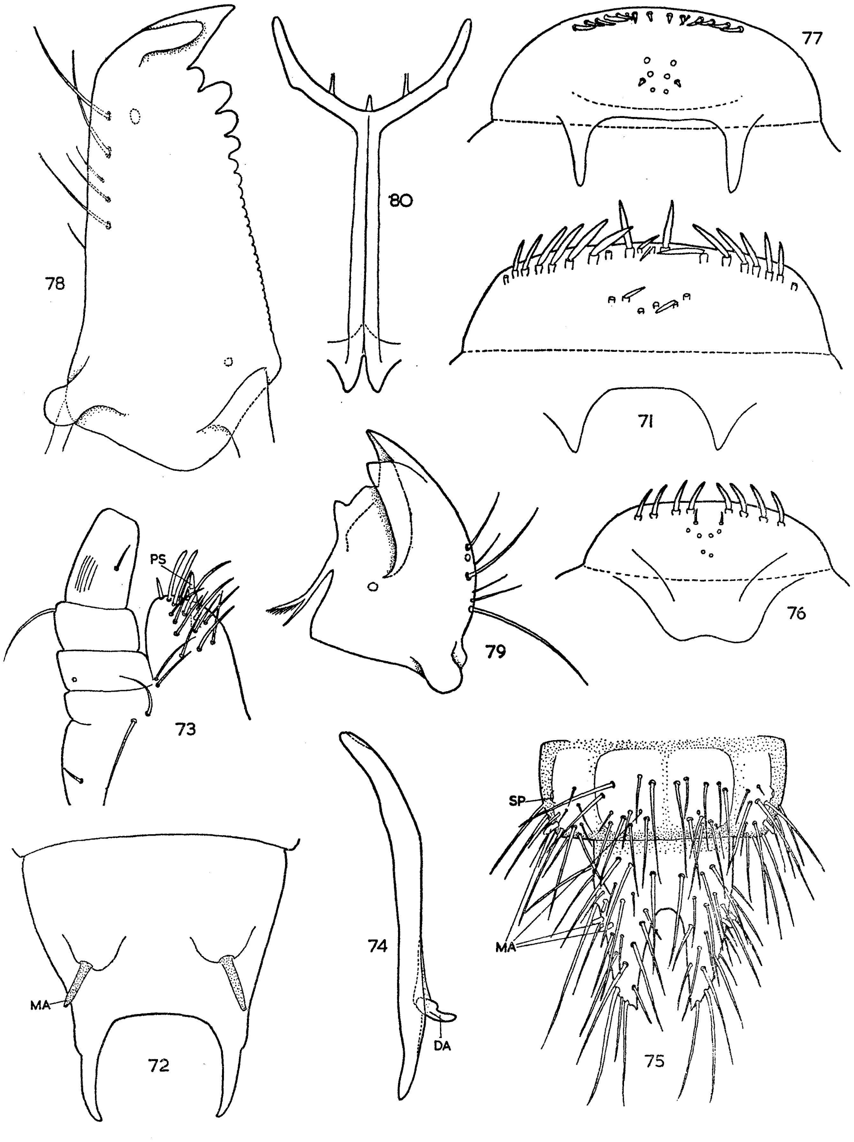
The inclusion of *Metaxina* in the Thaneroclerinae necessitates a revised definition of the group, as the New Zealand genus does not show the broad front tarsi and constricted base of the prothorax, which contribute so much to the characteristic facies of other Thaneroclerines. It is perhaps possible that these features have been secondarily lost in *Metaxina*, but it seems more probable that the genus is a primitive Thaneroclerine type, to be numbered among the notable relicts of the New Zealand fauna. The characters of the supposed *Metaxina* larva, described below, would accord with this hypothesis—the absence of a gular tubercle and the presence of well developed urogomphi are both likely to be primitive features.

### *Description of Supposed Larva of* Metaxina ornata *Broun*

With the general features of Cleridae and of the subfamily Thaneroclerinae, except that the gular tubercle, present in all other described Thaneroclerinae larvae (*Thaneroclerus*, *Zenodosus*, *Isoclerus*), is lacking and distinct urogomphi (absent in other known larvae of the group) are present. Notal sclerotisations of thorax (fig. 54) distinctive.

*General form.*—Relatively short and broad, resembling larvae of Melyridae-Haplocneminae, with relatively long and conspicuous vestiture of curved setae.

*Head.*—Head capsule (fig. 53) almost parallel-sided, about one and two-thirds as long as wide, median epicranial suture extending for more than a quarter of its length, endocarina not discernible; mandibles of typical Clerid form, apex single toothed, cutting edge with 2 backward projecting spines near base; maxillary mala with peduncle of pedunculate seta about as long as its large spine, about 7 other large spines on apex of mala; a conspicuous suture at base of labium, in line with hind margins of cardines; five ocelli on each side, arranged in usual Cleroid pattern; labrum dorsally with a pair of pedunculate spines similar to those of maxillary mala; epipharynx with a median group of 8 sensillae; antennae with segment 1 about twice as long as wide, about as long as 2 and 3 together, 2



Figs. 71–80.—Melyridae. (71–73) *Pelecophora* sp., larva: (71) epipharynx; (72) outline of abdominal segment 9, dorsal view; (73) apical part of right maxilla, ventral view. (74) *Haplocnemus impressus* Marsh., adult: median lobe of aedeagus, laterally. (75) *Lobonyx aeneus* F., larva: abdominal segments 8–9, dorsal view. (76) *Dasytes* (*Arthracanthus* Broun) sp., larva: epipharynx. (77) *Idgia* sp., larva: epipharynx. (78) *Danacaea nigritarsis* Kust., adult: right mandible, ventral view. (79) *Troglops capitatus* Er., larva: left mandible, ventral view. (80) *Ebaeus pedicularis* Schrk., adult: met-endosternite, dorsal view.

quadrate and very slightly narrower than 1, 3 about as long as 2 and half as wide as 1, sensory appendage of 2 ventral to and a little more than half as long as 3.

*Thorax.*—With a single large dorsal sclerotisation of pronotum and mesonotum, metanotum with 3 sclerotisations (fig. 54); legs strongly sclerotised and pigmented, of moderate length.

*Abdomen.*—Without distinct dorsal or ventral ampullae; tergum of segment 9 with a large dark nearly circular sclerotisation, which bears a pair of small upturned pointed urogomphi on a common base posteriorly and at its most lateral points a pair of pale membranous protuberances (? glands); spiracles moderately large, bicameral with lateral air-tubes relatively large and posteriorly directed.

A single specimen was collected by scraping moss, lichen and bark off trunks of living *Nothofagus* trees at about 2900 feet (900 m.) in the Lewis Pass of the South Island, New Zealand. The larva was about 6·5 mm. long when fully extended, with the head capsule about 0·55 mm. wide—the size would be appropriate to a nearly full grown larva of *Metaxina.* No recognisable gut-contents could be seen in this specimen. The hind gut of an adult male of *M. ornata* from the Broun collection contained fragments of insect cuticle as well as dark, presumably detrital, material.

The revision by Corporaal (1939) of Thaneroclerinae did not include the genus *Cleridopsis* Champion (1912), which certainly belongs in the group. The subfamily appears to be the most distinct and isolated among living Cleridae, and some of its features are probably primitive in the family. Information about the habits of larvae or adults is rather scanty; some species, particularly *Thaneroclerus buqueti* Lef., are able to develop in stored vegetable products *etc.*, preying on adult and larval Anobiidae, *Ababa tantilla* Lec. has been reared from a fungus (Knull, 1951), while *Zenodosus sanguineus* Say, according to Böving & Champlain (1920) frequents dead trees attacked by Scolytidae *etc.*, like more normal Cleridae; I have obtained larvae, apparently of this species, from old Polypore fungi from Massachusetts.

In the adult stage, Tillinae are not always easy to distinguish from Clerinae, whereas in the larval stage they are more likely to be confused with certain Enopliinae—in fact there does not seem to be any larval character known that provides a satisfactory separation between the latter subfamily and Tillinae. The most primitive modern Tillinae are probably those in which the tarsal claws have only a single tooth, the closure of the front coxal cavities is comparatively narrow, and the antennae tend to be more or less clubbed—as exemplified in genera like *Gastrocentrum* Gorh., *Spinoza* Lewis, the fossil *Prospinoza* (described below), and *Pallenis* Lap. It is these forms that provide the main difficulty in separating Tillinae from Clerinae. The genera of this section differ from other Tillinae, but resemble certain Clerinae, in having the inter-coxal process of the basal ventrite depressed along the middle and with raised margins.

### ***Prospinoza*** gen. n.

*General form.*—Rather similar to that in recent species of *Spinoza* Lewis but with prothorax more elongate and cylindrical, somewhat as in *Gastrocentrum* Gorh.

*Head.*—Eyes rather small and widely separated, glabrous, with a rather shallow and ill-defined emargination opposite the antennal insertions. Antennae not extending beyond base of prothorax, somewhat moniliform, segments 3–7 elongate, 8–11 rather asymmetrically widened to form a loose club, segment 8 slightly transverse, 9–10 more so, 11 about as wide as 10 and distinctly elongate. Mouth-parts not distinctly visible in the type, labial palpi apparently with last segment more or less equilaterally triangular.

*Thorax.*—Prothorax about one and two-thirds as long as its average width, rather cylindrical, narrowed in basal part, front half and basal third nearly parallel-sided, separated by a sinuation; no trace of side edges; notum with a transverse procurved impression immediately before base; front coxal cavities narrowly closed behind. Metasternum about twice as wide as its median length, rather strongly convex on each side of its impressed median suture, the convexities sharply limited posteriorly along oblique lines which receive the protracted femora; anterior process between middle coxae (not well seen in the type) apparently sharp and laterally bordered. Elytra with regular rows of punctures, but not striae, in basal part, somewhat transversely constricted before middle, with narrow epipleura in basal half only, outer edges slightly explanate towards apex. Legs moderately ong; front femora considerably thicker than the others, which are of moderate thickness; trochanters small, triangular, posterior ones somewhat protuberant; tibiae moderately thick, with very small spurs; tarsi rather broad and flat, segment 1 easily visible from above, nearly as long as 2, 1–4 with well developed ventral adhesive lobes, 4 rather shorter than 3, 5 about as long as 3 and 4 together in middle line; claws divaricate, with a large basal tooth.

*Abdomen.*—With first ventrite longest, its intercoxal process strong, relatively broadly triangular with raised sides and a depression along the middle; a small portion of a sixth ventrite exposed apically; basal margin of first ventrite continued a short distance along its lateral edge.

Type species, *Prospinoza baltica* sp. n.

### ***Prospinoza baltica*** sp. n. (Pl. I, figs. 1–4)

General colour blue-black, somewhat metallic, with vestiture of long black projecting setae. Punctuation of the derm not very clearly seen, apparently nowhere dense. The long projecting setae are distributed over dorsal surface of head, prothorax and elytra and occur also along the outer edges of femora and tibiae; anterior and posterior faces of tibiae with short pale raised pubescence. Pronotum with punctuation rather sparse along a broad median band, rather dense at the sides. Scutellum transverse, densely pubescent. Elytra with regular rows of large punctures in basal half, dying out behind the transverse constriction, with scattered small punctures throughout; a reddish transverse fascia, interrupted at the suture, coinciding with the constriction, about two-fifths of way to apex; elytral vestiture with more numerous shorter semi-erect setae among the sparser long erect ones.

Overall length 7 mm., length of pronotum 2·1 mm.

Holotype (sex unknown) in the British Museum collection, reg. no. In. 18785, from Klebs' collection, Baltic Amber, East Prussia.

The genus *Prospinoza* seems to be closest to the existing *Spinoza* Lewis and *Gastrocentrum* Gorh.; it differs from both in the larger and blunter basal tooth of the tarsal claws and in having relatively longer antennae, in both of which respects it resembles *Pallenis* Lap. It might well represent a type ancestral to all three of these modern genera. This whole group of genera probably represents a primitive type among Tillinae, of which unfortunately no larvae have yet been described. The complete absence of the group from America (as far as known) may be connected with its mainly tropical habitats and the relatively recent origin of Tillinae altogether—only types of the subfamily capable of adapting themselves to cool conditions may have been able to reach America.

The Phyllobaeninae were until recently known as Hydnocerinae, while the name Epiclininae is now applied to what were called Phyllobaeninae. This particular nomenclatorial improvement, for which we are specially indebted to the American entomologist, Wolcott (1944), is an example of effects of recent modifications in the rules of zoological nomenclature. The increasing emphasis on typification, rather than definition, as the basis of higher groups like genera, has led to the revalidation of numerous generic names that were formerly ignored as "nomina nuda", among which are many first published in Dejean's *Catalogus Coleopterorum* of 1837. New generic names in this work were published with no more attempt at definition than an appended list of species. Dejean's new generic names were almost entirely (and very properly, according to the principles accepted at the time) ignored by his contemporaries and successors; some of them, like *Phyllobaenus*, were used by later authors in a sense different from Dejean's.

According to the characters given in my key, the Phyllobaeninae will probably include a number of ground-living African forms hitherto generally placed in Clerinae: *Apteroclerus* Woll., *Dozocolletus* Chevr., *Caridopus* Schk., *Brinckodes* Winkler, etc.

Within the large and diverse subfamily Clerinae, the New Zealand genus *Balcus* may possibly represent a rather primitive type. The only larva collected by me in New Zealand with the characters of Clerinae was a single specimen obtained from a leaf-litter sample at Wilton's Bush, Wellington, on 8th December, 1956. The specimen is very small, the overall length being about 4·5 mm. and the width of the head capsule 0·5 mm., and if it is a larva of *Balcus* probably represents an early second instar. The habitat is an anomalous one for Clerinae, as is the form of the spiracles (fig. 59).

In the entirely American Epiclininae (*olim* Phyllobaeninae), the described larvae resemble those of Enopliinae and differ from those of Clerinae, in having distinct dorsal ampullae on the abdomen; their relatively large intersegmental membranes in the abdomen are suggestive also of Tarsosteninae.

The Enopliinae are a rather heterogeneous group, for which no satisfactory larval characterisation has yet been formulated. The New Zealand *Phymatophoea* Pascoe (including *Mathesis* Waterh.) appears to be fairly close, in both adult and larval characters, to such American species as *Cregya oculata* Say. The larvae of *Orthopleura* Spinola and allied forms may be more or less parasitic; structural degeneracy associated with such habits is no doubt responsible for the difficulty in characterising these larvae as Enopliinae.

Tarsosteninae have not yet, as far as I am aware, been reported from New Zealand, but the introduction of either *Tarsostenus univittatus* Rossi or *Paratillus carus* Newm. into the country would not be at all surprising. The group is undoubtedly allied to Corynetinae (Korynetinae *auctt.*); larvae of *Tarsostenus* and *Paratillus* may be distinguished from known ones of Corynetinae by the possession of dorsal abdominal ampullae on at least segments 5 and 6, by the much smaller lateral air tubes of their spiracles, and by the possession of 4 or 5 ocelli on each side of the head; they are less easily separable from larval Enopliinae, perhaps the best character for this being the smaller number of ampullate abdominal segments in Tarsosteninae.

It is unfortunate that the known Corynetine larvae belong to the most advanced and distinctive group of the subfamily, the genera *Corynetes* and *Necrobia*; the larvae of forms like the Australian *Pylus* Newm. might be expected to be more primitive and more or less annectant to Tarsosteninae and Enopliinae. The uninverted aedeagus in the subfamily is correlated, at least in *Necrobia* species, with the male climbing on the back of the female in copulation. It is hardly likely that *Corynetes* and *Necrobia* would preserve a primitive condition lost in practically all other Cleroidea, so it is to be presumed that the uninverted condition of the aedeagus here is secondary. A similar condition was found in *Tillus transversalis* Charp., in which Crovetti (1962) reports a copulatory position similar to that seen in *Necrobia*. The liability of an inverted aedeagus to become secondarily re-erected in the course of evolution—there is no evidence that in Coleoptera this occurs by a 360° twist succeeding a 180° one as in male Diptera,—needs to be considered in relation to other groups of Coleoptera, notably Tenebrionidae.

## XI. Family 6. PHYCOSECIDAE

The genus *Phycosecis* Pascoe is known so far from the coasts of Australia and New Zealand; though one might expect it to occur in similar latitudes on the South American coast, no species of the genus (or family) has yet been reported from the continent. The species, which are entirely apterous, probably all live on rejectamenta above high water mark on the shore, mainly of sandy coasts. Another described genus that might possibly belong in this family is *Alfieriella* Wittm. (1935), known to me only from the fairly full description of *A. rabinovitchii* Wittm. from Egypt. *Alfieriella* appears to differ from *Phycosecis* in several respects, notably the length of the head in front of the antennae, the smaller and rounder front coxae, the cavities of which are said to be open behind, the greater separation of the middle and hind coxae, the long basal abdominal sternite, *etc.*; if it does not belong in this family, the genus will probably prove to be Cucujoid or Dermestoid. The genus *Phycosecis* having been entirely omitted from Junk's *Coleopterorum Catalogus*, I append here a catalogue of the family.

PHYCOSECIDAE Crowson, 1955; Tenebrionidae *pars* Pascoe, 1875, Masters, 1885–7; Trogositidae *pars* Masters, 1896; Lea, 1899; Hudson, 1934.

*Phycosecis* Pascoe, 1875, *Ann. Mag. nat. Hist.* (4) **16** : 213–4; Broun, 1880, *Manual of the New Zealand Coleoptera* I, 358–9; Masters, 1886–7, *Proc. Linn. Soc. NSW* (2) **1** : 259–380; id. 1896, *Ibid.* (2) **10**; Champion, 1894, *Trans. ent. Soc. Lond.* **1894** : 364; Lea, 1899, *Proc. Linn. Soc. NSW* **23** : 546–7. *Dermestes* partim Fabricius, 1792, *Entomologia Systematica* I : p. 234.

**limbata* Fabr., 1792 (type in Banks Collections, British Museum); *discoidea* Pascoe (type in B.M. coll.), Broun, 1880; *atomaria* Pascoe, 1875 (type in B.M. coll.), Broun 1880 NEW ZEALAND
*litoralis* Pascoe, 1875 (type in B.M. coll.); *algarum* Pascoe, 1875, type in B.M. coll. AUSTRALIA
*ammophilus* Lea, 1899 W. AUSTRALIA
*hilli* Lea, 1921, *Mem. Queensl. Mus.* **7** : 188 N. QUEENSLAND

## *Key to Adults of Described Species of* Phycosecis

1 Vestiture of prothorax and elytra composed of short erect narrow scales. *New Zealand* . . . . . . . . . . . . . . . **limbata** F.
– Vestiture of prothorax and elytra composed mainly of recumbent scales. *Australia* . . . . . . . . . . . . . . . . . . 2
2 Elytra with dense vestiture of overlapping rounded scales **litoralis** Pasc. (**algarum** Pasc.)
– Recumbent scales of elytra elongate, not overlapping each other laterally 3
3 Scales of elytra broadly ovate, not strongly contrasting in shape with those of the prothorax, which are also elongate . . . . . **hilli** Lea
– Scales of elytra narrow and linear, those of pronotum dense and nearly circular . . . . . . . . . . . . . . . . . **ammophila** Lea

The synonymy of *litoralis* and *algarum* was established by Lea (1899); from the study of fairly extensive material I have concluded that the New Zealand *Phycosecis* belong to a single rather variable species for which Fabricius's name must take priority. Either this species or *litoralis* might be made the type of the genus; I here select *limbata* on the grounds that it is the best-known and most widely represented species in European collections.

## *The Principal Characters of* Phycosecis

### *Adult*

With the general characters of Polyphaga-Cucujiformia-Cleroidea. Small, apterous species of relatively broad form, dorsal surface with more or less scaly vestiture.

*Head.*—Relatively large, almost circular in outline, eyes small, lateral, entire, convex, composed of relatively few convex ommatidia, middle of dorsal surface with a longitudinal impression, gular sutures relatively short and fairly widely separated; genae (fig. 63) with an anterolaterally directed prominent conical tubercle with a small vesicle at its apex. Antennae with insertions lateral, not covered by sides of frons, 10-segmented with a large 1-segmented club (fig. 63). Mandibles bidentate at apex, with a blunt tooth near middle of cutting edge, behind which is a setose prostheca, no trace of a molar part. Labrum transverse, its apex evenly rounded. Maxillae with a group of strong hooked spines near apex of lacinia, rest of armature of lacinia and whole of armature of galea consisting of much more slender curved setae; palpi with segment 1 small, 2 wider and slightly elongate, 3 about as wide as 2 and slightly shorter than it, 4 at least twice as long as 2, rounded at sides and distinctly narrowed to apex. Labium with mentum transverse, very slightly narrowed in front, anterior margin emarginate, prementum very transverse, narrower than mentum, distinctly widened to apex; ligula broad, slightly bilobed at apex, setose; palpi with basal segment small, palpiger-like, segment 2 obconical, elongate, segment 3 similar to apical segment of maxillary palpi.

*Thorax.*—Prothorax with well marked complete side edges; front coxae small, ovate, not projecting, their cavities closed behind by meeting of long hypomeral process with slightly widened tip of prosternal intercoxal process; prothorax constricted posteriorly to a distinct basal collar, its front margin strongly produced over the head, almost as in Bostrychoidea, side margins produced into tooth-like processes in front. Mesothorax with coxal cavities quite or almost closed outwardly by the sterna, trochantins hidden, coxae separated by about same distance as front coxae. Sternopleural suture indistinct. Scutellum relatively large, transversely triangular. Elytra rounded at sides, with punctures quite irregularly arranged, epipleura well marked and complete. Metathorax with sternum short, nearly parallel-sided (fig. 64), a median longitudinal impression extending about half its length. Episterna very large, strongly widened posteriorly, epimera not visible. Hind coxae small, oval and not quite as widely separated as the middle coxae, extending laterally not quite as far as lateral edge of metasternum. Met-endosternite consisting of a pair of widely diverging arms bearing the widely separated anterior tendons (fig. 64), with a short weakly sclerotised median area and a strong median ventral keel extending somewhat in front of it.

*Abdomen.*—With 5 visible sternites (ventrites), first slightly longer than the others and bearing strongly margined recesses receiving hind coxae and a sharp triangular intercoxal process; none of ventrites margined at sides. Tergites of segments 1–5 transparent and membranous, tergite 6 distinctly pigmented and somewhat sclerotised, spiracles lying in membrane beyond its edges, tergite 7 more strongly pigmented and sclerotised, extending laterally to include the spiracles within its edges, tergite 8 in male large and fully exposed. Aedeagus nearly or quite inverted when retracted, apex of tegmen bilobed and setiferous, its lateral parts separated from its basal median strut by membranous areas (fig. 65); median lobe broad, obtuse, and curved laterally.

## *Description of Larva of* Phycosecis limbata *F.*

General habitus resembling that of typical Melyrid larvae, setae of dorsal surface relatively short and sparse but rather stout.

*Head* (fig. 66).—With distinct epicranial suture and no endocarina, frontal sutures markedly sinuate; hypostomal rods strongly developed, extending to occipital foramen, curved and somewhat convergent posteriorly. Ocelli, 6 on each side, all with distinct lenses, 5 in the usual Cleroid pattern, sixth in position of pigment spot in *Phloiophilus* and *Protopeltis.* Labrum distinctly emarginate in middle, epipharyngeal sensillae characteristic (fig. 68). Antennae with segments 1 and 2 very short and transverse, 3 elongate and cylindrical; segment 2 with a large conical sensory appendage postero-ventrally to segment 3 and nearly as long as it. Mandibles (fig. 67) with 2 strong apical teeth, the ventral one slightly shorter, a blunt tooth near middle of cutting edge, lacinia mandibulae represented by a relatively broad appendage bearing 6 or 7 stout setae on its apical and posterior part. Maxillae of Melyrid type, with transverse cardo, elongate stipes, and a small vestige of articulating area between the two. Cardo with a strong ventral seta near its outer angle, stipes with a strong discal seta in basal half, a seta on outer margin in front half, and 2 at base of mala. Mala comparatively narrow, rounded apically with about 5 strong hooked spines along its apical and inner end, dorsal face with a short pedunculate seta and numerous normal setae. Palpi with apical (third) segment about twice as long as wide, considerably tapered to apex and with outer edge strongly sclerotised, penultimate segment slightly wider than base of apical one, strongly transverse and with a strong seta on outer apical angle, segment 1 slightly broader than 2 and about as long as it; palpiger relatively large and with a strong seta near outer basal angle. Labium with mentum very elongate, parallel-sided, a pair of ventral setae near middle and another towards apex, prementum transverse, more strongly sclerotised and pigmented, narrowed to its base, which is emarginate, bearing a prominent obtuse finely setose ligula and 2-segmented palpi, of which segment 1 is slightly transverse and 2 slightly elongate; a pair of strong ventral setae just behind bases of the palpi.

*Thorax.*—With pronotal sclerite fairly large and dark, approximately semicircular with a pale median line, mesonotal sclerites roundish and separated by about their own diameter, metanotal sclerites more widely separated, smaller and more irregular in shape. Coxae rather widely separated, legs moderately long strongly sclerotised and pigmented; coxae with 4–5 strong setae along anterior ventral edges, trochanters partially divided, apical part with 4 ventral setae, femora with 2 strong setae on anterior face, 1 on posterior face, tibiae with about 10 setae each. Tarsungulus long and slender, with a strong ventral seta.

*Abdomen.*—With distinct paired sclerites on segments 1–8 which become larger and more conspicuous posteriorly—a pleural sclerite behind and a little below each spiracle, a laterotergal sclerite, and a pair of discal tergal sclerites (fig. 69), each sclerite bearing 1 or 2 strong setae. Ninth segment, excluding urogomphi, nearly as long as its basal width, sides converging to apex, dorsal side fairly uniformly pigmented and sclerotised; urogomphi nearly straight, tapered and parallel with apical points only slightly upturned; two irregular transverse rows of more or less strong setae on tergum, urogomphi with many setae arising from distinct nodes. Segment 10 ventral, membranous and pygopod-like. Ninth abdominal tergite with several minute pores, but no distinct glands on abdominal segments 1–8. Spiracles all annuliform; thoracic pair situated ventrally in front part of mesothorax, abdominal ones lateral and before middle of segments.

Larvae were collected by me together with adults, on the remains of a dead bird on the sandy shore at Ruakaka, near Whangarei, New Zealand, on 14th November, 1956, and in similar circumstances at the Sandspit, near Dunedin, New Zealand, on 31st December, 1956. The gut contents of two larvae of which slide preparations were made consisted apparently entirely of insect fragments, as did the gut-contents of two adults studied.

In the ocelli, and the form of the frontal sutures, perhaps also the strong hypostomal rods, the *Phycosecis* larva may be more primitive than the known Melyrid types, and shows resemblances to some more primitive Cleroids. In the undivided tegmen of the aedeagus, however, *Phycosecis* may be less primitive than *Acanthocnemus*, and most other features of adult Phycosecidae may well be derivative in relation to Acanthocneminae. If the *Acanthocnemus* larva, when discovered, proves to have the same essential features as *Phycosecis*, it may prove more satisfactory to transfer the former genus to a re-defined Phycosecidae, or to transfer *Phycosecis* to Melyridae.

## XII. Family 7. MELYRIDAE

### (including Malachiidae, Dasytidae, Rhadalidae and Prionoceridae *auctt.*; Zygiidae Jacobson)

The present group is very easily distinguished in the larval stage, but rather less easy to define on imaginal characters. It will include the genus *Acanthocnemus* Perris, placed with *Phloiophilus* by Jacobson (1913) and Pic (1926), which is aberrant in having a well-marked 3-segmented antennal club, in its simple tarsal claws, and in the distinctly double tegmen of its aedeagus (fig. 70). The closest affinities of Melyridae would appear to be to Phycosecidae, and through *Phloiophilus* to primitive Peltidae; a direct link with Cleridae seems hardly possible, in spite of the Melyrid-like larvae of Thaneroclerinae and the suggestion of Leconte (1861) that the genus *Rhadalus* linked the two families. The analogies in both adult and larval characters between certain Melyridae and the Cantharoidea have long been noted, and many have taken them as indicative of a direct relationship; they are certainly striking enough to call for some comment and explanation. On the basis of the phylogenetic ideas developed here and in my previous works (Crowson, 1955, 1960) there can be no direct connection between Cleroidea and Cantharoidea, and particular similarities between Melyridae and Cantharidae will need to be explained as resulting from parallel or convergent development. In the adult stage, those Melyrids which most resemble Cantharids in structure also resemble them in habits, being much more free-living and floricolous than the majority of Cleroidea—species of both groups probably rely a good deal on their distasteful properties for protection. My own experience, and such ecological information as there is in the literature, indicate that larval Melyridae also show a trend towards more or less free-living habits and away from the subcortical or lignicolous associations of typical Cleroidea.

The existence of eversible lateral glands in adult Malachiinae may well have been an important factor in making possible the conspicuous mode of life of these insects—the defensive glands, which are present in both sexes, need to be distinguished from the "excitators" of Matthes (1962). The existence of dorsal glands, presumably repugnatorial, has long been known for Cantharid larvae; Gardner (1931), in describing a larva of the Malachiine genus *Carphurus*, seems to have been the first to record similar structures in the Melyridae. Fiori (1960, 1961) has studied the glands of Malachiine larvae in some detail, and gives details of their histological structure and some information on the nature of the secretion. My own attention was first drawn to the defensive glands of Melyrid larvae in 1958, by the South African entomologist, E. C. G. Bedford, who told me of an unpublished observation by a student of his, Miss de Wet, of drops of liquid exuding from the first and eighth abdominal segments of stimulated or irritated larvae of *Astylus astromaculatus* Blanch. Mr. Bedford very kindly sent abundant material of the larva of this species for study; examination of cleared preparations of the larvae revealed the presence of large reservoirs and ducts at the appropriate points at the sides of the first and eighth abdominal terga. On studying a cleared specimen of a European larva of *Melyris rufiventris* Boh., representing the same subfamily (Melyrinae) as *Astylus*, similar though rather smaller reservoirs and ducts proved to be present on the same segments.

From the observations of Gardner, Fiori and myself, one or two pairs of glands with well-marked tubular sclerotised orifices seem to be present on all three thoracic and the first nine abdominal segments in all Malachiine larvae studied. From my own observations, similar glands are present in corresponding positions in larval Prionocerinae (*Idgia* spp. from Ceylon and the Congo, and a presumed *Lobonyx* larva from Spain). In *Haplocnemus* and a number of Dasytinae, dark coloured subcuticular patches are often visible on the larval abdominal segments, usually two pairs each on segments 1–8; in these larvae the reservoirs seem not to be cuticle-lined and do not show up well in cleared slide preparations.

### *The Food of Adult and Larval Melyridae*

From such scanty published information as I have seen, it would appear that Melyrid larvae are usually carnivorous; the much more extensive available information concerning the food of adult Melyrids likewise suggests carnivorous habits for many species (particularly in Malachiinae), but there are reports also of a number of species taking vegetable food (*e.g.* pollen), particularly in Dasytinae. I have observed gut-contents in microscopic preparations of both adults and larvae of a number of species in this family, as follows.

HAPLOCNEMINAE

*Rhadalus* sp.: female, California—pollen grains.

*Haplocnemus* sp.: female, Europe—few insect setae and fragments of cuticle in a mass of unidentifiable material.

*Trichoceble floralis* (Ol.): female, Europe—numerous insect fragments, apparently of Aphididae.

PRIONOCERINAE

*Lobonyx aeneus* F.: male, Europe—dense mass of pollen grains; larva from pupal cell—hind gut contained fibrous vegetable material with a few apparently insect setae.

*Prionocerus bicolor* Redt.: male—hind gut with mass of dense apparently detrital material, no evident pollen grains or insect fragments.

*Idgia* sp.: larva, Ceylon—gut with numerous fragments of insect cuticle and setae, including parts of compound eye.

DASYTINAE

*Dasytes helmsi* Sharp: male, Australia—pollen grains in hind gut.

*D. derbesii* Sol.: male, Chile—mass of pollen grains in hind gut.

*D.* sp.: female, Europe—pollen grains in fore gut.

*D.* (*Arthracanthus*) sp.: female and male, New Zealand—pollen grains in fore gut.

*Henicopus armatus* Luc.: female, Spain—mass of pollen grains in hind gut.

*Graellsinus praticola* Waltl: male, Spain—ditto.

*Dasytiscus rufitarsis* Luc.: male, Europe—pollen grains and xylem fibres in hind gut.

*Dolichophron* sp.: male, Europe—pollen grains in hind gut.

*Amauronia* sp.: female, Europe—mass of insect fragments in hind gut.

*Halyles* sp.: male, New Zealand—ditto.

*Dasyrhadus impressicollis* Reitt.: male, California—?insect fragments in hind gut.

MELYRINAE

*Cerallus* sp.: male, Europe—mass of pollen grains in gut.

*Astylus atromaculatus* Blanch.: larvae, S. Africa—gut-contents of three specimens examined all included fragments of insect cuticle mixed with more or less detrital and, in one specimen, some evident vegetable material.

MALACHIINAE

*Balanophorus* sp.: female, Australia—insect fragments in hind gut.

*Collops quadrimaculatus* F.: male, N. America—ditto.

*Anthocomus fasciatus* L.: female, England—pollen grains and insect fragments in hind gut.

*Ebaeus pedicularis* F.: female, Europe—numerous insect fragments in gut, also some apparent pollen grains.

*Attalus dasytoides* (Perris): female, Europe—mass of pollen grains in gut, also some detrital material and apparent insect fragments.

?*Laius* sp.: larva, Australia—insect fragments in gut.

*Malachius* sp.: England—insect fragments, apparent pollen grains and detritus in hind gut of larva.

?*Troglops capitatus* Er.: larva, Spain—insect fragments in gut.

Undetermined Malachiine larva: Spain—ditto.

## *The Subdivisions of Melyridae*

There can be few groups of Coleoptera whose general system is currently in a more confused state than is that of Melyridae. Good comprehensive works on the group are almost non-existent, the most useful general treatment of it so far being probably that of Jacobson in his *Beetles of Russia and Western Europe* (1911), which provides keys as far as the genera for practically the entire Palaearctic fauna, with bibliographic catalogues of species. Unfortunately, few libraries in the West have this work, which suffers the additional disadvantage of being written in Russian, and has consequently been little used outside Russia. In Jacobson's system the family is called Zygiidae and divided into three subfamilies, Malachiini (=Malachiinae *mihi*), Zygiini (= Phloiophilidae + Acanthocneminae + Haplocneminae + Dasytinae + Melyrinae *mihi*) and Prionocerini (= Prionocerinae *mihi* minus *Lobonyx*). Jacobson's Zygiini are further subdivided into the tribes Dasytina (= Dasytinae *pars major* + Haplocneminae *mihi*), Danacaeina (= Dasytinae *pars mihi*) and Phloeophilina (= Phloiophilidae + Acanthocneminae *mihi*). Schilsky has provided keys to species for many of the Palaearctic genera, and Blaisdell made partial revisions of some North American genera of the group. The European Malachiinae were monographed by Abeille de Perrin (1891), and Marshall (1954) published a key to the world genera of this group.

The Melyridae have provided—and still provide—a happy hunting ground for certain prolific describers of new species, whose definitions are characteristically brief and often followed by the words (or their equivalent in the appropriate language) "type in my collection". The group is a fairly extensive one, with something like 200 described genera and some thousands of species. My own studies have been largely based on the British Museum collection, which in this family is neither as complete nor as well ordered as it is in some other groups. The system of subfamilies proposed here must be considered as tentative and provisional, and requires to be checked carefully against many more species and genera than I have had the time or opportunity to study.

## *Key to Subfamilies of Melyridae: Adults and Larvae*

1 ADULT: antennae with well-marked 3-segmented club; hypomeron of prothorax with a characteristic pit adjacent to sternopleural suture; claws simple; aedeagus with divided tegmen (fig. 70); male tarsal formula 4–5–5. LARVA: not described . . . (1) ACANTHOCNEMINAE

– ADULT: antennae never with so well marked a club; hypomeron of prothorax without such a pit; claws usually toothed or appendiculate; aedeagus with undivided tegmen . . . . . . . . . . . 2

2 ADULT: first 2 ventrites connate; elytra with sharply marked epipleura at least in basal half; last segment of maxillary palpi usually broadened at apex or securiform; median lobe of aedeagus with a dorsal appendage (fig. 74). LARVA: head with 2 ocelli on each side, the larger one anterior—a line through the two would pass through the antennal foramen; abdominal tergite 9 usually with a special appendage at the middle at each side (*cf.* fig. 72) . . . . . . . . . . (2) HAPLOCNEMINAE

– ADULT: all ventrites freely articulated; if epipleura sharply marked in basal half of elytra, last segment of maxillary palpi not at all broadened at apex; median lobe without a dorsal appendage. LARVA: if head with 2 ocelli on each side, they are one above the other, and a line through them would not intersect the antennal foramen . . . . . 3

3 ADULT: tarsal segment 1 shorter than 2; claws more or less toothed but never with membranous appendages; elytral epipleura distinct at least in basal half; tentorial cross-bar absent; sternopleural suture of mesothorax well marked. LARVA: body with more or less dense vestiture of long projecting setae; head with 4 ocelli on each side; dorsal glands distinct on abdominal segments 1 and 8 . . . . . (3) MELYRINAE

– ADULT: tarsal segment 1 usually at least as long as 2; claws often with membranous appendages; epipleura usually becoming indistinct before middle of elytra. LARVA: body vestiture usually of relatively sparse and not very long hairs; if head with 4 ocelli on each side, dorsal glands present on at least 8 abdominal segments . . . . . . 4

4 ADULT: prothorax with lateral exsertile vesicles; sternopleural sutures of mesothorax obsolete; head without a tentorial cross-bar; met-endosternite of Malachiine type (fig. 80). LARVA: head with 4 ocelli on each side; 1 or 2 pairs of dorsal glands with well marked tubular and often annulated orifices on thoracic and abdominal segments 1–9 . (6) MALACHIINAE

– ADULT: prothorax without lateral exsertile vesicles; met-endosternite usually not of Malachiine type. LARVA: head with 5, 3, 2 or 1 ocelli on each side; dorsal glands never with sclerotised tubular orifices . . 5

5 ADULT: tarsal claws simple or somewhat thickened in basal part, never with membranous appendages; tentorial cross-bar incomplete; head more or less rostrate, eyes often emarginate. LARVA: distinct paired dorsal sclerites present on abdominal segments 1–8, halves of head capsule usually meeting ventrally behind labium; 2 pairs of lateral eversible glands present on abdominal segments 1–9 (fig. 75) (5) PRIONOCERINAE

– ADULT: tarsal claws usually with membranous appendages; tentorial cross-bar usually complete; head not or scarcely rostrate, eyes entire. LARVA: without dorsal sclerites on abdominal segments 1–8; halves of head capsule not meeting ventrally; abdominal segments with a pair of dorsal and a pair of lateral glands, which are not eversible and do not have conspicuous openings . . . . . . . . . . (4) DASYTINAE

The single genus, *Acanthocnemus* Perris, of Acanthocneminae is perhaps closer to *Phloiophilus* and Peltidae than is any other known Melyrid type, and might reasonably be regarded as on the whole the most primitive of living Melyridae. The single well established species, *A. nigricans* Hope, seems likely to be of Australian origin (*cf.* Champion, 1922), but has been introduced into many of the warmer regions of the Old World. It is curious, considering the wide distribution recorded by Champion (*t.c.*), that there have been so few recent records of this species. The distinctly divided or "double" tegmen of the aedeagus (fig. 70) links this insect with Peltidae and Trogossitidae; another male character, the 4-segmented front tarsi, links *Acanthocnemus* with the otherwise very different Malachiinae. The pits on the hypomera of the prothorax presumably mark the openings of glands—which might well be an adaptation enabling the insect to survive in ant-infested habitats.

It is rather surprising that an apparently well defined group such as the Haplocneminae has escaped recognition hitherto. The probable reason is that museum systematists dealing with Melyridae have hitherto spent nearly all their time in examining specimens glued down on cards. The connation of the two basal ventrites is quite easily visible in dried specimens without special preparation (though I first noticed it in cleared slide mounts); it is perhaps a rather unexpected feature in a "Malacoderm" type of beetle, though paralleled among the Heteromera, *e.g.* in Elacatidae (Othniidae). As a rule, carded specimens of Haplocneminae can be recognised as such by their stout form, securiform palpi, sharply marked epipleura and rather thick antennae, even without examining the ventrites. An unfortunate mistake by Saalas (1917), who described a *Haplocnemus* larva as *Dolichosoma* and attributed a *Dasytes*-type larva to *Haplocnemus*, has not helped matters. Neither of Saalas's larvae were reared, and both attributions were admittedly speculative. Larvae similar to those described as *Dolichosoma* by Saalas were collected by me on two separate occasions at Dalkeith Old Oak Wood, near Edinburgh, and also in Windsor Forest; *Haplocnemus* was recorded from the Edinburgh locality more than a century ago (Murray, 1853), and is reasonably common in Windsor Forest, while *Dolichosoma* has never been recorded from Scotland, or even the north of England, and is not included in the very thorough list of Windsor Forest Coleoptera by Donisthorpe. It is possible that the supposed *Haplocnemus* larva of Saalas, which is very similar to known larvae of *Dasytes* spp., might really belong to *Dolichosoma*, which is certainly a member of the Dasytinae by its imaginal characters.

Professor Thure Palm lent me larvae, determined by rearing, of *Trichoceble memnonia* from Sweden, which proved to have the same essential characters as *Haplocnemus*, as do larvae of *Pelecophora* sp. from Mauritius, kindly lent by Dr. Jean Vinson. I have confirmed the adult characters of Haplocneminae on the following species, mainly in the British Museum collection:—

*Haplocnemus palaestinus* Baudi, *Diplambe abietum* Kies., *Trichoceble floralis* Ol., *Julistus oertzeni* Schilsky, *Ischnopalpus subcostatus* Schilsky, *Cymbolus rufopiceus* Gorh., *Eucymbolus cyaneus* Champ., *Pelecophora interrupta* Alluaud, *Donaldia maindroni* Pic, *Malthacodes pictus* Waterh., *Xamerpus maculatus* Pic, *Anthriboclerus scotti* Schklg. The last mentioned species was described as a Clerid, and is still listed under Corynetinae in Corporaal's revised catalogue of that family. A female of *Rhadalus* sp., from California, sent to me by Hugh B. Leech, proved to have the essential features of this subfamily.

One of the most notable features of the Haplocneminae is the sclerite articulated to the (morphologically) dorsal side of the median lobe of the aedeagus. In *Haplocnemus* itself (fig. 74) this sclerite is relatively small, but in the Mascarene *Donaldia* (see Vinson, 1946) and to a lesser degree in *Pelecophora* it is much larger. The condition in *Donaldia* suggests that this sclerite might even be homologous with one part—presumably the anterior—of the divided tegmen of *Acanthocnemus*.

Most adult Haplocneminae are probably to a considerable extent carnivorous, as indicated by the gut-contents of specimens of *Haplocnemus* and *Trichoceble* examined by me, and also by Vinson's report of insect fragments in the gut of adults of species of *Pelecophora* and *Donaldia* examined by him (Vinson, 1946). *Rhadalus*, according to the single female specimen examined by me, may be exceptional in its pollinivorous habits. Identifiable gut contents were not found in Haplocneminae larvae examined by me, nor have I seen published records of their food.

The Haplocneminae seem to be represented in all the main zoogeographical regions except the Australian; like most groups of Melyridae, they are most richly developed in the Mediterranean region.

The Melyrinae as defined in my key correspond to the Dasytidae-Melyrinae of

Pic (1929) minus the genera *Cymbolus* and *Eucymbolus*, which are part of my Haplocneminae. The ocelli of the larvae, like the tentorium and to a certain extent the metendosternite of the adult, suggest an affinity of this group to Malachiinae, while the general habitus, both larval and adult, rather recalls the Haplocneminae. The species are no doubt predominantly pollinivorous in the adult stage; the larvae of *Astylus atromaculatus* Blanch, introduced into South Africa from the Neotropical region, are reported to be herbivorous and injurious, though my observations on their gut-contents indicate that these larvae are at least partially carnivorous, like all other Melyrid larvae for which we have any definite indications of the food.

A notable feature of the distribution of Melyrinae is the entire absence of the group from tropical Asia and the Australian region; apart from one doubtful genus it seems to be lacking also in Madagascar, despite the abundant representation in Africa. The very distinct tribe Astylini is exclusively neotropical.

The Dasytinae are a rather heterogeneous looking assemblage, of which regrettably few larval types have yet been identified. Larvae of *Dasytes coeruleus* DeG. and *Psilothrix nobilis* L. are fairly well known, and have been available for my study in the British Museum collection. From New Zealand I have two types of Dasytine larvae, corresponding presumably to the genera *Halyles* and *Dasytes* (= *Arthracanthus* Broun), but without conclusive evidence which is which. The Chilean material, sent to me for determination by F. di Castri, contains a number of very interesting and diverse types of Dasytine larvae, but none of these can yet be associated with particular adults. The same is true of various European Dasytine larvae collected by me. The discovery of larvae of *Danacaea* or similar genera would be an important contribution to our knowledge of Melyridae. The genus *Lobonyx*, hitherto always included in Dasytinae, is here transferred to Prionocerinae, mainly on the basis of a presumed *Lobonyx* larva, described later. *Dasyrhadus* Lec., placed with *Rhadalus* under Rhadalidae by Pic (1926), proves from my study of an adult of *D. impressicollis* Fall. to be Dasytine with no particular resemblance to *Rhadalus* or Haplocneminae.

As will be seen from the list of the gut-contents of Melyridae studied by me, adult Dasytinae seem to be mainly herbivorous and specially addicted to pollen. Denticulation of the basal part of the cutting edge of the mandibles (*cf.* fig. 78) would appear to be a fairly reliable indicator of pollinivorous propensities in this group, and it recurs with a similar connotation in Melyrinae, Prionocerinae and probably in other families. The few Dasytinae in which I found insect fragments in the gut—*Amauronia*, *Halyles* and perhaps *Dasyrhadus*—all had mandibles with no trace of denticulation, like those of Haplocneminae and Malachiinae.

The habitats and habits of larval Dasytinae have been inadequately investigated, but appear to be diverse. Larvae of *Dasytes coeruleus* have generally been reported from dead wood attacked by borers, while those of *Psilothrix* have most often been found inside the stems of herbaceous plants. In New Zealand, I found Dasytine larvae in leaf-litter, in dead tree-fern rachises, and under bark, and have found unidentified Dasytine larvae in similar habitats at various European localities.

In numbers of species and genera, the Dasytinae rival the Malachiinae, and in geographical range they even exceed that group, being represented not only in all the main zoogeographical regions but also in New Zealand and Chile.

The Prionocerinae have been universally recognised, since the time of Lacordaire, as an isolated group of subfamily or even family status, comprising only the old-world genera *Prionocerus* Perty and *Idgia* Castelnau. The principal features hitherto relied on to distinguish the group have been the more or less large and sharply emarginate eyes, and the simple tarsal claws. Both these characters however are subject to a certain amount of qualification—for example, Champion (1919) described two Chinese species of *Idgia* in which the tarsal claws are said to be "distinctly widened to about the middle", and in the same two species the eyes are described as "small, distant"; similar features are described also for *Idgia dasytoides* Champ. from Burma, which is said also to have a *Dasytes*-like facies. Champion (*t.c.*) stresses two other general features of the Prionocerinae studied by him—the front tibiae having only a single apical spur, and the combs on the three basal segments of the male front tarsus. Larvae of *Idgia*, first described by Gardner (1929), certainly differ markedly from other known Melyrid types and thus might be taken to support the traditional isolation of Prionocerinae. It was thus surprising for me to find larvae agreeing in all essentials with those of *Idgia*, near Ronda in southern Spain. No Prionocerinae have been recorded from the Mediterranean region, or anywhere nearer Spain than Asia Minor or tropical Africa. Processes of consideration and exclusion applied to all Melyrid types known to occur in southern Spain led to a probable identification of these larvae as *Lobonyx aeneus* F. A re-study of the adult of this species revealed some notable similarities to Prionocerinae; for example, the front tibiae have only a single spur, the male has well developed combs on segments 2–3 of the front tarsus and some trace of one on the first segment, the wing-venation is practically identical with that of *Idgia*, the mouth-parts are very similar to those of Prionocerinae, the met-endosternite and aedeagus and the form of the mesosternum and pleura, are all more or less similar in *Lobonyx* and Prionocerinae. Furthermore, Champion (1920) described two new species of *Eulobonyx* (generally treated as a subgenus of *Lobonyx*) in which all three basal segments of the male front tarsus had well-developed combs, the head is markedly elongate (as in Prionocerinae) with the vertex "angularly depressed between the eyes", and in one of these species the prothorax is as long as its width—in *L. aeneus* it is markedly transverse and in Prionocerinae more or less elongate. In consideration of these facts I have transferred *Lobonyx* (and *Eulobonyx*) to a re-defined Prionocerinae.

Available information indicates that adult Prionocerinae are floricolous and at least to some extent pollinivorous, and that the larvae are at least partially carnivorous —in these respects this subfamily resembles Dasytinae. Information concerning the normal habitat and prey of larval Prionocerinae is very inadequate. Presumed larvae of *Lobonyx aeneus* were found by me in cells—probably pupal—in the bark near the base of a large living oak tree (*Quercus* sp.); larvae probably of *Idgia* I collected under bark of a large fallen tree in Ceylon, but very similar larvae were found in the soil in the Parc National de la Garamba, Congo, by G. de Moulin.

Distributionally, the Prionocerinae are notable in having no known representatives in the New World, or in Madagascar; the main centres of the group are in tropical Asia and Africa, with some representation also in the southern fringes of the Palaearctic region.

The Malachiinae are here treated last, as being on the whole the most modern and successful group of Melyridae, and the one showing fewest primitive features. The fact that several of the genera occurring in tropical Africa, e.g. *Pseudocolotes*, *Ebaeus*, *Hedybius*, *Apalochrus*, have species also in Madagascar indicates considerable facility in this group at crossing sea barriers. The adults are active, usually floricolous, often brightly coloured (and possibly aposematic), and appear to be at least to a considerable extent carnivorous. Many of the species show more or less marked sexual dimorphism, the males in particular often possessing striking secondary sexual characters. Matthes (1962) has studied these in some detail in connection with the mating behaviour of a number of Central European species.

According to available information, larval Malachiinae seem, like other Melyridae, to be to a large extent carnivorous. The habitats of the larvae are evidently diverse—few of the species seem to be particularly associated with dead trees and bark-beetles or borers, the majority having been found on the ground, on or in living plants, or in old fungi. These habitats are very similar to those of larval Cantharidae, to which group, as we have already mentioned, both larval and adult Melyridae present considerable analogies. Larvae which I have attributed to *Troglops capitatus*

Er. were found together with adults of this species in an old, much eaten fungal fruit-body of *Fomes* or an allied genus; the determination, though probable, is thus uncertain.

### *Melyridae: Synopsis of Larval Types Studied*

1 Head with 2 ocelli on each side, the larger one anterior; a line through the two would pass through the antennal foramen. Tergite of abdominal segment 9 often with a membranous appendage or group of setiferous tubercles near the middle of each side (fig. 72). Haplocneminae . . . . . . . . . . . . . . . . . . . 2

– If head with 2 ocelli on each side, they are one above the other and a line through them would not intersect the antennal foramen. Tergite of segment 9 without such special structures near the middle of its sides 5

2 Abdominal tergite 9 with a cluster of 3 setiferous nodules near the middle of each side; urogomphi relatively long, widely separated, with their apices strongly upturned; setal vestiture of upper surface relatively short and inconspicuous . . . . . (undetermined larva from Chile)

– Abdominal tergite 9 without such a group of setiferous nodules, with a membranous appendage if urogomphi are long and widely separated; vestiture of upper surface rather long and conspicuous . . . . . 3

3 Urogomphi (fig. 72) long, widely separated, slender; dorsal setae of abdomen more or less plumose; abdominal tergite 9 with a long membranous appendage near middle of each side . . . . . ***Pelecophora*** sp.

– Urogomphi very short, or close together; dorsal setae all simple . . . 4

4 Urogomphi short, blunt, closely approximated; ninth abdominal tergite with a short large membranous appendage near middle of each side ***Haplocnemus impressus*** (Marsh.)

– Abdominal tergite 9 a large flat plate, bearing minute sharp widely separated urogomphi, without evident membranous appendages near middle of each side . . . . . . . ***Trichoceble memnonius*** Kiesw.

5 Tergal region of abdominal segments 1–8 (fig. 75) with at least 2 pairs of well marked pigmented sclerites. Urogomphi practically straight, more or less conical and bearing numerous setae almost to their tips. Two pairs of eversible membranous appendages (? glands) on abdominal segments 1–8, 1 pair posteriorly to the spiracles, 1 near the mid-dorsal line; similar glands in corresponding positions on thoracic segments and abdominal segment 9. Prionocerinae . . . . . . . . 6

– No well marked sclerites on tergal regions of abdominal segments 1–8; urogomphi more or less strongly curved upwards towards apex, their setae few and mainly in basal portion; dorsal and lateral glands, if present, not appearing as eversible appendages . . . . . . . 7

6 Halves of head capsule not quite meeting ventrally behind labium; basal segment of labial palpi less than twice as wide as long; antennal segment 2 not more than twice as wide as long, nearly as long as segment 1; ventral sclerites of thorax small, well marked, widely separated, bearing few setae. *Palaearctic* . . . . . . . . . . ***Lobonyx aeneus*** F.

– Halves of head capsule meeting ventrally behind labium; basal segment of labial palpi more than twice as wide as long; antennal segment 2 many times as wide as long, much shorter than 1; ventral sclerites of thorax larger, less well marked, bearing more numerous setae . ***Idgia*** sp.

7 Body with vestiture of long projecting hairs; head with 4 ocelli on each side; dorsolateral gland reservoirs present on abdominal segments 1 and 8 only, segments without distinct sclerotised glandular orifices;

urogomphi more or less short and blunt, not markedly upturned. Melyrinae . . . . . . . . . . . . . . . . . . . 8

– Body rarely with vestiture of long projecting hairs, if so head with 5 ocelli on each side; if head with 4 ocelli on each side, all trunk segments with paired sclerotised glandular orifices . . . . . . . . . . 9

8 Abdominal tergite 9 with a strong lateral tubercle outside the base of each urogomphus, the disc of the tergite with a deep depression, which is sharply bordered at the sides; setal vestiture less dense ***Melyris rufiventris*** Boh.

– Abdominal tergite 9 without lateral tubercles, its disc not markedly depressed; setal vestiture very dense . . . ***Astylus atromaculatus*** Blanch.

9 Dorsal glands of thorax and abdomen never with sclerotised tubular orifices; mandibular appendage with its posterior branch always plumose, anterior branch simple or plumose; head with 5 ocelli on each side, more rarely 4, 3, 2, or 1. Dasytinae . . . . . . . 10

– Dorsal glands of trunk with well marked tubular sclerotised orifices; mandibular appendage with its posterior branch simple, anterior branch more or less plumose (fig. 79); head with 4 ocelli on each side. Malachiinae . . . . . . . . . . . . . . . . . . . 17

10 Head with 5 ocelli on each side; abdominal tergite 9 sclerotised and markedly pigmented . . . . . . . . . . . . . . . . 11

— Less than 5 ocelli on each side; abdominal tergite 9 lightly sclerotised, much paler than urogomphi. *Chile* . . . . . . . . . . . 15

11 Trunk with rather dense vestiture of very long hairs, some of them at least as long as width of ninth abdominal tergite; inner margins of urogomphi forming a V-shape, which is only narrowly rounded at its point; abdominal segments 1 and 8 with eversible lateral vesicles. *Chile* . . . . . . . . . . . . . . . (? ***Arthrobrachys***)

— Setae of trunk always much shorter than width of abdominal segment 9; without such lateral vesicles on abdominal segments; inner margins of urogomphi enclosing a U-shaped figure . . . . . . . . . 12

12 Antennal segment 2 much wider than long, 3 considerably longer than it. *Europe* . . . . . . . . . . . . . . . . . . . ***Dasytes***

— Antennal segment 2 not or scarcely wider than long, about as long as 3. *Chile*, *New Zealand* . . . . . . . . . . . . . . . 13

13 Dorsal plate of abdominal segment 9 more or less uniformly pigmented; pronotal sclerotisations weak and inconspicuous (undetermined larva from Chile)

— Dorsal plate of abdominal segment 9 with posterior part much paler than front part; paired pronotal sclerotisations pigmented, evident. *New Zealand* . . . . . . . . . . . . . . . . 14

14 Pronotal sclerotisations forming a pigmented area of nearly circular outline, with a narrow median pale line . . . . . . . ? ***Halyles*** sp.

— Pigmented area of pronotum much more irregular in outline, the pale median line much widened posteriorly . ? ***Dasytes*** (=***Arthracanthus***) sp.

15 Head with 2 ocelli on each side, one above the other; sclerotised part of antennal segment 2 not forming a complete ring, interrupted on its outer side under the sensory appendage (larva from Quebrada de la Plata)

— Head with 1 or 4 ocelli on each side; antennal segment 2 forming a complete sclerotised ring . . . . . . . . . . . . . . . 16

16 Head with 4 ocelli on each side; inner edge of sensory appendage of antennal segment 2 more than half as long as segment 3; urogomphi parallel to each other . . . . . . . . (larva from Cerro El Roble)

— Head with 1 ocellus on each side; inner edge of sensory appendage not more than half as long as antennal segment 3; urogomphi distinctly divergent . . . . . . . . . . (larvae from many localities)

17 Dorsal glands with long, narrow, annulated tubular ducts. *Australian species* . . . . . . . . . . . . . . . . . . . 18

— Ducts of dorsal glands short, not annulated. *Larvae not Australian* . . 19

18 Postspiracular glands with tubular ducts present on abdominal segments 1–8 inclusive, similar dorsal glands on thoracic segments and abdominal segment 8 only, lateral glands also on segment 9; vestiture of dorsal surface rather long and sparse . . . . . . . . . . (? ***Laius*** sp.)

— Both postspiracular and dorsal tubular ducts present on abdominal segments 1–8 inclusive; vestiture of dorsal surface rather close and short (? Carphurini sp.)

19 Vestiture of dorsal surface of abdominal segments 1–8 composed of short more or less recumbent setae of equal length; orifices of glands of these segments short, not barrel-shaped . . . . . . . . . . . 20

— Tergites of abdominal segments 1–8 with several long erect setae in a transverse row near the hind margin, in addition to the close, short more or less recumbent pubescence; orifices of dorsal glands relatively long, barrel-shaped . . . . . . . . . . . ***Malachius*** spp.

20 Urogomphi of normal length, upturned and pointed at apex, bearing setae shorter than themselves; pubescence of dorsal surface closer and shorter, less conspicuous . . . . . . . . ? ***Troglops capitatus*** Er.

— Urogomphi very short, blunt, pale, bearing several strong setae that are much longer than the urogomphi; pubescence of dorsal surface longer and less dense, more conspicuous . (undetermined larva from Andalucia)

## XIII. Summary

The history and constitution of the superfamily Cleroidea are reviewed, and the group is re-defined on the basis of both adult and larval characters. The adaptive significance of some of the features of the group is discussed. A key to the families, for both adults and larvae, is provided; the Trogositidae of older authors is divided into two families Peltidae and Trogossitidae. The major subdivisions of each family are characterised, and a catalogue is provided of the known species of Phycosecidae, omitted from Junk's *Coleopterorum Catalogus.* A number of significant and previously undescribed larval types, including those of *Phloiophilus*, *Protopeltis*, *Diontolobus*, *Grynoma*, *Promanus*, *Chaetosoma*, *Metaxina*, *Phycosecis*, *Lobonyx* and *Haplocnemus* are characterised. New genera characterised are *Protopeltis* (Peltidae), *Necrobiopsis* (Peltidae-Egoliinae), and *Prospinoza* (Cleridae-Tillinae, fossil from the Baltic Amber).

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## Explanation of Figure Lettering

*D*, denticles of tibia
*GO*, glandular openings on abdominal terga
*MA*, membranous appendages
*MO*, molar part of mandible
*PS*, pedunculate seta of maxillary mala
*SP*, spiracle
*TA*, *TP*, anterior and posterior parts of divided tegmen

Except in figures 16 and 69, dotted areas are membranous or concave; parts seen by transparency are indicated by broken lines.

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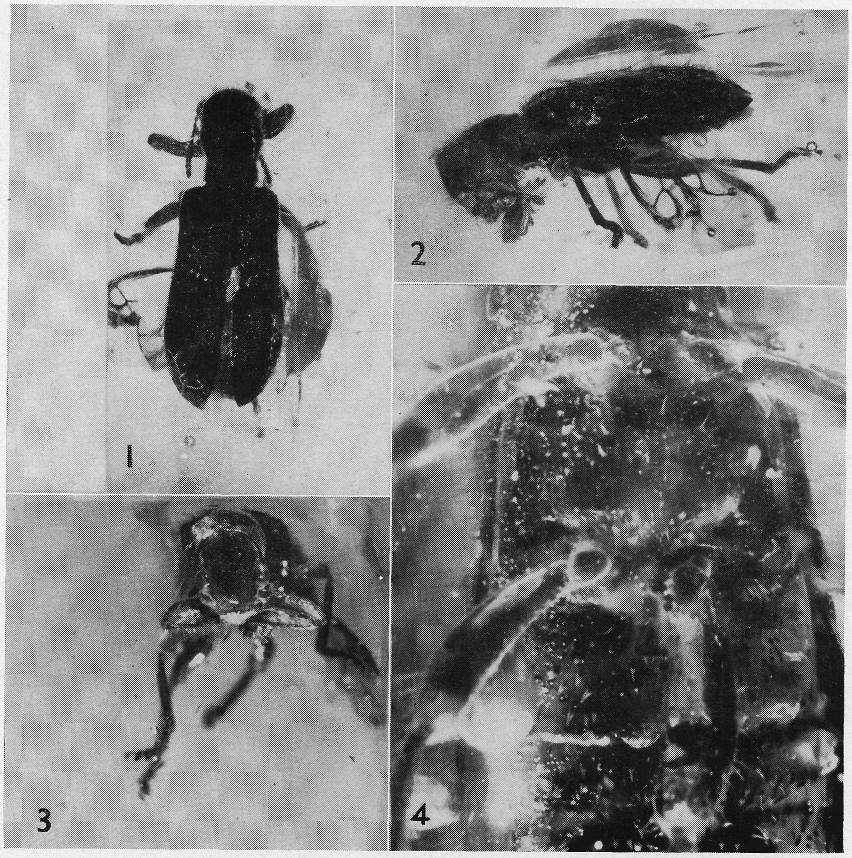

Fossil Cleridae from Baltic Amber.

FIG. 1.—*Prospinoza baltica* Crows., dorsal view of holotype.
FIG. 2.—*P. baltica*, holotype, left side view.
FIG. 3.—*P. baltica*, holotype, front view.
FIG. 4.—*P. baltica*, holotype, metathorax and base of abdomen, ventral view.