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Relationships of *Actizeta* and Cnemeplatiini (Coleoptera: Tenebrionidae)

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Abstract. The New Zealand genus *Actizeta* Pascoe, 1875 is transferred from the tribe Opatrini of the tenebrionoid lineage to the tribe Cnemeplatiini of the tentyrioid lineage in a new subtribe Actizetina. The Australian genus *Thorictosoma* Lea, 1921 is transferred from the tribe Ulomini of the tenebrionoid lineage to Cnemeplatiini in a new subtribe Thorictosomatina. The description of Pimeliinae is modified to incorporate additional taxa and characters. Cnemeplatiini sens.n. is defined, a key to subtribes and genera is presented, and *Actizeta* is described from adult and larval characters. Relationships of Cnemeplatiini are discussed, and the tribe Idisiini is identified as the most probable sister-group, on the basis of resemblances particularly in female genitalia and larvae. Characters of the ancestor of the tentyrioid lineage (subfamily Pimeliinae) are deduced. Attention is drawn to the taxonomic value of digitiform pegs on the terminal segments of maxillary and labial palpi, and larval endopleura.

Introduction

The relationships of the genus *Actizeta* Pascoe, 1875 have never been established satisfactorily. Both adults and larvae (here described for the first time) of *Actizeta* inhabit loose dry sand on coastal beaches in New Zealand where they consume dead organic matter. The adults are well adapted to this habitat structurally and they closely resemble tenebrionid genera from other parts of the world which also live in dry sand. *Actizeta* is re-described here because detailed study with the scanning electron microscope has brought much additional information relevant to determining its relationships.

The genus *Actizeta* Pascoe, 1875 was placed by its author in Tenebrionidae and compared superficially with *Ammobius*. Gebien (1910) in the Coleopterorum Catalogus listed *Actizeta* at the end of the Opatrinae among a very diverse assemblage of genera which appear to be 'genera incertae sedis', although not stated to be such; Hudson (1934) also listed it under Opatrinae. Gebien (1938–42) included *Actizeta* in the tribe Opatrini. Watt (1965) transferred *Actizeta* to Melanimini Koch, 1956 (a tribe of Opatrinae) on the basis of its simple aedeagus, failing to note that the aedeagus is inverted.

The subfamily Opatrinae as recognized by Español (1945), Koch (1956) and Medvedev (1968) is characterized by a deeply emarginate clypeus. Watt (1974b) included Opatrinae in the Tenebrioninae on the basis of both adult and larval characters, stating that: 'They may be a monophyletic group, but are not worthy of subfamily status'. In the analysis of Doyen & Tschinkel (1982), Opatrini s.l. tend to cluster with Helopini and Ulomini. However, the relationships of this group need not concern us any further here, because *Actizeta* does not belong to it, although it has a strongly emarginate clypeus (the clypeal emargination of Opatrinae is deep, almost V-shaped, but in *Actizeta* and its relatives it is evenly curved, almost semicircular).

Discovery of the larva of *Actizeta albata* showed that it has little in common with larvae of Opatrini, and caused me to examine the adult in more detail. The aedeagus proved to be inverted, abdominal defensive glands are absent, and the intersegmental membranes between abdominal sternites 5/6 and 6/7 are not exposed. These three characters together are diagnostic of Doyen & Lawrence's (1979) tentyrioid lineage or subfamily Tentyriinae, and of Watt's (1974b) interpretation of subfamily Pimeliinae (except for the tribes Pimeliini and Platyopini, in which the abdominal intersegmental membranes are exposed but the hinge position is medial as in Tentyriini, etc.). The term 'tentyrioid lineage' as used in this paper is equivalent to the subfamily Pimeliinae *sensu* Watt (1974b).

Lack of adequate comparative overseas material of Tenebrionidae in New Zealand prevented any further progress until I visited Professor Doyen, who gave me specimens of *Thorictosoma*, which he suggested is probably related to *Actizeta*. Access to the incomparable world collection of Coleoptera in the Natural History Museum, London (BMNH) has enabled me to assess the relation-

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ships of *Actizeta* both to *Thorictosoma* and to the tribe Cnemeplatiini.

Thorictosoma, hitherto in the tribe Ulomini, was placed in the tribe Cnemeplatiini by Doyen *et al.* (1990) and this placement is confirmed in the present study. Thus both *Actizeta* and *Thorictosoma* are now placed in Cnemeplatiini.

Notes on morphology of adults and larvae

Morphological terms used here are mostly explained and/or illustrated in Watt (1970, 1971, 1974a, b), Doyen & Lawrence (1979) and Doyen & Tschinkel (1982). Further comments are required to cover one adult and one larval structure which seem not to have been noted previously in descriptions of Tenebrionidae.

Digitiform pegs

Both adult and larval Coleoptera usually have proclinate, blunt-tipped, setiform structures on the dorsal surface of the maxillary palpi, parallel to the axis, and frequently on the labial palpi. The appearance of these in cleared preparations is shown for *Actizeta albata* in Fig. 1 (see also Watt, 1974a, figs 6, 10). In the scanning electron microscope (SEM) these structures are seen to lie in slits in the cuticular surface of, for example, the labial palp in *Tentyria schaumi* (see Fig. 3).

In the literature the structures have been variously referred to as proclinate blunt-tipped chemosensory setae (Watt, 1974a), scolopophorous organs, digitiform pegs, and digitiform organs (Crowson, 1981, and references therein). Their function is in doubt, but what experimental evidence there is suggests that they are receptive to vibrations rather than to chemical stimuli (Crowson, 1981). The term 'digitiform pegs', being descriptive of their appearance without implying anything of their function, is adopted here.

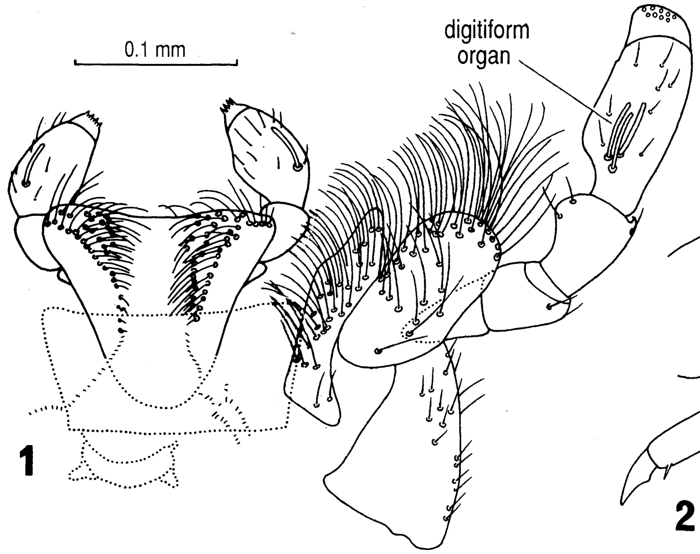
In adult Coleoptera, digitiform pegs are present on the dorsal or lateral surface of the maxillary palpi of almost all cleared preparations examined (superfamilies Caraboidea, Staphylinoidea, Byrrhoidea, Bostrichoidea, Cleroidea, Cucujoidea, Tenebrionoidea, Chrysomeloidea, Curculionoidea). Their number and position vary considerably, and are clearly of taxonomic significance. They may be almost anywhere on the dorsal or outer lateral surface, and their number varies from 1 to 32+, as noted by Watt (1974a).

One or more digitiform pegs are usually present on the dorsal or outer dorsolateral surface of the terminal segment of the labial palp in adult Tenebrionidae. These are usually fewer in number than those on the maxillary palpi. The position of digitiform pegs on the maxillary palpi seems to be constant within a genus, and sometimes a tribe (pers. obs.). In some genera the number of pegs on the maxillary palpi is quite constant, but in others it can vary between individuals of a single species.

Endopleuron

In many tenebrionid larvae there is a shallow to deep invagination of the body wall immediately adjacent to the anterior outer angle of each front coxa (Fig. 2). This structure is clearly an invagination of the pleural region, and hence is called an 'endopleuron'.

In adults of Polyphaga the 'endopleuron' is fused with the trochantin (Hlavac, 1972), although Lawrence (pers. comm.) suggests that the structure is not homologous with the endopleuron as discussed here (see below). The endopleuron of tenebrionid larvae is usually narrowly



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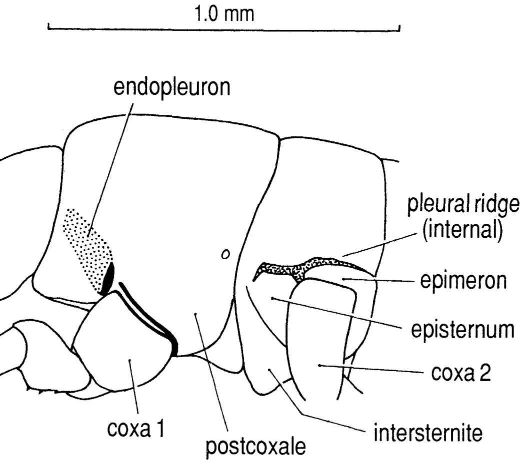

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Fig. 1. *Actizeta albata*, male, labium and maxilla, dorsal.

Fig. 2. *Actizeta albata*, larva, thorax, lateral (semi-diagrammatic; setae omitted).

open to the exterior just behind the proepisternum and in front of the trochantin (Watt, 1974b, fig. 87), so that with care a fine needle can be inserted through the opening into the invagination. Endopleura are present in larvae of many Tenebrionidae, but are most strongly developed in Pimeliinae. In *Tentyria*, *Pimelia*, *Coelus*, *Akis*, and probably many other genera, the endopleura extend backwards diagonally into the prothorax rather than projecting straight inwards towards the midline as in *Actizeta* (and in Tenebrioninae, Zolodininae, etc.).

Because endopleura are best developed in larvae of Pimeliinae, especially those which have very large, strong front legs, it is possible that they function primarily as attachments for the locomotor muscles of the front legs. If so, it is not clear why they remain open to the exterior, unless they also have a glandular function. No references to endopleura in beetle larvae could be found in the literature.

Lawrence (pers. comm.) has pointed out that the 'endopleuron' of Hlavac (1972) (which he suggests might better be called a cryptopleuron) represents the entire pleuron, which is internal in the polyphagan prothorax. This invagination of the pleural region occurs on all thoracic segments and is certainly homologous with the pleural apophysis. In tenebrionids with enlarged front legs, the prothoracic apophysis is more pronounced. This has been discussed briefly in Lawrence (1991).

Subfamily Pimeliinae

Pimeliariae Latreille, 1802. Acides Billberg, 1920. Akidinii auctorum. Erodiusidae Leach, 1985. Erodiini auctorum. Pimeliinae auctorum. Praocidae Eschscholtz, 1829. Praocini auctorum. Sepidiae Eschscholtz, 1829. Sepidiini auctorum. Tentyridae Eschscholtz, 1829. Tentyriinae auctorum.

Doyen & Lawrence (1979) cast doubt on the inclusion of Tentyriinae and Pimeliinae in a single subfamily, on the basis of the exposed intersegmental membranes between abdominal sternites in adults and the different number of setae on the labrum of the first-instar larvae in Pimeliini and Platyopini (Kelejnikova, 1971). Doyen & Tschinkel (1982) noted that although intersegmental membranes are visible between abdominal sternites 5/6 and 6/7 in Pimeliini and Platyopini, the hinge position is medial, as in Tentyriinae. Far too few first-instar larvae of either the tentyrioid or the tenebrionoid lineage are known to permit evaluation of the significance of number of setae. In the various phenetic and phylogenetic analyses of Doyen & Tschinkel (1982) Tentyriini, Pimeliinae and Zolodinini aggregate in all except two instances, with Tentyriini and Pimeliini more closely related to each other than to Zolodinini. In my opinion the larva of *Zolodinus* precludes the placing of Zolodinini in Pimeliinae – they are best regarded as separate subfamilies.

In addition to the adult abdominal characters linking Pimeliinae and Tentyriinae, the antennal sensilla are characteristically as in Fig. 4. Medvedev (1977) includes the following tribes in the tentyrioid lineage, on the basis of their antennal sensilla: Asidini, Molurini, Sepidiini, Nycteliini, Akidini, Pimeliini, Leptodini, Stenosini, Eurychorini, Nyctoporini, Idisiini, Lachnogyini, Epitragini, Tentyriini, Erodiini. I agree with the inclusion of these tribes in the tentyrioid lineage, and would add the Cnemeplatiini.

In both adult and larval characters the tentyrioid lineage, including Pimeliini and Platyopini, is clearly definable and appears to be a monophyletic group. Under the subfamily name Pimeliinae (which has priority over any other available name) Pimeliini was preferred as the name for the tentyrioid lineage by Watt (1974b) for reasons given in that paper. The description requires some additions and modifications to accommodate characters and taxa unknown or not adequately studied at the time, as follows.

Adult. Antennae not distinctly clubbed or with a 3-segmented club; sensilla setiform, grouped into dense rings apically on last 3 segments (Figs 5–7). Procoxal cavities closed behind externally, except in *Idisia*. Elytra rarely striate, but if so then with 10 striae and a scutellary striole, except in *Actizeta* (8-striate). Wings, if present, almost always without subcubital flecks. Hinge position between abdominal sternites 5–7 medial (Fig. 9). Abdominal defensive glands absent. Female genitalia very diverse.

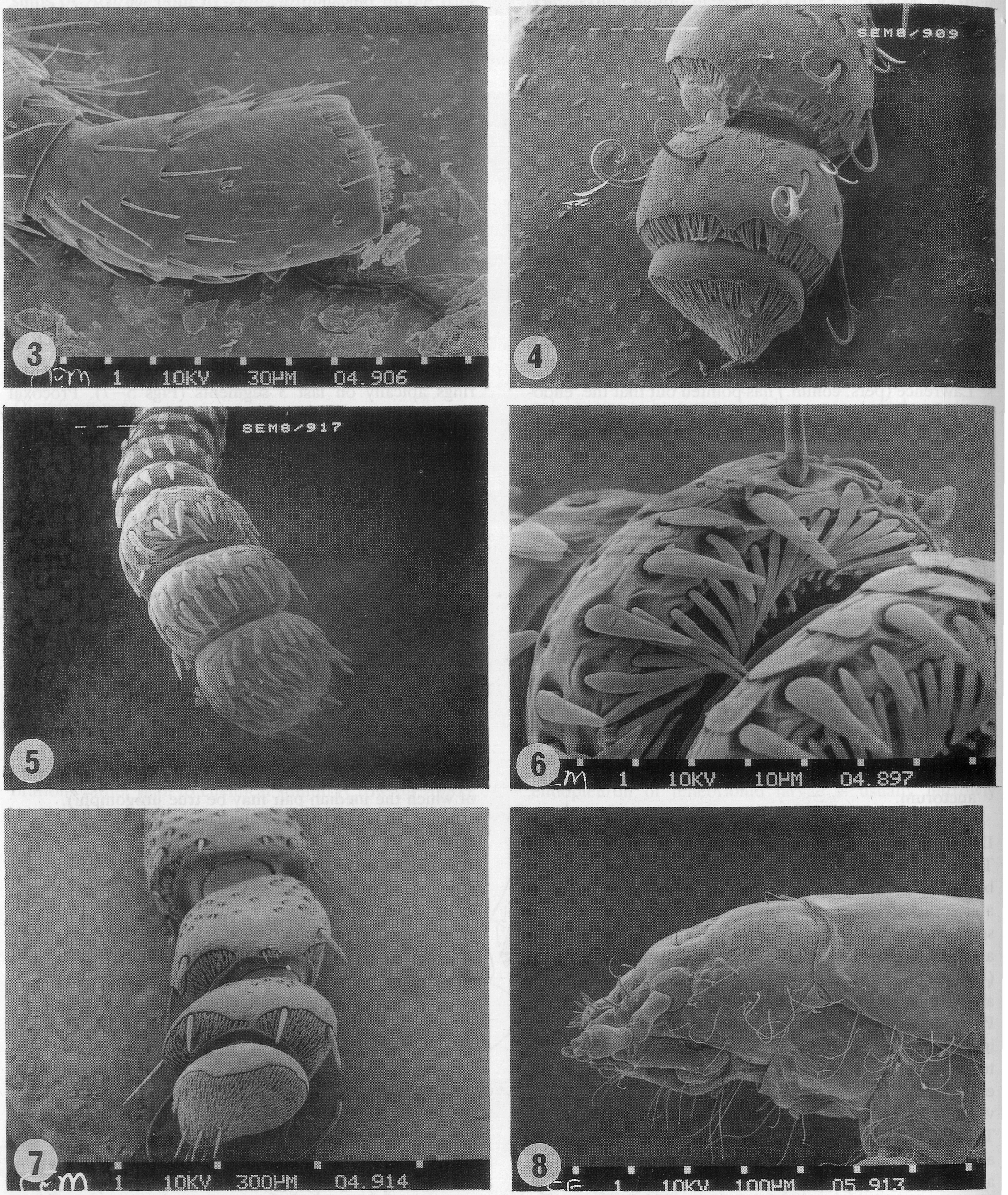
Larva. Lightly sclerotized except for head and terminal segment, slightly depressed, elongate. Mandibles with anterior part of dorsolateral edge carinate or explanate, and posterior part with a membranous elevation (usually dorsolateral, occasionally lateral) bearing at least 1 stout spiniform seta, and usually many; mola almost always strongly sclerotized. Hypopharyngeal sclerome almost always present, never tridentate, absent in *Actizeta*. Prothorax with deep endopleura usually extending diagonally backwards into thorax. Urogomphi rarely present (*Actizeta*, *Idisia*; *Akis* has 4 sharp apical and subapical projections, of which the median pair may be true urogomphi).

Tribe Cnemeplatiini

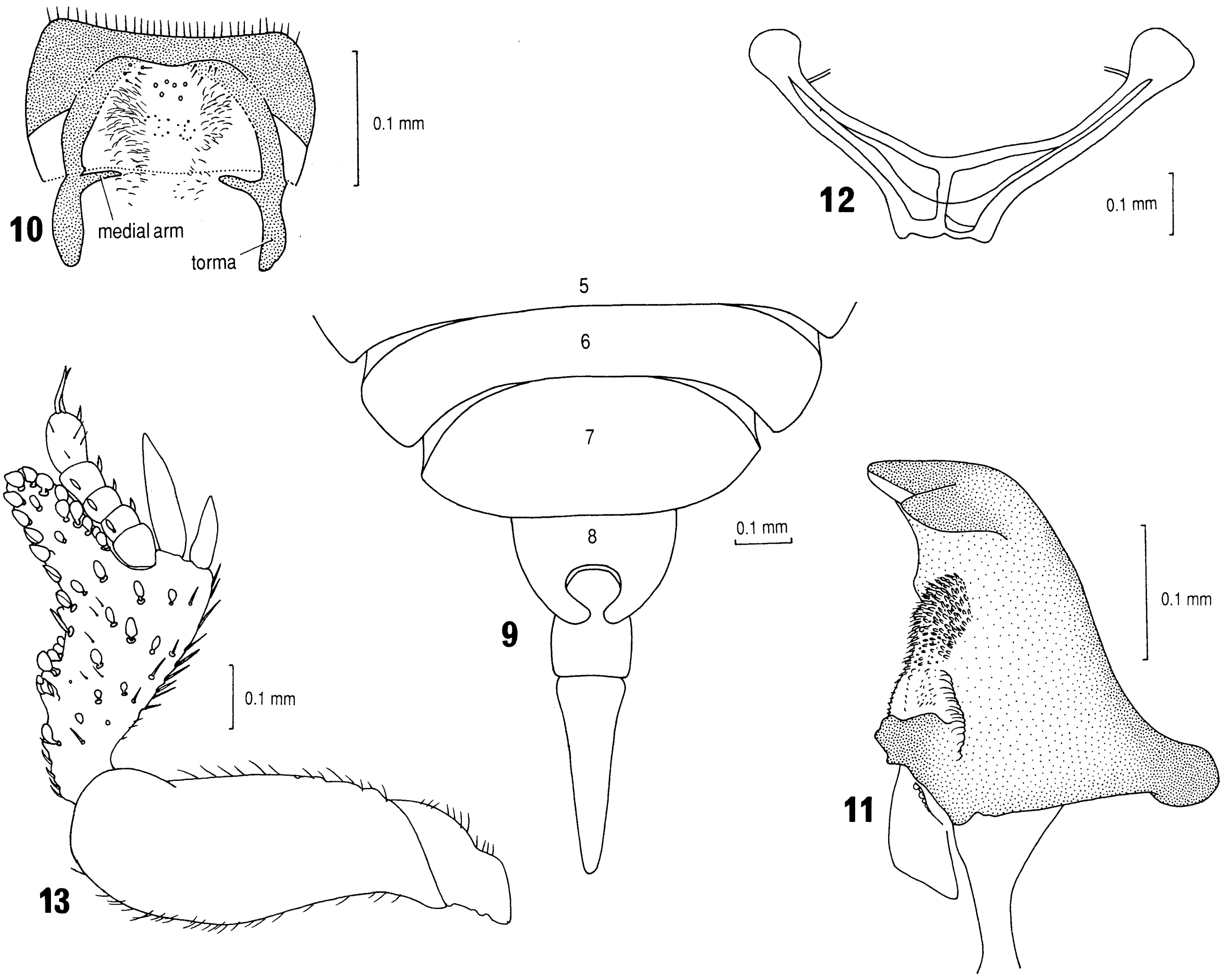
Cnemeplatiini Csiki, 1953: 117; Doyen & Lawrence, 1979: 367–368.

Adult. elongate and parallel-sided or oval, moderately convex, brown in colour, almost glabrous to densely pubescent, or clothed with erect and/or sessile scales.

Antennae short, always shorter than width of head, 11-segmented, the last 3 segments forming a club; club segments each bearing a dense ring of setiform sensilla in a circular depression around its apex, except in *Actizeta* (Figs 5, 6, cf. Fig. 7), where the rings are incomplete. Labrum small, largely concealed by clypeus, strongly transverse; clypeus deeply, almost semicircularly emarginate anteriorly, completely fused with frons; frontoclypeal suture obliterated; frontal canthus prominent, usually projecting as far laterally as eyes or further. Eyes usually convex, oval (vestigial in *Thorictosoma*), not or scarcely encroached upon anteriorly by canthus. Head slightly constricted, gradually or sharply, behind eyes to broad neck. Epipharynx with transverse tormae (Fig. 10), their



Figs 3–8. SEM studies. 3, *Tentyria schaumi*, labial palp; 4, *Pimelia cribra*, antenna; 5, *Actizeta albata*, antenna; 6, same, segments 9 and 10; 7, *Akis acuminata*, antenna; 8, *Actizeta albata*, larva, fore-end, lateral.



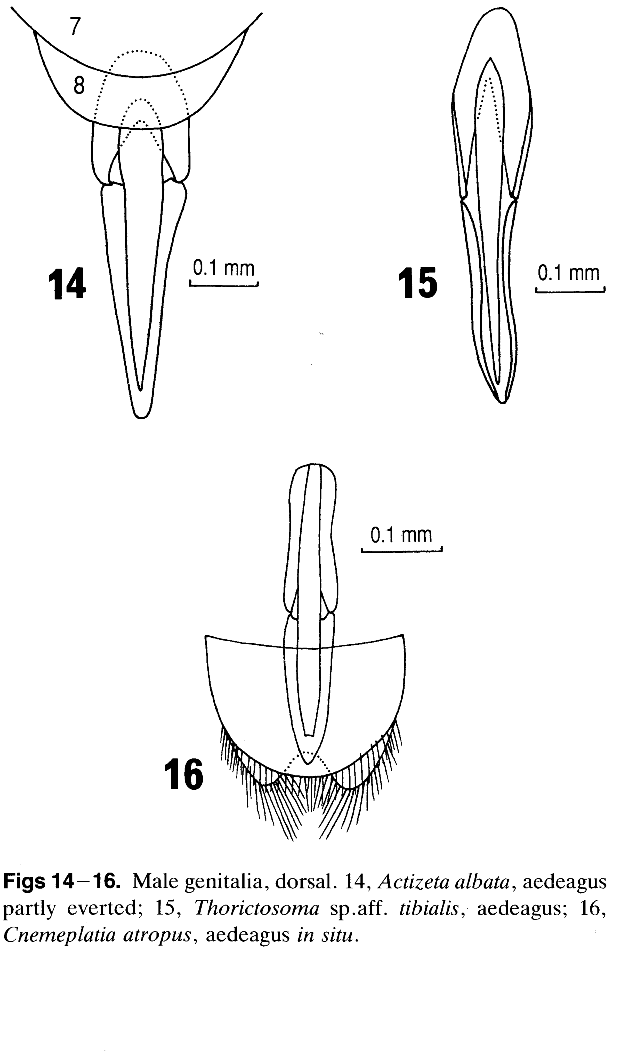
Figs 9–13. *Actizeta albata*, male. 9, terminalia, ventral, with sternites 6 and 7 deflexed; 10, epipharynx; 11, left mandible, ventral; 12, metendosternite, dorsal; 13, left front leg, dorsal.

medial arms directed mesad, not bent anteriorly or posteriorly. Mandibles variable, fairly elongate, each with strongly sclerotized apical and preapical teeth and variably developed cutting edge (strongest on right mandible); prostheca small (e.g. Fig. 11) or very small (*Thorictosoma*); mola prominent, either strongly developed and sclerotized (*Thorictosoma*) or reduced and very weakly sclerotized (*Cnemeplatia*). A membranous post-molar appendage present in *Actizeta*, not apparent in other genera. Maxillary palpi 4-segmented, with basal segment small and easily overlooked, and labial palpi 2-segmented; terminal segment of both palpi fusiform (see Fig. 11), that of maxillary palpi with 3 or 5 (*Thorictosoma*) digitiform pegs, that of labial palpi with 1. Mentum usually small, trapezoidal, leaving most of mouthparts, including cardo and stipes, exposed; in *Thorictosoma* mentum large, oval, covering most of mouthparts, including cardo and stipes. Galea and lacinia densely covered with curved bristles on inner face (see Fig. 1); lacinia without teeth; labium with a median area of bristles (*Thorictosoma*). Gular sutures short, widely separated, converging slightly. Ventral surface of head without pits, except for posterior tentorial pits.

Pronotum transverse, widest at or near anterior angles; posterior angles abruptly obtuse or completely rounded off (*Philhammus*). Prosternum before procoxae about as long as coxae; intercoxal process relatively narrow, broadened between coxae. Procoxal cavities closed behind externally, closed internally by a plate in the form of a spherical quadrant (see Watt, 1974b, fig. 72) with a single lateral aperture. Scutellum small, triangular. Elytra with 10 striae, 8 striae (*Actizeta*), or a lateral stria (*Thorictosoma*). Eipleura distinct in proximal half or indistinct and not reaching apex. Wings, if present, without anal cell and with only 3 anal veins in main group, of which only 1A and 2A reach the wing margin.

Mesocoxal cavities closed laterally by meso- and metasterna, not nearly reached by mesepimera, fairly narrowly separated. Metasternum transverse, more strongly so in wingless forms, with deep, curved grooves behind and parallel to hind margin of mesocoxae. Metendosternite with a short stalk and widely diverging arms (Fig. 12); anterior tendons inserted near apex of arms; laminae present in winged forms, absent in *Actizeta* and *Thorictosoma*. Trochanters heteromeroid. Legs, especially front legs, modified for digging. Front tibia broadly expanded at apex (e.g. Fig. 13), bearing scales or spines. Tibial spurs long on all legs, but larger and blade-like on front legs (Fig. 13). Front tarsi short, stout (Fig. 13), with last segment about twice as long as each other segment; middle and hind tarsi more elongate, and basal segment of hind tarsi longer than any other segment. On underside of tarsi a pair of stout, short spines at apex of each segment except the last, and usually a few sparse setae as well.

Abdominal sternites 5/6 and 6/7 hinged medially (Doyen & Tschinkel, 1982, fig. 41); intersegmental membranes not exposed. Abdominal defensive glands absent. Aedeagus inverted, with tegmen ventral (Figs 9, 14–16) and divided into apicale and basale; parameres completely fused. Tegmen and penis simple, without accessory lobes or processes. Female genitalia (Fig. 17) lacking an ovipositor; anus and vulva between tergite 8 and sternite 8. Internal organs simple; in *Thorictosoma* (Fig. 17) bursa with a glandular area near its base, apparently the functional spermathecal gland; *Cnemeplatia* and *Actizeta* (Figs 18, 19) with small spermatheca at or near apex of a large bursa.



Figs 14–16. Male genitalia, dorsal. 14, *Actizeta albata*, aedeagus partly everted; 15, *Thorictosoma* sp.aff. *tibialis*, aedeagus; 16, *Cnemeplatia atropus*, aedeagus *in situ*.

Size range 1.9–3.4 × 0.9–1.9 mm.

Larva. Only *Actizeta* (q.v.) is known.

Remarks. It will be noted in the above description that *Thorictosoma* differs from all other genera of Cnemeplatiini in its vestigial eyes, strongly developed mola, very small prostheca, large oval mentum covering the cardo and stipes, and absence of a small spermathecal gland of the type found in *Cnemeplatia* and *Actizeta*. However, it agrees with Cnemeplatiini in many other characters, and those in which it differs, except for the large mola, may be autapomorphies within the Cnemeplatiini.

The size of the mentum in Pimeliinae has been used for separating large groups of tribes; in fact Gebien (1937) used it as the main basis for his concept of the subfamily Tentyriinae, although as he noted, the tribe Asidini of the subfamily Asidinae (*sensu* Gebien) also has a large mentum concealing the mouthparts. Leconte & Horn (1883), although separating the subfamilies Asidinae and Tentyriinae on the basis of presence or absence of a mesocoxal trochantin (which correlates with lateral closure of the mesocoxal cavity by the meso- and metasterna), used the size of the mentum to separate tribes within both subfamilies. Koch (1955), who synonymized Asidinae with Tentyriinae, used the size of the mentum for the basic division in the first couplet of his key to tribes of Southern Africa.

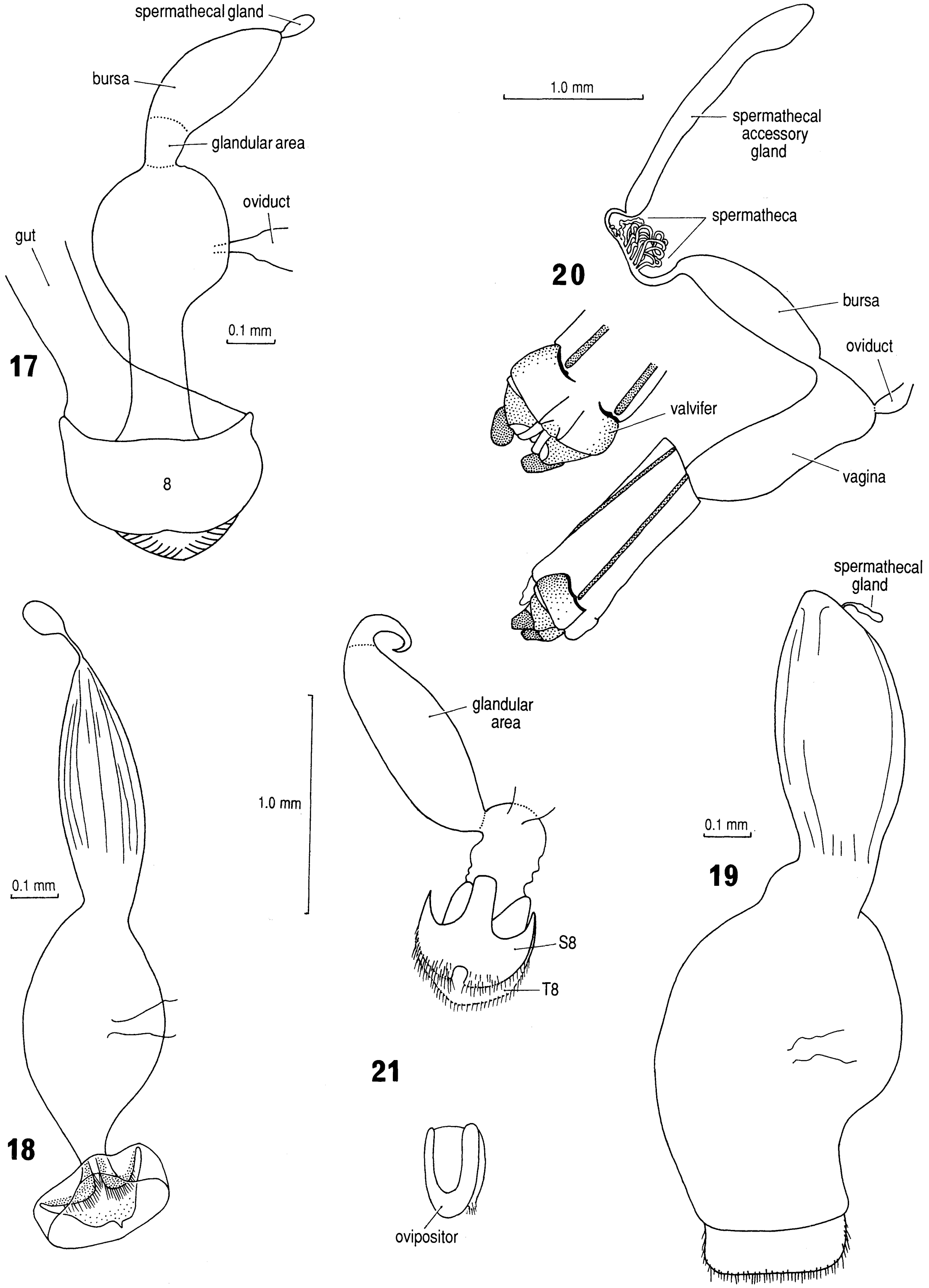
It seems likely that a large mentum has evolved independently more than once in Pimeliinae. Functionally it no doubt protects the ventral mouthparts from abrasive particles and dust when the beetle is digging. An enlarged mentum seems to be present in tribes and genera living primarily in semi-arid and arid conditions, or in sand dunes in moister climates.

Thorictosoma could not find a place in any tribe of Pimeliinae other than Cnemeplatiini. It is sufficiently distinct from all other genera, however, to be placed in a new subtribe, Thorictosomatina (see key, below). Of the remaining genera, *Actizeta* clearly is the sister-group of *Cnemeplatia* and *Philhammus*. It too is placed in a new subtribe, Actizetina (see key, below).

Relationships of Cnemeplatiini

Adult Cnemeplatiini have several derived characters, including a strongly emarginate clypeus, legs modified for digging, mesocoxae closed by the meso- and metasterna and lacking trochantins, reduced wing venation, absence of ovipositor, simplified internal female genitalia, and probably small size. Primitive characters include antennae with a distinct 3-segmented club, presence of wings in some genera, 10-striate elytra in some genera, and long tibial spurs.

Doyen & Lawrence (1979) state: 'Eventually it may be necessary to redefine the Lachnogyini to include Cnemeplatiini'. In Lachnogyini the antennae are considerably longer than the width of the head, the 3-segmented club is less distinct, the clypeus is not deeply emarginate anteriorly, the eyes are very short horizontally, elongate vertically,

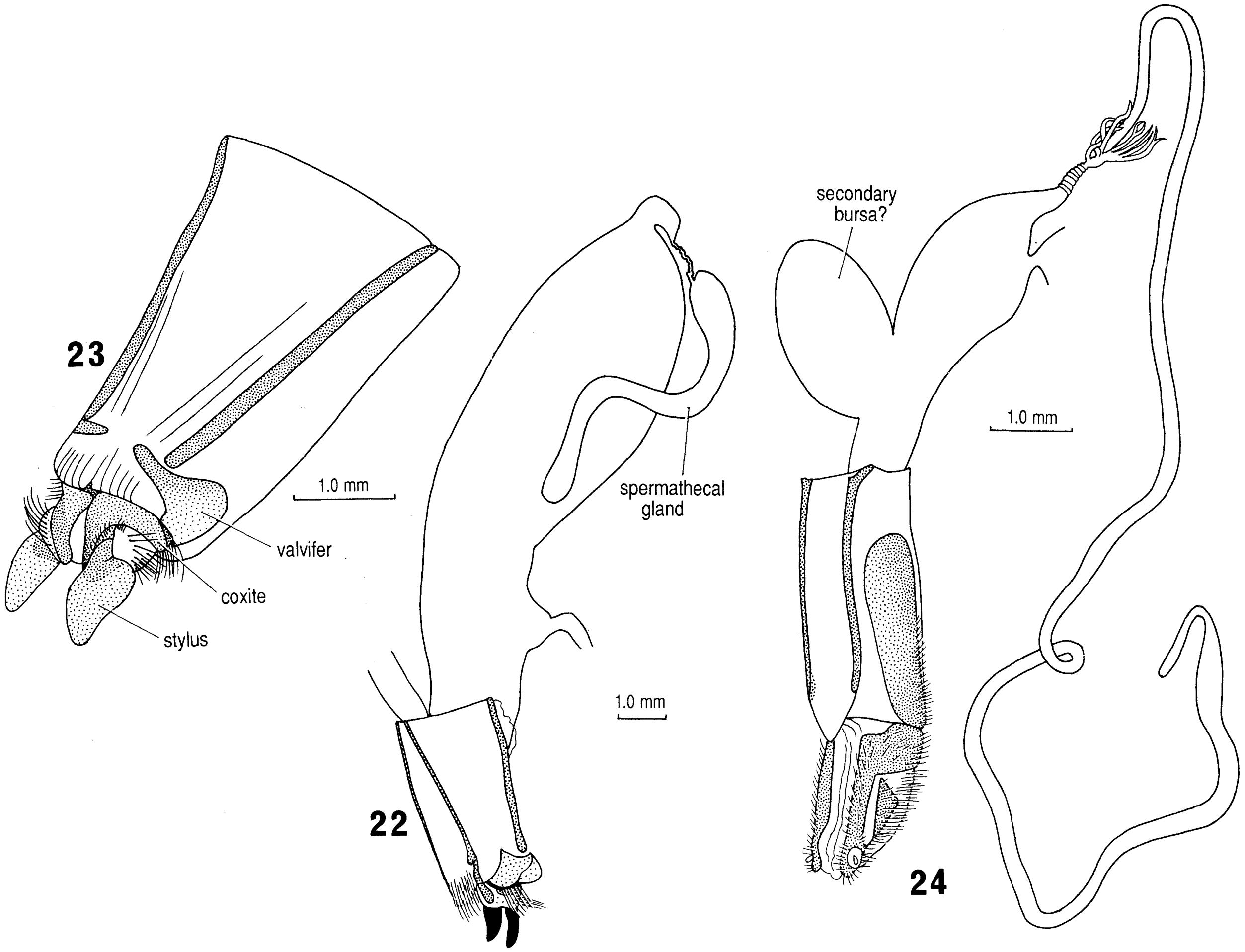


Figs 17–21. Female genitalia. 17, *Thorictosoma* sp.aff. *tibialis*, dorsolateral; 18, *Cnemeplatia indica*; 19, *Actizeta albata*, ventral; 20, *Lachnogya squamosa*, lateral; 21, *Idisia ornata*, ventral (ovipositor dorsolateral).

and encroached on by the canthus, the pronotum is widest at about mid length, and the legs are less modified for digging. In the female genitalia there is a well developed, apically strong sclerotized ovipositor, and internally a spermatheca comprising 8 convoluted, apparently unbranched tubules opening separately into the duct from the sausage-like spermathecal accessory gland to the bursa (Fig. 20). The wing of *Lachnogya* has a large subcubital fleck, otherwise unknown in Pimeliinae. This combination of characters is sufficient to exclude Cnemeplatiini from Lachnogyini. The two tribes do share many characters, and may have a more recent common ancestry than most of the rest of the Pimeliinae.

Medvedev (1973) established a tribe Idisiini for *Idisia* Pascoe, which he considered to be related to Lachnogyini. *Idisia* is the only known genuine tenebrionid outside the Zolodininae with externally open procoxal cavities, and is thus, at least in that respect, primitive. Idisiini agree with Cnemeplatiini in the strong 3-segmented antennal club, prominent, large, broadly oval eyes, elongate mandibles with reduced mola, mesocoxae with cavities closed by sterna and no trochantins, and 10-striate elytra with alternate intervals costate, as in Cnemeplatiina. In the female the ovipositor (Fig. 21) is reduced to lightly sclerotized curved plates, one dorsally and a pair ventrally; these represent respectively the proctiger and either paraprocts or coxites. The internal genitalia (Fig. 21) are simple and basically as in Cnemeplatiini.

The larva of *Idisia ornata*, described by Hayashi (1966), is basically similar to that of *Actizeta*, sharing such primitive characters as the presence of urogomphi and only 1 or 2 spiniform setae on the labrum, clypeus, and membranous elevations of the mandibles. The epipharynx is similar in the two genera, although *Actizeta* lacks spiniform setae near the anterior margin on either side that are characteristics of *Idisia* and most other pimeliine larvae. The larval mandibles of *Actizeta* (see Fig. 29) are unlike those of *Idisia* or any other known pimeliine larva. *Actizeta* is the only pimeliine known to me with a 2-segmented maxillary palp and without a hypopharyngeal sclerome in the larva (although the sclerome of *Idisia* is small). The legs of the two genera resemble each other, and differ from other known tentyrioid larvae in their claws, which are not finitely divided into a strongly sclerotized apical



Figs 22–24. Female genitalia. 22, *Pimelia cribra*, right lateral; 23, *P. cribra*, ovipositor, ventral (slightly oblique); 24, *Akis acuminata*, lateral.

lobe and weakly sclerotized base (see Fig. 31). The simple spiracles of *Actizeta* (see Fig. 34), lacking a filter or closing apparatus, may be unique for Pimeliinae; unfortunately Hayashi (1966) does not describe the spiracles of *Idisia*.

Some characters of the *Actizeta* larvae which seem *a priori* to be primitive are possibly derived from and related to its small size, e.g. the simple spiracles and absence of a hypopharyngeal sclerome. However, I have no doubt that the larvae of *Idisia* and *Actizeta* are the most primitive tentyrioids described so far. *Akis* larvae have projections that are probably urogomphi (Marcuzzi & Rampazzo, 1960), but do not otherwise resemble *Idisia* and *Actizeta*. That these primitive tentyrioid larvae are not closer to larvae of other soil-inhabiting Tenebrionidae ('Blapimorpha', Omophlini, Helaeini) than are the most advanced forms, but instead are closer to primitive forms inhabiting fungus and dead wood, confirms the opinion of Watt (1974b) and other recent workers that the tentyrioid lineage is not derived from any other soil-inhabiting group.

On present knowledge it is a reasonable hypothesis that Idisiini and Cnemeplatiini are sister-groups. The adults, however, are superficially different, for example in size, but these differences do not preclude them from being sister-groups. Further work is necessary to establish their relationships. As Cnemeplatiini is the only tribe of Pimeliinae occurring in Australia and New Zealand, one would expect it to be one of the most primitive tribes; and this is true on larval characters. In the adult, however, there are several obvious apomorphies in the deeply emarginate clypeus, 'closed' mesocoxae without trochantins, legs adapted for digging, absence of ovipositor, and simple internal female genitalia. These characters are probably all adaptive to life in dry sand and loose sandy soil, in which substrate the eggs are deposited directly while the female is digging.

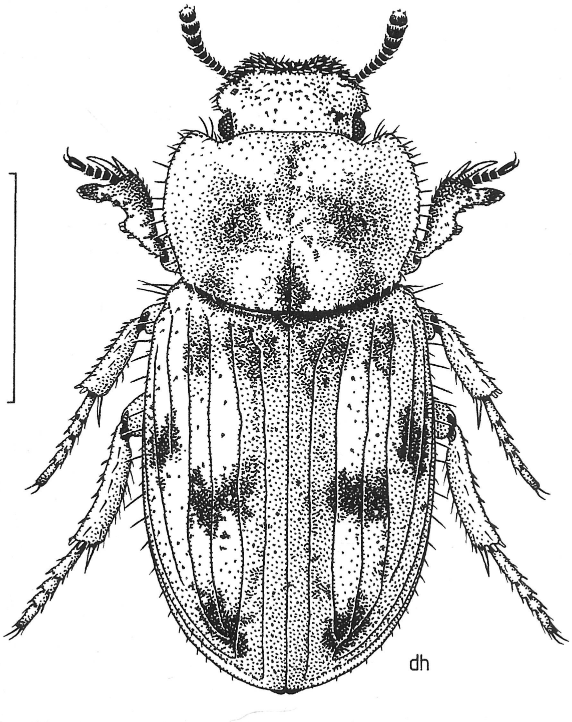


Fig. 25. *Actizeta albata* (Tahuna, Nelson), habitus, ×15. Artist: Des Helmore. Scale bar = 1 mm.

It seems that *Idisia* and Cnemeplatiini represent an early, specialized offshoot from the ancestral tentyrioid, which can be expected to have had antennae with a loose 3-segmented club, non-emarginate clypeus, circular or oval eyes, fusiform maxillary and labial palpi, small mentum, open procoxal cavities, 'open' mesocoxal cavities reached by the mesepimera, 10-striate elytra with epipleura well marked and extending to the apex, wings with full venation and a subcubital fleck, long, slender legs with moderate tibial spurs and without specializations for digging, abdominal ventrites hinged medially, with intersegmental membranes concealed, aedeagus inverted, ovipositor simple, well developed, elongate, with broad paraprocts and small styli, and internal genitalia probably not unlike those of *Lachnogya* (Fig. 20) or possibly *Pimelia* (Fig. 22; and see below). The larva was probably not unlike that of *Idisia*.

Female genitalia of relatively few Pimeliinae have been described and illustrated so far. Watt (1974b) illustrated *Tentyria schaumi*, and Tschinkel & Doyen (1980) examined ten species, summarizing their findings with the observation 'All tentyrioids . . . as in lagriines'.

In addition to the female genitalia of genera already discussed (*Actizeta*, *Thorictosoma*, *Cnemeplatia*, *Lachnogya* and *Idisia*) I have illustrated *Pimelia cribra* (Figs 22, 23) and *Akis acuminata* (Fig. 24), as Pimeliini and Akidini have primitive somatic characters. Considering only these genera and *Tentyria*, the following character states are probably primitive: ovipositor well developed (*Lachnogya*, *Pimelia*, *Akis*, *Tentyria*); paraprocts broad sclerotized plates (*Akis*, *Tentyria*); styli small, simple (*Akis*); internal genitalia complex, with multiple, bursa-derived tubular spermatheca and spermathecal accessory gland (*Lachnogya*, *Akis*) and no secondary bursa (all except *Akis*). There is unlikely to be disagreement over the ovipositor characters, but regarding internal structure it could equally well be argued that the simpler bursa-derived spermathecal gland (*Actizeta*, *Cnemeplatia*, *Pimelia*, *Tentyria*) is primitive.

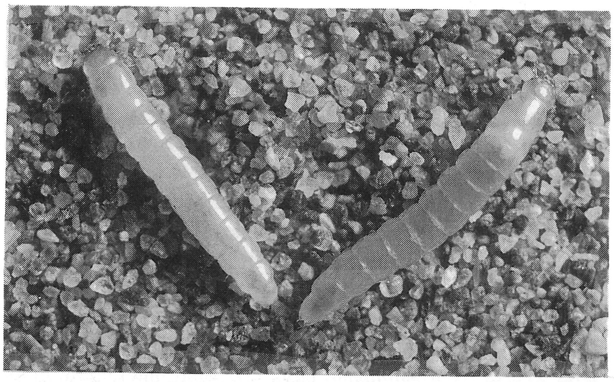


Fig. 26. *Actizeta albata* larvae (Pines Beach, Kaiapoi).

Study and illustration of female genitalia of many more tribes of Pimeliinae is needed to resolve this question.

Idisiini and Cnemeplatiini with female genitalia lacking functional ovipositors could not be directly descended from the ancestors of the large number of tentyrioid tribes with closed mesocoxal cavities but also with a well-developed ovipositor and a more complex female internal tract. It seems most likely that Idisiini/Cnemeplatiini are part of a lineage independent of the vast majority of tentyrioid tribes with closed mesocoxal cavities.

Although the adult of *Idisia* has open procoxal cavities as in Zolodininae, its larva does not show any special resemblance to that of *Zolodinus* (cf. Watt, 1974b). Doyen & Lawrence (1979) questioned the sister-group relationship between Zolodiniinae and Pimeliinae proposed by Watt (1974b). In Doyen & Tschinkel (1982) the tribes Pimeliini, Tentyriini and Zolodinini aggregate in all analyses. On adult characters *Zolodinus* differs little from the hypothesized tentyrioid ancestor, but its larva has features improbable for an ancestor of any known tentyrioid larva. Discovery of larvae of other primitive Pimeliinae and the other zolodinine genus, *Tanylypa*, may help to resolve this apparent incongruity.

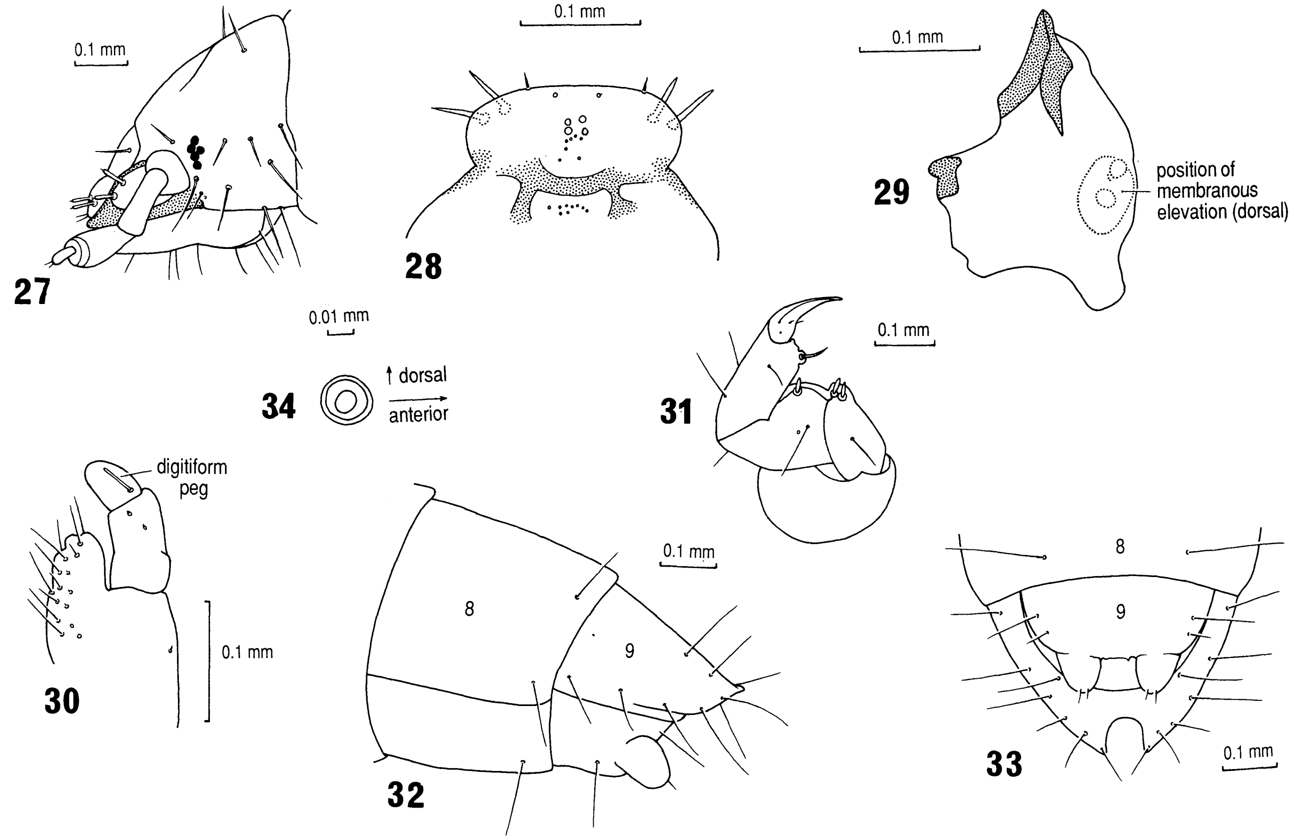
Species of *Cnemeplatia*, *Lepidocnemeplatia*, and *Philhammus* (=*Psilachnopus*) have been reviewed and keyed by Kaszab (1938, 1966, 1967). The key to Cnemeplatiini (below) is partly based on these papers. Perhaps *Philhamellus* Kaszab, 1962, established as a subgenus of *Philhammus*, should be raised to generic rank, but this requires further study.

Key to subtribes and genera of Cnemeplatiini

1 Mentum very large, oval, concealing almost all of mouthparts from below. Eyes vestigial. Prostheca of mandible very small; mola strongly developed. Elytra glabrous, with a single lateral stria in addition to the marginal stria. Female genitalia as in Fig. 17, with bursa functioning as a spermathecal gland. Australia .. subtribe Thorictosomatina (comprising the single genus *Thorictosoma* Lea, 1919)

– Mentum small, trapezoidal, not concealing mouthparts from below. Eyes well developed. Prostheca of mandible larger; mola weak (e.g. Fig. 11). Elytra not glabrous, bearing scales and/or setae, 8- or 10-striate (striae sometimes completely obscured by vestiture). Female genitalia with a small spermathecal gland attached at or near apex of bursa (Fig. 19) 2

2 Elytra with 8 clearly visible striae (the 5th short). Mandibular mola well sclerotized; membranous postmolar appendage present (Fig. 11). Aedeagal tegmen with apicale much longer



Figs 27–34. *Actizeta albata*, larva. 27, head, lateral; 28, epipharynx; 29, left mandible, ventral; 30, maxilla, dorsal; 31, front leg; 32, terminalia, lateral; 33, same, ventral; 34, second abdominal spiracle.

than basale (Fig. 9). Sternite 8 of male with a deep, almost circular excision (Fig. 9). New Zealand ... subtribe Actizetina (comprising the single genus *Actizeta* Pascoe, 1875)

– Elytra 10-striate, or striae completely obscured by dense, recumbent, scaly vestiture. Mandibular mola very weakly sclerotized; postmolar appendage absent. Aedeagal tegmen with apicale not longer than basale (Fig. 16). Sternite 8 of male at most emarginate (Fig. 16) ..... subtribe Cnemeplatiina . 3

3 Tibial spurs of middle legs long, stout, not much tapered, as long as tarsal segments 1 + 2. Tibial spurs of hind legs also long, stout, and not much tapered. Palaearctic, Guinea, Chad .... *Philhammus* Fairemaire, 1870

– Tibial spurs of middle legs slender, strongly tapered, sharp-pointed, shorter than tarsal segments 1 + 2. Tibial spurs of hind legs also strongly tapered and sharp-pointed 4

4 Body densely clothed with thick, scaly setae, usually completely concealing striae, which are evenly spaced with flat intervals. Basal segment of middle tarsus as long as segment 2. Nearctic, Neotropical, and Oriental regions .... *Lepidocnemeplatia* Kaszab, 1938

– Body not densely clothed with thick, scaly setae; striae clearly visible, with alternate intervals costate. Basal segment of middle tarsus shorter than segment 2. Palaearctic and Ethiopian regions .... *Cnemeplatia* Costa, 1847

Genus *Actizeta* Pascoe

Pascoe, 1875: 214; Broun, 1880: 359; Watt, 1965: 24.

Type species: *Actizeta ammobioides* Pascoe, 1875 (=*albata* Pascoe, 1875; see Watt, 1965: 24).

Adult (Fig. 25) oval, convex, dark brown; fresh specimens completely clothed with predominantly pale sessile scales, with some reclined elongate scales and erect bristles, especially laterally. Antenna as in Figs 5, 6. Labrum transverse, largely concealed by clypeus; apex arcuately emarginate, with a dense fringe of small bristles. Anterior margin of clypeus deeply emarginate (Fig. 25), continuous with canthus, the whole margin covered dorsally very densely with large, stout, blunt bristles inclined backwards. Eye medium or small, almost circular, situated mostly above level of canthus. Epipharynx transverse, with 2 longitudinal patches of fine setae near disc and sensory pits as indicated in Fig. 10. Medial arms of tormae projecting inwards. Mentum transverse, trapezoidal.

Pronotum transverse (Fig. 25), convex; surface minutely mamillate; anterior angles rounded, and posterior angles obtuse, not prominent but distinct; lateral margin with a row of stout bristles just above it and another just below. Prosternum with a few median bristles in front of intercoxal process, which is narrow, convex, and broadened between coxae. Scutellum small, triangular. Elytra convex, oval, little broader than pronotum; shoulders rounded; epipleural carina rounded, indistinct; epipleura consequently poorly defined, broad at base, narrowed to about one-quarter of length then continuing as a narrow, indistinct inflection almost to apex, bearing a row of bristles, these long and stout anteriorly, much smaller posteriorly. Elytra with 8 distinct striae in proximal half; striae 1–4 complete from base almost to apex, s3 joining s4 and s4 joining s2 on hind slope, s5 short and extending from shoulder almost to mid-length, s6 and s7 beginning progressively further behind shoulder, s8 (marginal) complete from base almost to apex; scutellary strioles absent. Hindwings absent. Mesosternum weakly depressed anteriorly; intercoxal process rather narrow, with a median depression; coxae separated by much less than their own diameter. Mesosternum short, little longer between coxae than the length of a coxa, with a deep median longitudinal sulcus and with deep, somewhat irregular curved grooves behind and parallel to hind margins of mesocoxae. Hind coxae fairly strongly transverse. Metendosternite (see Fig. 12) with a very short stalk and widely diverging arms, but without laminae.

Front legs approximately as in Fig. 13; outer margin of tibia only weakly emarginate in an undescribed species. Middle and hind legs with tibiae much less strongly expanded apically, bearing spinose bristles on all surfaces; tibial spurs spinose. Basal and apical segments of middle tarsus almost equal, segments 2–4 much shorter; basal segment of hind tarsus about 50% larger than apical segment, which is as long as segments 2 and 3 together; apex of each tarsal segment bearing a ring of spinose bristles.

Abdominal sternite 3 with intercoxal process rounded and depressed anteriorly; hind coxae slightly more separated than middle coxae; sternites 4s and 5s about equal in length, 6s much shorter, 7s slightly longer than 4s or 5s (somewhat foreshortened in Fig. 9). Segment 8 and aedeagus as in Fig. 9; aedeagus almost flat; sternite 8 with a deep, almost semicircular excision of posterior margin. Female genitalia as in Fig. 19.

Size range 2.1–3.5 × 1.0–1.7 mm.

Larva (based on *Actizeta albata*; Fig. 26) moderately elongate, slightly depressed, very slightly sclerotized, white or pale cream except for dark brown mandibles, medium brown claws, and black ocelli.

Antenna glabrous, with segment 2 slightly longer and much thicker than segment 1 (foreshortened in Fig. 8); sensorium at end of segment 2 an almost complete ring with a small vertical gap; segment 3 small, with 2 minute apical setae. Labrum oval, transverse, with 2 very stout setae on either side of disc and a pair of fine setae on anterior edge (Fig. 8). Clypeus with a seta on either side near lateral margin (Fig. 8). Frontal sutures and epicranial suture faint, Y-shaped. Ocelli contiguous, arranged as an anterior row of 3 and a posterior row of 2 (Fig. 27). Base of mandible contiguous with basal membrane of antenna. Epipharynx as in Fig. 28. Mandibles (Fig. 29) with a single apical tooth and well sclerotized dorsal and ventral cutting edges, the former projecting into a weak dorsal tooth near base; mola well sclerotized but small; mandibles each with a small dorsolateral membranous elevation (Fig. 29) bearing a pair of very stout, blunt bristles. Maxilla almost glabrous except for fairly sparse setae on inner surface (Fig. 30), with oblique cardo, oval articulating area, rounded mala, and 2-segmented palp (segments 1 and 2 fused); terminal segment of palp facing a single digitiform peg on outer part of dorsal surface. Ligula moderately developed; labial palpi 2-segmented. Hypopharynx without a sclerome.

Pronotum with a long seta near each anterior and posterior angle; meso- and metanota with a long dorsolateral seta on either side posteriorly. All thoracic segments with several long, fine ventrolateral setae and several other long, fine setae ventrally. Postcoxales of prothorax (see Watt, 1974b, fig. 87, for terminology) large and swollen, those of meso- and metathorax much smaller; intersternites between pro- and mesothorax and meso- and metathorax projecting strongly, each bearing several long setae. Front legs much larger and stouter than other legs, the femora almost twice the diameter of middle and hind femora; spinose bristles and setae as indicated in Fig. 31; middle and hind legs with a spinose bristle on inner surface of trochanter, 3 on femur, and 3 on tibia, in addition to some fine setae. Just above base of each front coxa is a diagonal oval opening in membrane between head and prothorax, leading into a moderately sclerotized, large, narrow endopleuron, approximately rectangular in outline, projecting towards midline of prothorax (see Fig. 2).

Abdominal tergites 1–7 glabrous dorsally, with a long seta on either side near posterior margin; tergite 8 with an additional pair of dorsolateral setae (Fig. 32); distinct laterotergites absent. Sternites 1–8 with a pair of long setae on either side; basal sternite with some shorter setae as well. Tergite 9 ending in 2 small urogomphi, separated by a semicircular excision (Fig. 33). Sternite 9 convex, transverse, with a pair of long lateral setae (Fig. 33). Sternite 10 represented by a pair of pygopods, each bearing 2 small setae. Thoracic spiracle oval, simple; abdominal spiracles (Fig. 34) with a circular peritreme, simple, with no filter apparatus or any discernible closing apparatus.

Length (in alcohol) up to 4.5 mm; maximum head width 0.6 mm.

Remarks. The two known species of *Actizeta* live on coastal sand dunes. *A.albata* is found particularly under and near the most seaward vegetation on foredunes, whereas the other (undescribed) species tends to occur further back. Gut contents seem to be plant material, presumably mostly dead. The undescribed species occurs around the North Island and northern South Island of New Zealand. It seems to be quite variable both within and between populations, and requires further study. *A.albata* extends much further southwards, but has not been found in the far south.

Actizeta albata Pascoe

Pascoe, 1875: 215, pl. 5, figs 5, 11, 11a; Broun, 1880: 360; Hudson, 1934: 85; Watt, 1965: 24 (syn. *ammobioides*). *Actizeta ammobioides* Pascoe, 1875: 215; Broun, 1880: 359–360.

Type material in the BMNH has been examined, and lectotypes have been designated (see below). In this genus specimens cannot be sexed reliably on external characters. As I believe that primary types should not be dissected unless it is essential for purposes of identification, they have not been sexed.

Lectotype of *albata*: 'Type [printed, in red circle]/ Waikato, N. Zealand [Pascoe, on oval lemon-tinted label]/Actizet albata type Pasc. [Pascoe]/Pascoe Coll. 93-60 [printed]/LECTOTYPE, *Actizeta albata* Pascoe, det J. C. Watt, 1965'. *Paralectotypes* (3), all bearing Pascoe Coll. labels and labelled as from either Waikato or New Zealand (2). Although the data on the paralectotypes is scanty, they are mounted identically to the lectotype on very small pieces of card, and are clearly members of the series on which Pascoe based his description.

Lectotype of *ammobioides* – left-hand specimen of two mounted on a single card: 'Type [printed, in red circle]/ NZ, Gt Barrier Id. [Pascoe, on oval lemon-tinted label]/ Actiz. ammobioides Type Pasc. [Pascoe]/Pascoe Coll 93-60 [printed)/LECTOTYPE (left-hand spec.) *Actizeta ammobioides* Pasc. (=*albata*) det. J. C. Watt, 1986'. *Paralectotype* – right-hand specimen mounted on its back on same card as lectotype.

Material examined. Adults: NEW ZEALAND (BMNH), many specimens, from Spirits Bay in the far north to mid Canterbury. *Larvae*: NEW ZEALAND, North Canterbury, Kaiapoi, Pines Beach, 1 Dec 1974 (J. C. Watt), ex loose, dry sand, 8 larvae (3 cleared, on slides, 1 dried and coated on SEM stub) associated with 15 adults. In this area only *A.albata* is known to occur. Essentially similar larvae from more northerly localities could include examples of undescribed species known to occur there.

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