

CLASSIFICATION OF THE ELATERIDAE (COLEOPTERA)**Relationships and classification of the subfamilies and tribes**By Jeffrey N. L. Stibick¹

Abstract: Keys and diagnostic descriptions are given for each subfamily and tribe of the Elateridae. Postulated phylogenetic relationships of the subfamilies are briefly discussed and charted, and a synthesis of adult and larval characters is given. The Sericosomina, Hypodesites and Cardiorhinites are synonymized under the Elateridae proper. The Campsosterninae are reduced to tribal status (Campsosternini, new status) under the Oxynopterinae. The Rostricephalini and Pectocerini are moved from the Oxynopterinae to the Pityobiinae. Within the Pyrophorinae, the fossil Protagrypnini are expanded to include the fossil Hynomorphina (= Hynomorphini), new status and the Desmatina (= Desmatini), new status here reduced to subtribal status within the nominate Protagrypnina. The Tetralobini are treated as a tribe with the nominate subtribe and the included Piezophyllina, new status reduced to subtribe. The Athoomorphinae are reduced to a tribe (Athoomorphini, new status) under the Oestodinae. A new subfamily, the Aplastinae, is established for a number of genera left without names by the removal of the Plastocerinae, now Plastoceridae, to the Cantharoidea by Crowson (1972). A new tribe, the Sphaenelaterini, is erected in the Oestodinae to contain certain extant and fossil species hitherto difficult to place. The Hemioptinae are reduced to synonymy under the Oestodinae. The tribal name Prisahypini, a nomen nudum, is validated herein to allow its use in this paper. The generic names *Prisahypnus*, *Insulahypnus* and *Australeus* are likewise validated by fixation of the type species of each.

This paper is the first of a series on the Elateridae and establishes a framework for subsequent articles. The comparatively unsettled state of the taxonomy of the higher taxa makes it impossible to produce a paper of this nature to which all parties will agree in every detail. One problem has been the tendency of various authors to treat many, if not most higher taxa (subtribes, tribes, subfamilies) as subfamilies of equal rank. This has resulted in a division of the Elateridae into as many as 44 subfamilies. For a number of reasons, including purposes of reference and classification, this arrangement has not been satisfactory. The rationales for the present concept are found in Hyslop's 1917 paper on the phylogeny of the Elateridae, Gurjeva's 1969 paper on some trends in the evolution of click beetles and her later 1974 work on the thorax of click beetles along with a proposed classification, Crowson's 1961 paper on new characters of classificatory importance, and more importantly, Ôhira's basic 1962a study on the larvae; the authors tended to recognize a comparatively small number of subfamilies with tribes inclusive. This trend is followed in the present work, and the resulting classification, which rests on a synthesis of adult and larval characters, is fundamentally conservative.

An outline of the subfamilies and tribes recognized in this paper, showing on one side adult characters and on the other larval characters, all linking the various taxa,

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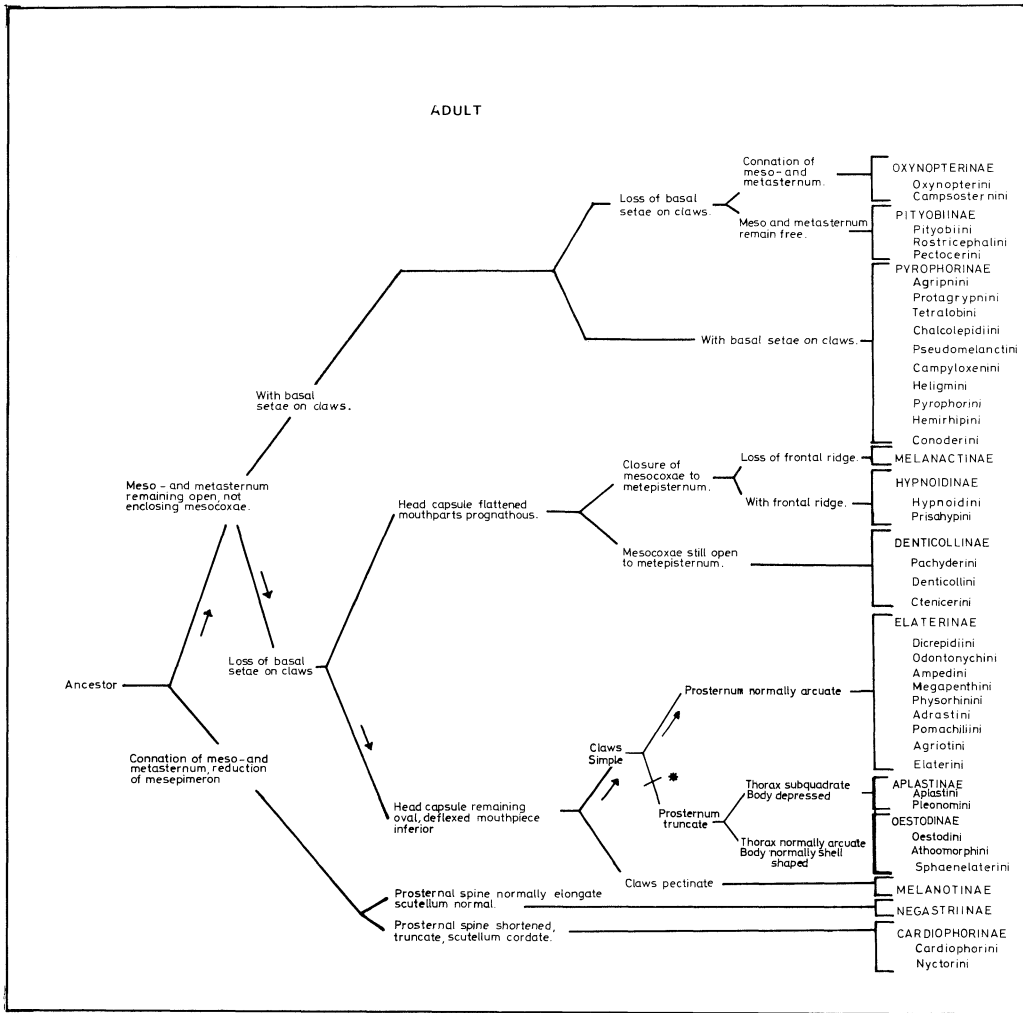
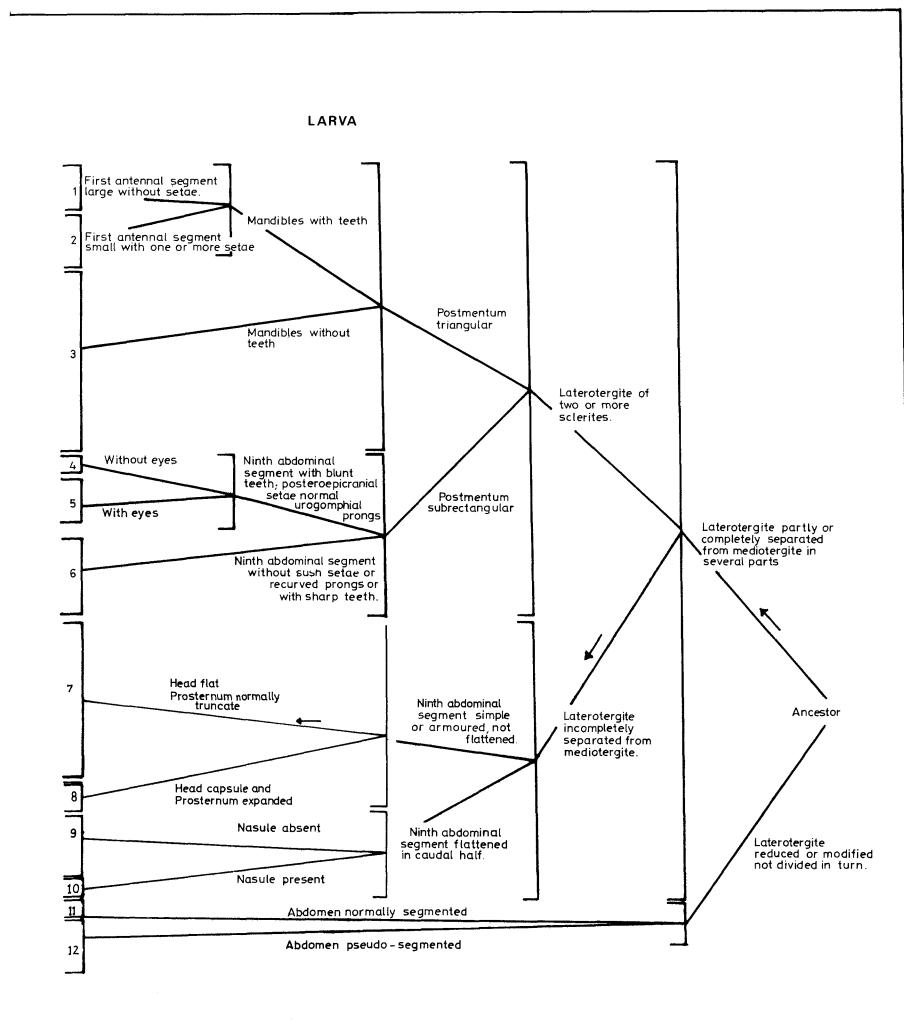


FIG. 1. Phylogenetic chart of the Elateridae showing adult characters on the left half and larval characters on the right half. Arrows represent the probable direction of basic elaterid stock. The asterisk (*) stands for the divergence of Throscidae, Cerophytidae, Eucnemidae and Cebrionidae. Primitive character states are as follows. *Adult*: mesocoxae open to mesepimeron and mesepisternum, mesepimeron of comparable size to mesepisternum: setae present at base of claws; head capsule more or less oval, deflexed, mouthparts inferior, frons simple, without carina above or between

is shown in FIG. 1. Agreement between the 2 sets of characters would help to produce the best possible comparative relationship of the taxa. While this has been attempted, there are some points of disagreement, chiefly in the degree of relationship.

It is unfortunate that the larval stages of most elaterids are unknown and that known forms are mostly from Europe and North America. Gaedike (1969) has published a valuable bibliography of the literature on the larvae (355 species) known to



antennae; prosternal spine elongate; scutellum shield-shaped; prosternum normally arcuate, covering mouth-parts. *Larva*: laterotergite part of mediotergite, spiracle undeveloped, small and embedded in mediotergite; 9th abdominal segment simple, normally ovoid, without ornamentation, caudal notch, prongs, flattening, etc.; abdomen normally segmented; postmentum subrectangular; eyes present; galea 2-segmented; head cylindrate; mandibles simple, with single point and with teeth; prosternum undivided.

date. These, plus a few additional records, come from every subfamily recognized here and 28 of the 53 tribes and subtribes, but of the species, the majority are in the Denticollinae and Elaterinae. For the above reasons a larval diagnosis is provided for each subfamily only, as tribal descriptions may prove to be in error and should await the definitive tribal placement of the genera.

The background to the following discussion on relationships and classification is

provided by Dolin (1968) who postulated the origins of the family as somewhere between the Triassic and Miocene eras as a result of his studies on adult wing variation, larval structures and fossils. More recently Dolin (pers. commun.) has changed this probable time of origin to coincide with the Lower Jurassic.

The most important adult characters on which the classification presented herein is based are (1) the arrangement and size of the plates surrounding the mesocoxal cavity; (2) the basal setae of the claws; and (3) the shape of the head and consequent position of the mouthparts. The most important larval characters are (1) the separation, breakup or reduction of the laterotergite; (2) the various modifications of the 9th abdominal segment; and (3) the shape of the postmentum. Additional larval characters which help distinguish subfamilies are (a) sensory appendices present on 2nd antennal segment, spiracle separate from mediotergite and with spiracular sclerite; (b) circular sensory appendages present on 2nd antennal segment, spiracle as in (a); (c) spiracle as in (a), spiracular sclerite may be reduced; (d) prosternum complete, not divided, spiracle as in (a), may be variously placed from laterotergite; (e) prosternum divided, spiracle as in (d); (f) spiracle as in (d); (g) spiracle embedded in mediotergite; (h) head corrugated transversely on dorsum; (i) nasule absent or greatly reduced, spiracle as in (g); (j) nasule present, spiracle as in (g); (k) head depressed, mandible single, galea 1-segmented, caudal notch present, spiracle small, no spiracular sclerite, fitting within laterotergite; (l) head cylindrical, mandible cleft, galea 2-segmented, no caudal notch, spiracle as in (k) but with lateral ambulatory papilla.

In FIG. 1 four basic subdivisions of the family can be seen when either adult or larval characters are considered. The oldest subdivision leads to the Negastrinae-Cardiophorinae lineage. On larval characters, Ôhira (1962a) postulated that the Cardiophorinae should constitute a distinct family in its own right. I disagree, because the adult form has closed metacoxae with reduced mesepimeron similar to the Negastrinae, possesses the ability to click, and is elateriform in all particulars. Its chief unique features are a truncate prosternal spine and a (usually) cordate scutellum. The larva is unusual, but all the modifications seem to be specialized adaptations as a consequence of long evolutionary separation. A few primitive features remain, such as the unsclerotized 9th abdominal segment, which, except for the anal lobes, is quite uncomplicated and not too unlike the 9th segment of the Elaterini, and the simple, divided laterotergite upon which pseudosegmentation has been imposed.

The Negastrinae are associated phylogenetically with the Cardiophorinae in this paper. This is based on the adult having the same arrangement of sclerites grouped around the mesocoxal cavity with a reduced mesepimeron, and the larva having a single but reduced laterotergite. It may seem that the mesocoxal characters just noted are not significant because they occur in certain Pyrophorinae, but as in the case of *Lanecarus* Ôhira (Agriotini), the mesepimeron is not reduced in size and the simple connation of the sterna appears to be a separate development which has appeared in different groups at different times. Again, the single negastrine laterotergite seems to show a relationship to those groups with 2 (or 3) separate, reduced fragments.

This reasoning would then place the negastrines near the Denticollinae lineage (postmentum subrectangular; head capsule of adult flattened). However, I notice that the spiracle of the Denticollinae lineage is generally well developed, large, distantly placed (though sometimes close) from the laterotergite and with its own spiracular sclerite. That of the negastrine is small and not developed, is fitted within a concavity of the laterotergite and is without any spiracular sclerite. The laterotergite of the *Cardiophorinae* is also shaped to hold a small, undeveloped spiracle (plus a special, lateral, ambulatory papilla). The *Pyrophorinae* lineage is similar to the Denticollinae lineage except that the spiracular sclerite is often reduced to a vestigial remnant and the spiracle is sometimes underdeveloped. In the *Elaterinae* lineage the spiracle (usually well developed) is still embedded in the mediotergite. There is also evidence, incomplete to be sure, that the bifurcate male parameres found within both the negastrines and *cardiophorines* are unique to them. These parameres are known for *Negastrius* and *Zorochrus* on the one hand and for *Cardiophorus* and *Dicronychus* on the other (e.g., Leseigneur 1972, save that in *Negastrius*, plate 25, p. 114, the parameres should have shown details of the apical section, much as given for *Zorochrus* in plate 27, p. 121). Another structure, the form of the 9th abdominal segment, especially the caudal notch and prongs, is a feature peculiar to the negastrine and probably only analogous to the other groups whose 9th segment also possesses a caudal notch and prongs. Finally, the 1-segmented galea is a distinctive development not found elsewhere and indicates an ancient ancestry.

In FIG. 1 it is implied from the adult schema that the Denticollinae stem arose from the *Elaterinae* stem, but from the larval schema we see that it would have arisen from basic *Pyrophorinae* stock. Part of this discrepancy may be due to differing rates of evolution and divergence in the larval and adult forms and partly to the absence of good "indicative" characters in adult elaterids.

The arrangement of the Denticollinae and *Elaterinae* lineages is in general agreement with that of Ôhira (1962a). It seems plausible that the *Elaterinae* lineage represents the ancestral elaterid stock and that the Denticollinae lineage diverged from it, or at an earlier time from the *Pyrophorinae* lineage as indicated by the larva. The flattened, prognathous head of the adult and the combination of a subrectangular postmentum and divided laterotergite of the larva distinguish the Denticollinae lineage. It is difficult to decide which of the 2 larval characters is the more important phylogenetically, but the presence of a spiracle with a spiracular sclerite also indicates a link to the *Pyrophorinae* lineage, as noted in FIG. 1. The subrectangular postmentum, of course, is a link to the *Elaterinae* lineage. These considerations also preclude placing the Denticollinae (in the strict sense Denticollina) as a separate family as suggested by Jagemann (1950) and disputed by Leseigneur (1972). Within the lines leading to the *Elaterinae*, *Aplastinae*, *Oestodinae* and *Melanotinae*, it is difficult to decide which division came first. However, the pectinate claws of the adult and distinctively plated and scalloped 9th abdominal segment of the larva seem to point to the *Melanotinae* as a specialized offshoot. The *Oestodinae* also seem to have devel-

oped some specialized characters, such as a truncate prosternum in the adult; prongs plus a notched, 9th abdominal segment and loss of the nasule in the larva. However, the facies of this group is not at all too different from that of the Elaterini, whose larvae by possession of a relatively simple 9th abdominal segment appear to be representative of ancient stock. Also, the adults of the Sphaenelaterini have not developed the profoundly truncate prosternum or approximate to contiguous mesosternal coxae of the more advanced oestoid tribes. Finally, the Aplastinae, on the basis of larval characters, seem to be a very close derivative of the Elaterinae, differing chiefly by the development of a greatly produced prosternum which covers the mouthparts, externally expanded mandibles and a transversely corrugated head. In FIG. 1 it is implied that the adult was derived from basic Oestodinae stock. This again may be due to differing rates of evolution and divergence in the larval and adult forms and absence of indicative characters in the adult as discussed for the Denticollinae-Elateridae divergence.

In the adult, the Denticollinae lineage seems to have been basically maintained, because the mesocoxae have remained open to the mesepimeron and mesepisternum, while various points separate the larva, which together indicate close relationships among the Denticollinae, Hypnoidinae and Melanactinae. However, differences between the Melanactinae and the others are such as to require further study.

The Pyrophorinae lineage, as indicated, is a basically ancient group which has for the most part retained an apparently archaic feature—a basal seta or basal setae on the claws. The larvae appear to be distinguished by the triangular postmentum, probably a more recent development (reduction of the subrectangular postmentum of other groups). The larvae are generally predacious and often rather specialized, e.g., the termitophilous *Oxynopterus* Hope and *Scaphoderus* Candèze (Kalshoven 1955). Loss of the basal setae and retention of the toothed mandibles in the larva distinguish the Pyrophorinae and the more generalized Oxynopterinae and Pityobiinae, which tend toward great elaboration and specialization in the adult. The schema separates the Oxynopterinae from the Pityobiinae by connation of the meso- and metasternal plates in the adult and by loss of setae and enlargement of the 1st antennal segment in the larva.

In the following pages, author citations are given in accordance with the International Code of Zoological Nomenclature under Articles 36, 39, 40 and 50. This includes retention of the date of a replaced name (Recommendation 40A).

As it is felt that ample drawings for the characters mentioned will be found in the literature cited, drawings have not been provided in this paper. Ôhira (1962a) is a good reference for the larvae. Leseigneur's excellent 1972 monograph of the French Elateridae is useful for the adult characters mentioned.

CLASSIFICATION

The classification that follows recognizes 12 subfamilies. Nine of these are in turn subdivided to give 37 tribes. Five tribes are again divided to give 20 subtribes.

The keys provided herein serve as a guide to the subfamilies and tribes for the adult form. Descriptions of the adult are also provided down to tribal level. Keys and descriptions of the larval form are given only to subfamily. Synonymies presented list the original reference only for each name. Comments are made to give some indication of the status and size of each taxonomic group. Subtribes are only listed in this paper, as their limits remain imprecisely defined at present.

Family ELATERIDAE Leach, 1815

Elaterites Leach, 1815.

Ludiites Candèze, 1863.

Hypodesites Candèze, 1863. **New synonymy.**

Cardiorhinites Candèze, 1863. **New synonymy.**

Steatoderini Schwarz, 1906a.

Sericosomina Hyslop, 1917. **New synonymy.**

Adult. Body elongate; head with labrum visible and free, clypeus not distinct, maxillary palpi 4-segmented; antennae 11–12 segmented and near (not between) eyes and under frontal margin if 1 is present; thorax with globose front coxae, prosternum either truncate or more usually lobed in front, procoxal cavities lateral to a prosternal spine which is produced posteriorly and loosely received in a mesosternal fossa, prothorax freely joined to mesothorax and usually capable of rapid movement on basal joint which usually produces a jumping movement of the body, often with audible snapping noise; tarsi of 5 segments on all pairs of legs; abdomen with 5 (rarely 6) visible and usually separate and equally distinct sternites, the last 2 connected by a membranous suture.

Larva. Body straight, elongate and cylindrical; head with labrum fused with clypeus and anterior margin of frons into a nasule or labrum absent, maxillae and labium elongate and fused, frontoclypeal area usually lyre-shaped; thorax with legs present, well developed, subequal and 5-segmented; abdomen with 9 abdominal segments visible dorsally and 10th segment lying ventrad to 9th and enclosing anus, spiracles biforous.

KEY TO SUBFAMILIES OF ELATERIDAE—ADULTS

1. Mesocoxae open to mesepimeron and/or the mesepisternum, mesepimeron normal size *or* with setae on base of claws 2
- Mesocoxae closed to mesepisternum and a reduced mesepimeron by connation of mesosternum and metasternum; no setae on base of claws 10
- 2 (1).² Setae present at base of claws or mesosternum and metasternum connate *or* with luminous areas near pronotal hind angles *or* with deep grooves in the prosternal sutures for the antennae or anterior tarsi 3
- Setae absent from base of claws though possibly present elsewhere on claws; mesosternum and metasternum separated by distinct suture; no luminous areas near pronotal hind angles; prosternal sutures closed to open anteriorly, sometimes feebly depressed in shallow trough 4
- 3 (2).³ Claws usually with setae at base; mesosternum and metasternum either separate or connate **Pyrophorinae**

2. For the sake of conformity, certain taxa with nonsetate claws go to couplet 3. These are the Oxynopterinae, Campyloxenini, certain Agrypnini and perhaps the fossil Protagrypnini (claws unknown).

3. Pyrophorinae without setae have a separate meso- and metasternum. The *approximans* group of *Metablax* (Oxynopterinae) from New Zealand have a distinct suture. They appear to retain a smooth strongly raised central area of the meso- and metasternum characteristic of the Campsosterninae, but may be distinguished from other New Zealand elaters which key to this couplet by possession of an acutely pointed elytron.

Claws without setae at base, setae may be present between or on outside of claws; mesosternum and metasternum connate **Oxynopterinae**

4 (2).⁴ Head capsule flattened, prognathous 5
 Head capsule oval, deflexed 7

5 (4).⁵ Mesocoxae closed to mesepisternum by mesepimeron and mesosternum 6
 Mesocoxae open to mesepisternum or very rarely closed by sternal plates, in which case mesepimeron is of normal size **Denticollinae**

6 (5). Frons without ridge **Melanactinae**
 Frons with ridge **Hypnoidinae**

7 (4). Frons ridged at least over antennae, sometimes obsolete towards middle, or if ridge completely absent then prosternal lobe present, arcuate in front 9
 Frons without ridge between and above antennae, broadly rounded or strongly declivous, or carinate over antennal insertions at best; prosternum truncate 8

8 (7). Thorax normally arcuate (if depressed, then normally, evenly arcuate on sides), or globular or elongate and subcylindrical; body normally shell-shaped **Oestodinae**
 Thorax subquadrate or quadrilateral, rarely convex in front or middle depressed; body depressed, flattened **Aplastinae**

9 (7). With a thick and strongly protruding frontal pad between and above antennae or frontal ridge completely absent and antennal sockets strongly protruding above surface of frons; antennae bipectinate or pectinate in ♂, serrate in ♀; tarsi usually simple, without lobes, or rarely 4th is lobed, claws simple, with simple basal lobe **Pityobiinae**
 Without above combination of characters; frontal ridge various, often obsolete in middle or arcuate towards labrum, but if thick and protruding then 2 or more tarsal segments are lobed, claws simple to serrate; antennae serrate to pectinate in ♂, various in ♀ 10

10 (9). Claws simple to serrate, frontal ridge various, often obsolete in middle to thick and protruding **Elaterinae**
 Claws pectinate, frontal ridge usually prominent to more rarely obsolete **Melanotinae**

11 (1). Prosternal spine normally elongate; scutellum never cordate **Negastriinae**
 Prosternal spine short, truncate; scutellum usually cordate **Cardiophorinae**

KEY TO THE SUBFAMILIES OF ELATERIDAE—LARVAE

1. Laterotergite of 2 or more sclerites or incompletely separated from mediotergite 2
 Laterotergite of 1 separate sclerite 11

2 (1). Ninth abdominal segment with caudal notch 3
 Ninth abdominal segment without caudal notch or with 2 prongs 8

3 (2). Postmentum triangular 4
 Postmentum subrectangular 6

4 (3). Mandibles with teeth 5
 Mandibles without teeth **Pyrophorinae**

5 (4). Second antennal segment smaller than 1st, with sensory appendices; no setae on 1st segment **Oxynopterinae**
 Second antennal segment larger than 1st, with circular sensory appendages, at least 1 seta on 1st segment **Pityobiinae**

6 (3). Ninth abdominal segment with blunt teeth; urogomphial prongs normal; posteroepicranial setae present 7
 Ninth abdominal segment without posteroepicranial setae or with recurved urogomphial prongs or with sharp teeth **Denticollinae**

7 (6). Eyes absent **Melanactinae**
 Eyes present **Hypnoidinae**

4. Beware of unnaturally twisted heads in preserved specimens and of highly developed protruding frontal ridges which make the head appear flattened.
5. *Hypolithus littoralis* (Eschscholtz) has open mesocoxae. It is found under driftwood on North Pacific beaches (Hypnoidinae).

- 8 (2). Ninth abdominal segment simple or armored, not flattened in caudal $\frac{1}{2}$ 9
 Ninth abdominal segment flattened in caudal $\frac{1}{2}$ 10
- 9 (8). Prosternum normally truncate in front, not covering mouthparts; mandibles not produced externally **Elaterinae**
 Prosternum greatly produced in front, covering mouthparts; mandibles greatly produced externally **Aplastinae**
- 10 (8). Prongs and caudal notch present on 9th abdominal segment **Oestodinae**
 Prongs and caudal notch absent, 9th abdominal segment platelike, scalloped **Melanotinae**
- 11 (1). Abdomen normally segmented; caudal notch on 9th abdominal segment; galea 1-segmented **Negastriinae**
 Abdomen pseudosegmented; no caudal notch; galea 2-segmented **Cardiophorinae**

I. Subfamily OXYNOPTERINAE Candèze

Oxynopterides Candèze, 1857.

Adult. Head capsule more or less oval, deflexed, mouthparts inferior; antennae of ♂ long laminate or serrate, frons deeply foveate medially; pronotum explanately broadened and flattened, prosternum normally arcuate anteriorly, prosternal spine normally elongate, mesosternum and metasternum connate, suture indistinct or absent; mesocoxae open to mesepimeron and mesepisternum; elytra usually spinose and may be notched at apex, scutellum shield-shaped, never cordate; claws simple, without setae, but often with projecting onychium bearing setae between.

Larva. First antennal segment bare, no setae present, 2nd antennal segment smaller than 1st and with 1 or more sensory appendices, 3rd segment very small, length about $\frac{1}{2}$ that of 2nd; mandibles simple with teeth, nasule present, galea 2-segmented, postmentum triangular; lateral tergite of 2 sclerites, spiracule well developed and separate from mediotergite, with spiracular sclerite; 9th abdominal segment with caudal notch.

Two tribes, Oxynopterini and Campsosternini, are placed within this subfamily. This has been done to keep the superfamilial structure of the Elateridae on a manageable level by including in a subfamily those groups with broadly recognizable common characters. Thus the Campsosterninae, whose larvae are dentately toothed and have serrate antennae as described above and whose adults possess no visible suture between meso- and metasternum nor setae on the claws, are here reduced to tribal status. There are, of course, great differences between the 2 tribes, which are highly attributable to their ancient lineage. Three characters exist in the adult which are worthy of mention and which might or might not have some bearing on common ancestry. These are the explanately flattened and broadened pronotum with prominent sides and hind angles, the usually spinose elytral apex and the deeply foveate frons.

The definition of the Oxynopterinae presented here makes it necessary to remove the genera *Pectocera* Hope (Tribe Pectocerini) and *Rostricephalus* Fleutiaux (Tribe Rostricephalini) from this subfamily and place them in the Pityobiinae.

KEY TO THE TRIBES OF OXYNOPTERINAE

- Antennae of ♂ with long lamella; elytra of either sex more or less broad, without striae . . . **Oxynopterini**
 Antennae of ♂ serrate; elytra of either sex more or less gradually acuminate and pointed towards apex, striae present **Campsosternini, new status**

Tribe OXYNOPTERINI Candèze

Adult. Head capsule more or less oval, deflexed, mouthparts inferior; antennae of ♂ with long lamella, frons deeply foveate medially; pronotum explanately broadened and flattened, prosternum normally arcuate anteriorly, prosternal spine normally elongate, mesosternum and metasternum connate, suture indistinct or absent; mesocoxae open to mesepimeron and mesepisternum; scutellum shield-shaped, never cordate, elytra very broad to apex, nonstriate, notched and spinose at apex; claws simple, without setae; tarsi simple, without pads or lobes.

A small tribe of 4 genera and less than a dozen species at present. The best known genus is *Oxynopterus* Hope whose larvae have been reported as predacious on termites (Kalshoven 1955).

Tribe CAMPSOSTERNINI Fleutiaux, **new status**

Campsosterninae Fleutiaux, 1927.

Semiotinae Golbach, 1970 (nec Gurjeva, 1974, Semiotini).

Adult. Head more or less oval, deflexed, mouthparts inferior; antennae of ♂ serrate, frons deeply foveate medially; pronotum explanately broadened and flattened, prosternum normally arcuate anteriorly, prosternal spine normally elongate, mesosternum and metasternum connate, suture indistinct or absent; mesocoxae open to mesepimeron and mesepisternum; scutellum shield-shaped, never cordate, elytra acuminate to apex, striate, spinose and usually mucronate at apex; claws simple, without setae; tarsi simple or lobed.

The tribe contains 5 genera, with nearly 200 known species of which about ½ are in *Semiotus* Eschscholtz.

In 1974 Gurjeva (1974) named a new tribe, the Semiotini, unaware that Golbach (1970) had already employed that name for a subfamily. I moved *Campsosternus* Latreille into the Semiotinae of Golbach, recognizing Campsosterninae as the senior family-group name in a paper recently published (Stibick 1976a), but was unaware of Gurjeva's paper until after publication.

Calder (1976) included the New Zealand genus *Metablax* Candèze and provided a key to the species. Three of the 5 species in this genus possess a sternal suture, and in a 4th the sterna are completely separate. The 5th species has fused sterna.

II. Subfamily PITYOBIINAE Hyslop

Pityobiinae Hyslop, 1917.

Adult. Head capsule oval, deflexed, mouthparts inferior, antennae of ♂ long laminate or bipectinate, rarely dentate, of ♀ serrate to serrulate, frontal ridge a thick projecting pad or absent and antennal sockets are strongly protruding; prosternum normally arcuate anteriorly, prosternal spine normally elongate, mesosternum and metasternum distinct, joined by a definite suture; mesocoxae open to mesepimeron and mesepisternum; scutellum shield-shaped, never cordate; claws simple, without setae.

Larva. First antennal segment with 1 or more setae, 2nd antennal segment larger than 1st, without sensory appendices but with circular sensory appendages, 3rd segment minute, length from 1/6 to 1/5 that of 2nd; mandibles simple, with teeth, nasule present, galea 2-segmented, postmentum triangular; lateral tergite of 2 sclerites; spiracle well developed and separate from mediotergite, with spiracular sclerite; 9th abdominal segment with caudal notch.

There are 3 small tribes in this subfamily with 5 genera and 16 species. Although the number of species is very small, the tribes recognized here are readily distinguished from each other. They are thus best left as separate taxa pending detailed studies of their relationships. One remarkable unifying feature is the sexual dimorphism of the antennae, which is always more elaborate in the male.

KEY TO THE TRIBES OF PITYOBIINAE

1. Frontal pad present, projecting between and above antennae 2
 Frontal pad absent, antennal sockets strongly protruding **Pectocerini**
2. Fourth tarsal segment lobed **Rostricephalini**
 Fourth tarsal segment simple, not lobed **Pityobiini**

Tribe PITYOBIINI Hyslop

Adult. Head capsule oval, deflexed, mouthparts inferior, antennae of ♂ bipectinate, of ♀ serrulate, frontal carina a thick projecting pad; prosternum normally arcuate anteriorly, prosternal spine normally elongate, mesosternum and metasternum distinct, joined by a definite suture; mesocoxae open to mesepimeron and mesepisternum; scutellum shield-shaped, never cordate; tarsi simple, not lobed, claws simple, without setae.

The tribe contains 1 genus, *Pityobius* LeConte, with 2 species. *Metablax* Candèze belongs in the Campsosternini and not here as suggested by Gurjeva (1973), as the mesosternum and metasternum are connate. LeConte (1853) described the adults of both species. The larva of *P. anguinus* LeConte is figured in Hyslop (1917) and Jewett (1946).

Tribe ROSTRICEPHALINI Fleutiaux

Rostricephalinae Fleutiaux, 1947.

Adult. Head capsule oval, deflexed, mouthparts inferior, frontal carina a thick projecting pad; antennae serrate, expanded apically; prosternum normally arcuate anteriorly, prosternal spine normally elongate, mesosternum and metasternum distinct, joined by a definite suture; mesocoxae open to mesepimeron and mesepisternum; scutellum shield-shaped, never cordate; tarsal segments 2 and 3 thickened, 4th lamellate; claws simple, without setae.

The tribe is represented by 1 monobasic genus only. Originally placed in a separate subfamily by Fleutiaux (1947), the genus was reduced to tribal status within the Oxynopterinae by Gurjeva (1973). The tribe is now placed within the Pityobiinae to fit the definitions of these subfamilies as presented herein, especially as regards the suture delimiting the mesosternum and metasternum and the absence of setae at the base of the claws.

Tribe PECTOCERINI Gurjeva

Pectocerini Gurjeva, 1973.

Adult. Head capsule oval, deflexed, mouthparts inferior; antennae of ♂ long laminate to rarely compressed and dentate or subserrate, serrate in ♀; frontal carina absent and antennal sockets strongly protruding; prosternum normally arcuate anteriorly, prosternal spine normally elongate, mesosternum and

metasternum distinct, joined by a definite suture; mesocoxae open to mesepimeron and mesepisternum; scutellum shield-shaped, never cordate; tarsae simple, without lobes but 3rd and 4th segments may be feebly dilate, claws simple, without setae.

The tribe was established by Gurjeva (1973) for *Pectocera* Hope and *Ceroleptus* Fleutiaux. *Julodischema* Thompson, long associated with *Ceroleptus* but little known, must be added. These taxa contain 13 species in all. As with the Rostricephalini, the Pectocerini are placed in the Pityobiinae because of the presence of setae at the base of the claws.

Little is known about this tribe. Fleutiaux (1947) briefly discussed 3 of the 9 species of *Pectocera* and Ôhira (1962b) studied the larva of *Pectocera fortunei* Candèze.

III. Subfamily PYROPHORINAE Candèze.

Pyrophorites Candèze, 1863.

Adult. Head capsule variously developed, generally oval, deflexed, mouthparts inferior; antennae, frons and pronotum various; prosternal lobe normally arcuate, even prominent, prosternal spine normally elongate; mesocoxae may be open or closed to mesepimeron and mesepisternum; scutellum shield-shaped, never cordate; claws simple, with seta or setae at base, sometimes scattered setae elsewhere on claws.

Larva. Mandibles simple, without teeth on inner side, nasule present, galea 2-segmented, postmentum triangular; laterotergite of 3 sclerites; spiracule separate from mediotergite, well developed to somewhat reduced, with spiracular sclerite, this also may suffer reduction; 9th abdominal segment with caudal notch and no prongs, usually with prominent tubercles on dorsum, these absent only in the Conoderini.

This is a large, extremely varied subfamily which is consequently hard to define. Outside of a few exceptions, adults have at least 1 seta at the base of the claws. One such exception involves certain species in *Danosoma* Thomson and it seems probable that these species lost this character fairly recently, although there is as yet no formal study of their relationship to the other species in the Agrypnini.

Ten tribes are placed in the Pyrophorinae although most have been considered to be independent subfamilies by other authors at various times. Nevertheless, the diagnostic characters given seem to reasonably outline a subfamily which is sufficiently recognizable and distinct from the other subfamilies listed in this paper. The characters of the larvae also strongly indicate that this arrangement is feasible.

A good deal of work has been carried out by several authors on various Pyrophorinae tribes. Laurent (1967) published a summary on the Tetralobini with keys to what are here recognized as subtribes and to the genera. Arnett et al. (1969) provided keys to the North American genera of Pyrophorinae, while earlier Arnett (1952) presented a review of the North American Agrypnini. Costa (1975) presented a dissertation on the bioluminous tribes. The synonymization of the Hemirhipini under Pyrophorini by Arnett et al. (1969) has been reversed by Costa (1975), who is followed in this paper. Costa also established the tribe Heligmini to include most of the old nonluminous genera of the "Pyrophorini." A comprehensive treatise on the Agrypnini of the world was presented by von Hayek (1973).

Citation of the name Pyrophorinae (Pyrophorites Candèze, 1863) with the family-

group taxa herein presents problems, as it is not the oldest valid family-group name (cf Code, Article 23,d,i). The oldest name available is *Tetralobites* LaPorte (1840), followed by *Agrypnides* Candèze (May 1857), *Chalcolepidiides* Lacordaire (June 1857), and *Conoderini* Fleutiaux, 1919 (1859). However as presently used the accepted name is *Pyrophorinae*, with inclusion of all the tribes listed here. For the sake of stability this practice will be followed until such time as the exact ranking of the various taxa becomes settled. It should perhaps be added here that the next choice of a subfamily name in general usage which would preserve stability and universality in nomenclature is *Agrypninae*.

KEY TO THE TRIBES OF PYROPHORINAE

1. Antennae received in deep prosternal pleural grooves *or*, very rarely, prosternal pleural sutures grooved for reception of anterior tarsi 2
- Antennae not received in deep prosternal pleural grooves, the latter closed or open at front with shallow excavation at best 3
- 2 (1). Prosternum, mesosternum and mesepisternum all simple, without cross sutures of any sort **Agrypnini**
- Prosternum transversely sutured anteriorly; mesosternum divided by cross suture between mesosternal fossa and mesepisternum; mesepisternum also divided by cross suture **Protagyrypnini**
- 3 (2). Meso- and metasternum connate between mesocoxae, suture absent or indistinct **Chalcolepidiini**
- Meso- and metasternal suture distinct between mesocoxae 4
- 4 (3). Front a thick, projecting pad with transverse trough or vertical groove between eyes . **Tetralobini**
- Frontal carina either entire, relatively fine and sharp or absent 5
- 5 (4). Fourth tarsal segment lobed or broadened beneath; no luminous areas near pronotal hind angles; antennae 11-segmented **Conoderini**⁶
- Fourth tarsal segment as narrow as 3rd, or if (rarely) lobed, then with luminous spots near pronotal hind angles; antennae variably segmented 6
- 6 (5). Claws without setae at base; anal cell present in wings; with luminous areas on pronotum **Campyloxenini**
- Claws with setae at base; anal cell absent; luminous areas present or absent 7
- 7 (8). Second antennal segment appreciably smaller than 3rd, antennae serrate, of 11 segments; without luminous spots on pronotum **Pseudomelanactini**
- Second and 3rd segments of antennae subequal, or if 2nd short then antennae of 12 segments or pronotum has luminous spots 8
- 8 (7). With luminous spots on the pronotum and/or on the abdomen **Pyrophorini**
- Without luminous spots on the pronotum or abdomen 9
- 9 (8). Antennae usually serrate, more rarely pectinate, 2nd and 3rd segments various but 3rd usually longer to (rarely) subequal; mesosternal cavity more or less inclined (rarely horizontal), sides inconspicuous; colorful species from Central and South America **Heligmini**
- Antennae usually laminate or flabellate, rarely serrate, 2nd and 3rd segments usually subequal and moniliform, 3rd often with small tooth and rarely larger than 2nd; colorful species with horizontal mesosternal cavity and thick sides, unicolorous species with sloping mesosternal cavity and inconspicuous sides **Hemirhipini**

6. Becker (1973) lists 2 exceptions with simple tarsi which otherwise would key out here. These are small (under 7 mm) light brown species from Southern California and Mexico with a *Ctenicera*-like frons (carina over antennae directed downward and mesally, becoming obsolete near labrum). See text under *Conoderini*.

Tribe AGRYPNINI Candèze

Agrypnides Candèze, 1857.

Octocryptites Candèze, 1892.

Adelocerini Du Buysson, 1893.

Cavicoxumidae Pic, 1928.

Laconini Gurjeva, 1973 (?).

Adult. Prosternal sutures with deep grooves for reception of antennae, rarely grooved posteriorly for reception of anterior tarsi; frontal carina absent, vague or more or less present above to variously developed between antennae, frons more or less concave, mouthparts inferior; prosternal lobes normally arcuate or even prominent, prosternum simple, without cross or transverse sutures, propleuron and metasternum may be either grooved for tarsae or antennae or not; mesosternum and mesepisternum simple, not divided by cross sutures, meso- and metasternum with distinct suture or suture indistinct or absent; scutellum shield-shaped, never cordate; tarsi various; claws with seta(e) at base (rarely absent).

This is a large tribe with 19 genera and approximately 1000 known species. The largest genus is *Agrypnus* Eschscholtz. Von Hayek (1973) lists 409 species.

Citation of the family-group name Agrypnini follows von Hayek (1973), Leseigneur (1972) and other recent authors. The use of Adelocerini by Arnett (1952, 1962) and Arnett et al. (1969) may have followed on from Du Buysson's usage (Du Buysson 1893) as suggested by von Hayek (1973).

The name Laconini is listed as a synonym, as the genus *Lacon* LaPorte is included by von Hayek (1973) under the Agrypnini. Von Hayek did not mention Laconini and the only reference to it that I have found is in Gurjeva's paper (Gurjeva 1973) which lists *Lacon* LaPorte, *Sulcilacon* Fleutiaux, *Trachyilacon* Motschulsky, *Brachyilacon* Motschulsky and *Agraeus* Candèze in the tribe Laconini. However, von Hayek listed *Sulcilacon* as a synonym of *Lacon* and the others as synonyms of *Adelocera* Latreille. The latter genus together with 7 other genera was placed in the Adelocerini by Gurjeva (1973).

The Agrypnini had been in need of comprehensive study for some time. As this is a group with many interesting large elaters, a number of workers had studied various individual genera or regional faunas. Because of the restricted nature of these studies, these workers were generally unaware of a wide range of variation in many of the classic diagnostic characters that they employed. Many species and genera which were named as a consequence of these relatively restricted studies were found on more detailed analysis (von Hayek 1973) to have been established on very tenuous grounds. In the process of von Hayek's exhaustive revision, 35 genera were synonymized under the appropriate, oldest name, and 1 genus was taken out of synonymy. At the specific level, further work remains to be done, but von Hayek has corrected the older mistakes, placing 23 names in synonymy, retrieving 11, and giving 471 new combinations, in addition to giving the location of the type material and designating 406 lectotypes.

Von Hayek also synonymized the Octocryptites of Candèze under Agrypninae. This synonymy is followed here, as I agree that *Octocryptus* Candèze belongs within

the Agrypnini as that tribe is delineated herein. Ôhira & Becker (1973), while discussing the elaterids of Nepal, also mentioned *Octocryptus*, but retained the subfamilies and cited the following characters to separate *Octocryptus* from other agrypnid genera: lack of setae on the tarsal claws, lack of a cubital crossvein; and small movable styli on the ovipositor. The 1st character does not appear valid. The genus *Danosoma* Thomson, as defined by von Hayek, lacks basal setae on the claws. This character is probably the result of reduction from the original state in the ancestors of *Danosoma*, which probably had setae on the claws. In the collection of the British Museum (Natural History) there is a single specimen of *Danosoma fasciata* Linnaeus in which the outside claw of the right middle tarsus has 1 seta at the base in the exact place where a basal seta of an agrypnid is normally found. Such an example is probable evidence of throwback. As a consequence, lack of basal setae should not be regarded as evidence that *Octocryptus* (or other properly included taxa) should not belong to the Agrypnini and to the Pyrophorinae in turn, at least until definite (preferably larval) evidence to the contrary is produced. Nor should a taxon possessing basal setae be assigned outside the Pyrophorinae without good proof to support the assignment, for the present evidence suggests that basal setae, when present, indicate a generalized and ancient relationship, if the above and other factors such as the very great diversification of the Pyrophorinae are true (cf discussion under Conoderini).

The 2nd character, lack of a cubital crossvein, is found in various pyrophorinid groups such as the Pseudomelanactini, Heligmini and Pyrophorini. It would be necessary to examine all pyrophorinid taxa to ascertain the "tribal" diagnostic value of this character. The same comments apply to the movable styli on the ovipositor.

Tribe PROTAGRYPNINI Dolin

Protagrypnini Dolin, 1973.

Adult. Frontal carina present, straight, frons flat, mouthparts inferior, propleuron with deep grooves for reception of antennae; prosternum arcuate anteriorly, hiding mouth, with narrow semicircular or straight suture anteriorly; mesosternum divided by cross suture between mesosternal fossa and mesepimeron; mesepimeron also divided by cross suture; scutellum shield-shaped, not cordate; tarsi simple; claws not known.

This tribe is made up of 5 fossil genera with 13 species, all from the Jurassic, which I have never seen. This is the only fossil family-group taxon so far recognized in the Elateridae. The sutured prosternum, mesosternum and mesepimeron are unique. The prominently grooved prosternal sutures leave no doubt of this group's close relationship to the Agrypnini. Dolin (1975b) elevated the group to subfamily with 3 included tribes. I have elected to retain the original tribal status with 3 subtribes in order to maintain the concept of the subfamilies and tribes as arranged in the present paper. Dolin (1973) dealt with the taxonomic position of many other fossil genera ascribed to the Elateridae by earlier authors. He removed some of these from the Elateridae and placed them in various other families. His classification will be largely followed in my subsequent papers in this series.

Subtribe *PROTAGRYPNINA* Dolin, 1973, **new status**

Subtribe *HYPNOMORPHINA* Dolin, 1975b, **new status**

Hypnomorphini Dolin, 1973.

Subtribe *DESMATINA* Dolin, 1975b, **new status**

Desmatini Dolin, 1973.

Tribe *TETRALOBINI* LaPorte

Tetralobites LaPorte, 1840.

Phyllophoridae Hope, 1842.

Adult. Frons as a thick, projecting pad with transverse trough or vertical groove between eyes, mouthparts inferior, antennae and tarsi not received in deep grooves; prosternal sutures excavated in front, prosternal lobes normally arcuate; meso- and metasternum with distinct suture; scutellum shield-shaped, never cordate; tarsi lamellate; claws simple, setae present at base and often elsewhere on claws.

This tribe comprises 4 genera and 63 species. The majority of species (42) are in the genus *Tetralobus* Peletier. Laurent (1967) treated this group extensively as a subfamily and divided it into 2 tribes (herein regarded as subtribes).

Subtribe *TETRALOBINA* LaPorte, 1840

Subtribe *PIEZOPHYLLINA* Laurent, 1967, **new status**

Piezophyllini Laurent, 1967.

Tribe *CHALCOLEPIDINI* Lacordaire

Chalcolepidiides Lacordaire, 1857.

Alaites Candèze, 1874.

Adult. Frons more or less inflexed, concave, mouthparts inferior, frontal carina absent, indistinct or vaguely present, antennae and tarsi not received in deep grooves; prosternal sutures more or less excavated in front, usually somewhat shallowly impressed (but not excavate), its prosternal lobe normally arcuate; meso- and metasternum connate, suture absent or indistinct; scutellum shield-shaped, never cordate; tarsi simple; claws simple, setae present at base and sometimes elsewhere on claws.

The present definition of this tribe restricts it to 11 genera with nearly 300 species. The genera *Semiotus* Eschscholtz, *Campsosternus* Latreille and *Oistus* Candèze have been removed to the Oxynopterinae (Campsosternini) on the basis of absence of setae at base of the claws and the toothed mandibles of the larvae. Neboiss (1967) revised the Australian species.

Tribe *PSEUDOMELANACTINI* Arnett

Pseudomelanactini Arnett, 1967.

Adult. Frons more or less inflexed, mouthparts inferior, frontal carina absent, antennae and tarsi not received in deep grooves, 2nd antennal segment appreciably smaller than 3rd, of 11 segments; prosternal sutures excavated in front, vaguely impressed, prosternal lobe normally arcuate; meso- and metasternum with distinct suture; scutellum shield-shaped, never cordate; tarsi simple; claws simple, setae present at base.

At present, 2 genera and 6 species are recognized. However, more species probably exist in the Australian region. These may be known species at present under *Agrypnus* Eschscholtz or *Lanelater* Arnett.

The validity of this tribe is open to question. Perhaps the general facies as an apparent *Melanactes* LeConte or *Lanelater* Arnett is sufficiently characteristic. From the former, it is easily separated by the pyrophorine head, mouth and claws and, from the latter, by the lack of deeply excavated grooves for the antennae. However, the 2 included genera are not so easily separated from the Hemirhipini, the chief distinguishing feature being the short, 2nd antennal segment (Arnett 1967, Arnett et al. 1969). The length of this segment is subject to some variation, and when the fauna is more exhaustively studied it may well prove to be unreliable. Nevertheless, a complete study of all relevant characters may yet support the separation and retention of this tribe, for its distinctive facies are easily recognized.

Tribe CAMPYLOXENINI Costa

Campyloxeninae Costa, 1975.

Adult. Frons inflexed, curved downwards, mouthparts inferior, frontal carina present, antennae and tarsae not received in deep grooves; luminous areas present on pronotum, prosternal sutures (not known), prosternal lobe normally arcuate anteriorly; meso- and metasternum with distinct suture; scutellum shield-shaped, never cordate; anal cell present in wings; tarsi simple; claws simple, without setae at base; indistinct luminous areas on abdomen.

The tribe comprises 1 genus and species only. Costa (1975) established a subfamily, citing the absence of setae on the base of the claws, the presence of an anal cell and the stylus and elongate baculum of the female as distinguishing features. However, the relationship of the more primitive Campyloxenini to the other luminous tribes seems clear, as indicated by the diffuse nature of the luminous areas and retention of the anal cell in the wings. It seems, therefore, that the diagnostic setae on the base of the claws have been lost, much as in *Danosoma* Thomson or *Octocryptus* Candèze (Agrypnini). The form of the female genitalia is not unique (cf the styli of *Octocryptus*).

Tribe HELIGMINI Costa

Heligmini Costa, 1975.

Adult. Frons more or less inflexed or flat, curved downwards, mouthparts inferior, frontal carina absent to slightly carinate, antennae and tarsi not received in deep grooves; antennae usually serrate, more rarely pectinate, 2nd and 3rd segments vary in length but 3rd usually longer to (rarely) subequal; pronotum without luminous spots, prosternal sutures closed or excavated anteriorly, prosternal lobe normally arcuate; meso- and metasternum with distinct suture, mesosternal cavity more or less inclined to (rarely) horizontal, sides inconspicuous; scutellum shield-shaped, never cordate; tarsi simple; claws simple, setae present at base; abdomen without luminous areas.

This tribe contains 11 genera and 26 species (Costa 1975). The genera involved were, for the most part, previously placed in the old nonluminous Pyrophorini, but the Pyrophorini are now restricted to luminous forms. At present all known species are found in Central and South America. Costa's paper covers the group extensively,

with keys and descriptions down to the specific level. Phylogenetic considerations led Costa to establish 4 subtribes as listed below.

Subtribe HELIGMINA Costa, 1975

Subtribe ALAMPINA Costa, 1975

Alampina Costa, 1975.

Subtribe EUPLINTHINA Costa

Euplinthina Costa, 1975.

Subtribe COMPSOPLINTHINA Costa

Compsoplinthina Costa, 1975.

Tribe PYROPHORINI Candèze

Adult. Frons more or less inflexed or flat, curved downwards, mouthparts inferior, frontal carina absent or well developed, antennae and tarsi not received in deep grooves; antennae serrate from the 4th, rarely the 3rd, segment onwards; pronotum with luminous spots, prosternal sutures closed to slightly open anteriorly, prosternal lobe normally arcuate; meso- and metasternum with distinct suture, mesosternal cavity generally sinusoidal; scutellum shield-shaped, never cordate; tarsi simple; claws simple, setae present at base; abdomen with or without luminous areas.

Following Costa (1975), there are 11 genera with 95 species in the Pyrophorini. About ½ the species belong to *Pyrophorus* Bilberg and *Pyrearinus* Costa. Costa excluded *Hifo* Candèze, *Hifoidea* Schwarz and (with reservations) *Photophorus* Candèze from the tribe. However, for the present these 4 genera may be regarded as belonging to the Pyrophorini on an 'Incertae Sedis' basis. Costa has mentioned that *Hifo* has a lobed, 4th tarsal segment and this may place *Hifo* near the Conoderini; *Hifoidea* has a wedge cell in the wing and no setae on the claws which might place it near the Campyloxenini, while *Photophorus* has setae on the claws but has no evident suture between the mesosternum and metasternum and this would put it near the Chalcolepidini.

Costa (1975) also excluded *Hemirhipus* Berthold from the Pyrophorini, and by doing so disagreed with Arnett et al. (1969) who synonymized the Hemirhipini under the Pyrophorini. In effect, this means that the Hemirhipini must be resurrected to include all those taxa formerly under that name, and this will be done in the next paper of this series (cf Hemirhipini).

At present all known species are found throughout Central and South America, the West Indies and the southwestern through southern United States. Studies by Costa (1975) led to the establishment of 3 subtribes, as listed below.

Subtribe PYROPHORINA Candèze

Subtribe NYCTOPHYXINA Costa

Nyctophyxina Costa, 1975.

Subtribe HAPSODRILINA Costa

Hapsodrilina Costa, 1975.

Tribe HEMIRHIPINI Candèze

Hemirhipides Candèze, 1857.

Adult. Frons more or less inflexed or flat, curved downwards, mouthparts inferior, frontal carina absent to prominent, antennae and tarsi not received in deep grooves; antennae usually laminate or flabellate, rarely serrate, 2nd and 3rd segments usually subequal and moniliform, 3rd often with small tooth, rarely larger than 2nd; pronotum without luminous spots, prosternal sutures closed, excavate or pseudoexcavate anteriorly, prosternal lobe normally arcuate to sometimes straight anteriorly; meso- and metasternum with distinct suture, colorful species with horizontal mesosternal cavity and thick sides, unicolorous species with sloping mesosternal cavity and inconspicuous sides; scutellum shield-shaped, never cordate; tarsi simple; claws simple, setae present at base; abdomen without luminous areas.

As stated earlier, Costa (1975) dropped *Hemirhipus* Berthold and allied genera from the Pyrophorini, in effect reversing Arnett et al.'s (1969) decision to synonymize the Hemirhipini under the Pyrophorini. Consequently, I will resurrect the Hemirhipini in the next paper of this series. As can be seen from the key to tribes and diagnoses, it is difficult to separate the Hemirhipini, as now recognized, from the Heligmini. Costa (pers. commun.) believes the key, as presently devised, is good, though not definitive. She also observed that some of the genera of Hemirhipini should be in the Chalcolepidini, a point which stresses the need for further study and is further highlighted by an unrelated move by Dolin (1975a), who also recognized the Hemirhipini, but included *Chalcolepidius* Eschscholtz and *Alaus* Eschscholtz, which in the present work are placed in the Chalcolepidiini.

At present, 18 genera containing less than 60 species make up this tribe. The largest genus is *Hemirhipus* with 15 species.

Tribe CONODERINI Fleutiaux, 1919 (1859)

Conoderinae Fleutiaux, 1919.

Monocrepidiites Candèze, 1859.

Adult. Frons more or less inflexed or flat, curved downwards, mouthparts inferior, frontal carina well developed above and between antennae, more or less straight and well separate from labrum; antennae and tarsi not received in deep grooves; prosternal sutures closed, prosternal lobe normally arcuate; meso- and metasternum with distinct suture; scutellum shield-shaped, never cordate; tarsi with 4th segment broadened or lobed beneath; claws simple, setae present at base.

There are 14 genera with perhaps 800 species, chiefly in the genera *Conoderus* Eschscholtz, *Aeolus* Eschscholtz and *Heteroderes* Latreille in the tribe. Delimitation of some of the genera may be difficult and it is believed that the 3 main genera will eventually be broken into smaller, more manageable taxa. Such a study has yet to be published, although several persons have reportedly been at work on the problem.

Becker (1973), when studying *Ctenicera sleeperi* Becker and *C. pilatei* (Champion), considered that the 2 species could not be in the Pyrophorinae (near *Conoderus* Esch-

scholtz) because of their nonmargined frons and simple tarsi, despite the fact that both possess setae at the base of the claws. In fact, Becker believes that there has been too much reliance placed on the setae at the base of the claws as a diagnostic character. He concluded, however, that the larvae and females of these species, when discovered, will help in their correct generic placement.

There is no proof that the above 2 species do belong in *Ctenicera* Latreille. Although a carina is present, it is merely obliterated mesally near the labrum in a *Ctenicera*-like manner. The absence of a lobe on the 4th tarsal segment could well be the loss of a character, rather than its absence in the ancestor. It is even harder to accept Becker's argument that a significant character, such as setae at the base of the claws, can be independently acquired. (Certain *Ctenicera* from New Zealand possess setae on other areas of the claws, but not at the base, and consequently are not relevant to the present case.) Finally, Becker cited the lack of a cubital crossvein and noted that it is also absent in pyrophorids, while *Ctenicera*, or at least those species examined by Becker, do possess such a crossvein.

As *C. sleeperi* and *C. pilatei* key out to the Pyrophorinae and, except for the simple tarsi, are identifiable to the Conoderini in the present study, they are regarded as belonging here until larvae become available to help settle the question.

The tribal name Conoderini is used herein following Recommendation 40A of the Code, since *Conoderus* Eschscholtz is the senior synonym to *Monocrepidius* Eschscholtz (type genus) and the replacement tribal name must take the date of the name replaced.

IV. Subfamily MELANACTINAE Candèze

Melanactides Candèze, 1857.

Adult. Head capsule flattened, prognathous, mouthparts prognathous, frons without ridge; prosternum normally arcuate anteriorly, scutellum oblong; mesocoxae open to mesepimeron but closed to mesepisternum; meso- and metasternum distinct, joined by a definite suture; tarsi simple, without pads; claws simple, without setae.

Larva. Head with posteroepicranial setae, mandibles simple, with teeth, nasule present, eyes absent, galea of 2 segments, postmentum subrectangular; prosternum not divided; laterotergite of 2 sclerites; spiracle separate from mediotergite, well developed and with spiracular sclerite; 9th abdominal segment with caudal notch and normal urogomphi divided into 4 prongs, inner prongs small, outer prongs very long and corniform.

This small subfamily contains 6 species in a single genus, all from North America. The adults, which are large, smooth, black beetles, at least 20 mm in length, are additionally characterized by the form of the mesosternal cavity, the sides of which are so raised and swollen as to be protuberant. Their larvae seem to have characters reasonably distinct from that of denticolliniform larvae, otherwise they might be placed within the Denticollinae along with the Hypnoidinae.

Arnett (1967) pointed out that other elaterid genera may belong here but that further study is required.

V. Subfamily HYPNOIDINAE Schwarz 1906 (1860)

Cryptohypnites Candèze, 1860.

Hypnoidini Schwarz, 1906a.

Hypolithinae Fleutiaux, 1928.

Adult. Head capsule flattened, mouthparts prognathous, frons ridged; prosternum normally arcuate anteriorly; scutellum various but never cordate; mesocoxae open to mesepimeron but closed to mesepisternum; meso- and metasternum distinct, joined by a definite suture; tarsi simple, without pads; claws simple, without setae.

Larva. Head with posteroepicranial setae, eyes present, mandibles simple, with teeth, galea of 2 segments, postmentum subrectangular; prosternum divided; laterotergite of 2 sclerites; spiracle separate from mediotergite, well developed, with spiracular sclerite; 9th abdominal segment with caudal notch and normal urogomphi divided into 4 prongs.

This subfamily has been extensively monographed [Stibick 1976b (Part I); Stibick 1978 (Part II); *Part III (The Hypnoidinae of Eurasia)*, *Part IV (The Hypnoidinae of India)*, and *Part V (The Hypnoidinae of New Zealand, Fossil Hypnoidinae and Indexes)* have been accepted for publication in *Eos* in Volumes 53, 54 and 55, respectively, but are not yet in press].

The Hypnoidinae are a small, rather homogenous group best known through certain grain pests in the genus *Hypnoidus* Dillwyn. The subfamily status of the Hypnoidinae may be questioned because of a close, derivative relationship to the Melanactinae. However, they are undeniably distinct. Otherwise they would be placed in the Denticollinae, as has been done by other authors. Such a move would also logically require subordination of the Melanactinae, a clearly delimited group. For this reason, until and unless a thorough and complete investigation of the various Denticollinae tribes and subtribes is undertaken, the position should remain as it is.

Reasons for using the name Hypnoidinae are given in my paper (1976b) on this group. Briefly, both Hypnoidini and Hypolithinae were proposed as replacement names when it was discovered that the genus *Cryptohypnus* Eschscholtz was a junior synonym of *Hypolithus* Eschscholtz. The name Hypnoidini was proposed in 1906 by Schwarz on the assumption that *Hypolithus* was also a junior synonym of *Hypnoidus*. This was not true as *Hypolithus* was established in January of 1829 (Eschscholtz 1829) and *Hypnoidus* in November of the same year (Dillwyn 1829). Although this assumption was not correct, and these genera are now considered to be good separate entities, the name Hypnoidini still takes precedence over the name Hypolithinae which was first used by Fleutiaux (Fleutiaux 1928).

KEY TO THE TRIBES OF HYPNOIDINAE

Prosternal lobe feebly developed; scutellum generally oblong; New Zealand only . . . **Prisahypini, n. tribe**
 Prosternal lobe moderately to strongly elongate; scutellum usually flat, generally truncate anteriorly
 and as wide or wider than long;⁷ Northern Hemisphere, South America **Hypnoidini**

7. One exception, the very rare *Desolakerus* Stibick, from the southwestern deserts of North America, has a convex and oblong scutellum.

Tribe HYPNOIDINI Schwarz

Adult. Head capsule flattened, mouthparts prognathous, frons ridged, eyes only feebly prominent, scarcely expanded laterally, prosternal lobe moderately to greatly elongate and normally arcuate anteriorly; scutellum usually flat, generally truncate anteriorly, generally little longer than wide to sometimes wider than long or rarely convex and oblong; mesocoxae open to mesepimeron but closed to mesepisternum; meso- and metasternum distinct, joined by a definite suture; tarsi simple, without pads; claws simple, without setae.

A small tribe of 8 genera, 58 species, usually found in cold to temperate regions of North America, South America, Europe and Asia. A key to the larvae occurring on the North American Atlantic seaboard is given in Stibick (1969). Ôhira (1973) added the genus *Homotechnes* Candèze, with 2 included species, to the tribe. It is possible that it belongs in the Ctenicerini, but the matter must receive further study.

PRISAHYPINI Stibick, **new tribe**

Prisahypini Stibick, 1976b. Nomen nudum.

Adult. Head capsule flattened, mouthparts prognathous, frons ridged, eyes usually prominent and greatly expanded laterally; prosternal lobe only feebly expanded and normally arcuate anteriorly; scutellum always rather elongate, longer than wide; mesocoxae open to mesepimeron but closed to mesepisternum; meso- and metasternum distinct, joined by a definite suture; tarsi simple, without pads; claws simple, without setae.

The tribal and included generic names were first given in Stibick 1976b without reference to included species. The 3 genera were characterized in a table on page 207. To validate the generic names so treated, species are now associated for the first time. The type-species is given for each genus, as follows:

Prisahypnus Stibick, **new genus**

Prisahypnus Stibick, 1976b: 169, 207. Nomen nudum.

Type-species: *Cryptohypnus frontalis* Sharp, 1877. Present designation.

Insulahypnus Stibick, **new genus**

Insulahypnus Stibick, 1976b: 165, 207. Nomen nudum.

Type-species: *Cryptohypnus longicornis* Sharp, 1877. Present designation.

Australeeus Stibick, **new genus**

Australeeus Stibick, 1976b: 169, 207. Nomen nudum.

Type-species: *Cryptohypnus powelli* Sharp, 1877. Present designation.

The above genera are all endemic to New Zealand and together possess at least 9 species, including undescribed species.

VI. Subfamily DENTICOLLINAE Reitter, 1905 (1857)

Campylides Candèze, 1857.

Denticollini Reitter, 1905.

Lepturoidini Schwarz, 1906.

Adult. Head capsule flattened, mouthparts prognathous, frons ridged, either complete or obsolete in middle; prosternum normally arcuate anteriorly but lobe can have a straight, leading edge or be truncate; scutellum various but never cordate; mesocoxae open to both mesepimeron and mesepisternum; meso- and metasternum distinct, joined by a definite suture; tarsi various, with or without pads; claws simple, rarely pectinate, without basal setae.

Larva. Head with or without any posteroepicranial setae, mandibles simple, with teeth, nasule present, galea of 2 segments, postmentum subrectangular; laterotergite of 2 sclerites; spiracle variously separate from mediotergite, well developed and with spiracular sclerite; 9th abdominal segment with caudal notch and recurved prongs or sharp teeth.

The subfamily name, as cited above, follows Recommendation 40A of the Code, since *Denticollis* P. & M. is the senior synonym to *Campylus* F-W (type genus) and the replacement subfamily name must take the date of the name replaced.

This is one of the largest subfamilies, with about 219 genera and subgenera and thousands of species. Little is known about most of the taxa involved and there is disagreement as to the status of the various taxa. I recognize 3 tribes, of which the Denticollini, with 10 subtribes, is the largest and most diverse. These subtribes have often been treated as tribes or even subfamilies by other authors.

KEY TO THE TRIBES OF DENTICOLLINAE

1. Frontal carina either complete between the eyes (often projecting), or (rarely) absent 2
 Frontal carina not complete, obsolete in middle **Ctenicerini**
2. Tarsal segments 2 to 4 broadened and slightly depressed, all segments sometimes lobed, 4th
 bilobed or broadened and emarginate at tip **Pachyderini**
 Tarsal segments, if lobed, feebly widened at most **Denticollini**

Tribe PACHYDERINI Fleutiaux, 1919 (1859)

Eudactylites Candèze, 1859.

Pachyderinae Fleutiaux, 1919.

Adult. Head capsule flattened, mouthparts prognathous, frons ridged, complete; prosternum normally arcuate anteriorly; scutellum various but never cordate; mesocoxae open to both mesepimeron and mesepisternum (rarely closed); meso- and metasternum distinct, joined by a definite suture; tarsi with segments 2 to 4 broadened and slightly depressed, all segments sometimes lobed, 4th bilobed or broadened and emarginate at tip; claws simple or toothed at base, without setae.

This is a small tribe of 9 genera and about 70 species. No one genus is predominant. Van Zwaluwenburg (1959) removed this tribe to the Conoderini (Conoderinae), plus the genera *Anathesis* Candèze, *Simodactylus* Candèze, *Melanthoides* Candèze and *Pachyderes* Guerin. Ôhira (1970a, 1971), with the exception of *Anathesis*, did the same with the above genera. However, none of these genera have setae on the base of the claws and the larvae are not pyrophoriniform. In fact, the adult and larval characters of

Simodactylus place this genus in the Ampedini, and I have done that here. The other genera referred to above remain in the Pachyderini.

The generic name *Eudactylus* Salle, 1855 was replaced by *Platycrepidius* Hyslop, 1921. This normally calls for similar replacement of the subfamily name. However, Fleutiaux (1919) named and based the Pachyderinae on the related genus *Pachyderes* Guerin, 1834 and Schenkling (1925) followed this, listing *Eudactylites* Candèze, 1859 as a synonym. The name Pachyderinae has since been widely established in the literature and is maintained here under Article 40 (a) of the Code.

Tribe DENTICOLLINI Reitter, 1905 (1857)

Adult. Head capsule flattened, mouthparts prognathous, frons either ridged and complete, often projecting or completely absent; prosternum either normally arcuate, sometimes short, rarely truncate (in which case frons is strongly ridged), prosternal sutures double or single, may be excavate in front; scutellum various but never cordate; mesocoxae open to both mesepimeron and mesepisternum; meso- and metasternum distinct, joined by a definite suture; tarsi simple or lobed, if lobed then segments feebly widened at most; claws simple, or rarely pectinate, without basal setae.

This is the largest tribe of the Elateridae and contains 8 subtribes, 130 genera and thousands of species. The subtribe Denticollina has often been regarded as the only one correctly belonging to the subfamily. In 1 instance (Jagemann 1950) the Denticollina were raised to family level. Leseigneur (1972) presented the case for retaining this group in the Elateridae, based on a study of its typical elateriform larvae and imagos. In the present paper the other subtribes are associated in this subfamily on the basis of the commonly shared characters given in the diagnosis of adults and larvae of the Denticollinae. They are readily grouped in this way and perhaps further research will show that the Hypnoidinae and Melanactinae should also be placed here.

Certain characters not mentioned, specifically the presence of a 6th abdominal segment, the pointed metasternum and approximate mesosternal coxal cavities and the short, truncate anterior lobe of the prosternum have been cited by various authors to recognize the Denticollinae. However, some of these features may be compromised. For example, Fleutiaux's Toxognathinae (Fleutiaux 1940), placed under Physodactylina in this paper, was characterized by having a truncate prosternum, and his Anischinae (placeable here) characterized by having a short prosternum and no frontal carina (Fleutiaux 1940). I have not been able to examine the genera *Toxognathus* Fairmaire and *Anischia* Fleutiaux, much less review all the genera involved to resolve the question or to clarify the status or ranking of the higher taxa as set by Fleutiaux (1947). Again, some of the genera and species in the various subtribes listed below seem to have mesocoxae separated by varying distances and the metasternum, in consequence, more or less pointed to truncate. It is obvious that a comprehensive study of all the taxa listed herein is necessary to establish whether or how these taxa should be separated into subtribes, tribes or subfamilies, or indeed transferred elsewhere.

The Nyctorini as defined by Semenov-Tian-Shanskij & Pjatakova (1936) and apparently placed in the Denticollinae by these authors, was transferred to the Cardiophorinae by Gurjeva (1974).

It must finally be mentioned that Schenkling (1927a), not Rudolph (1973), was the first to raise *Dimites Candèze* (herein regarded as a subtribe) to subfamily rank.

Subtribe *ATHOUINA* Candèze, 1859

Athoites Candèze, 1859.

Limoniina Jacobson, 1913.

Subtribe *DENTICOLLINA* Reitter, 1905 (1857)

Subtribe *HEMICREPIDIINA* Champion, 1894 (1863)

Asaphites Candèze, 1863.

Hemicrepidiini Champion, 1894.

Subtribe *PHYSODACTYLINA* Fleutiaux, 1892

Physodactylini Fleutiaux, 1892.

Taxognathinae Fleutiaux, 1940.

Taxognatini Gurjeva, 1974 (error).

Subtribe *CREPIDOMENINA* Candèze, 1863

Crepidomenites Candèze, 1863.

Subtribe *SENODONIINA* Schenkling, 1927 (1863)

Allotriites Candèze, 1863.

Senodoniinae Schenkling, 1927a.

Subtribe *DIMINA* Candèze, 1863

Dimites Candèze, 1863 (nec Rudolph, 1973, *Diminae*).

Beliophorina Jacobson, 1913.

Subtribe *ANISCHINA* Fleutiaux, 1936

Anischinae Fleutiaux, 1936.

Tribe *CTENICERINI* Fleutiaux, 1936 (1863)

Corymbitites Candèze, 1863.

Ctenicerinae Fleutiaux, 1936 (nec Neboiss, 1956).

Adult. Head capsule flattened, mouthparts prognathous, frons flat, ridged but incomplete, obsolete in middle; prosternum normally arcuate anteriorly; scutellum various but never cordate; mesocoxae open to both mesepimeron and mesepisternum; meso- and metasternum distinct, joined by a definite suture; tarsi simple; claws simple, without basal setae.

This is a large tribe which has not been studied as a discrete taxon to date. There are 33 genera and probably 300 or more species; the number of species is difficult to determine due to piecemeal studies and isolated descriptions published over the years. *Ctenicera* Latreille, is the largest genus and accounts for possibly 2/3 of the known species.

The tribal name as cited above follows Recommendation 40A of the Code, since *Ctenicera* Latreille, 1829 is the senior synonym to *Corymbites* Latreille, 1834 (type genus). Neboiss (1956) was apparently unaware of Fleutiaux's 1936 paper in which the name Ctenicerinae was also proposed as a replacement for *Corymbites* (Corymbitinae).

VII. Subfamily ELATERINAE Leach

Adult. Head capsule oval, deflexed, mouthparts inferior, frons various; prosternum normally arcuate anteriorly; scutellum various but never cordate; mesocoxae open to both mesepimeron and mesepisternum; meso- and metasternum distinct, joined by a definite suture; tarsi various, with or without pads; claws either simple or serrate, without basal setae.

Larva. Nasule present, mandibles simple, with teeth, galea of 2 segments, postmentum subrectangular; prosternum normally truncate in front, exposing mouthparts; laterotergite incompletely separated from mediotergite at most; spiracle more or less well developed, embedded in mediotergite; 9th abdominal segment without caudal notch or prongs, simple in shape but often variously ornately armored or with point at apex.

This is the largest subfamily, with 180 genera and subgenera. There are 9 tribes which many authors treat as subfamilies. While I have reservations on the limits of several of these tribes, others seem fairly well defined. The reservations center on the Agriotini, which seem to be a heterogeneous grouping. *Agriotella* Brown, *Dalopius* Eschscholtz and *Agriotes* Eschscholtz (*criddlei* group) have larvae with setiferous tubercles on a pointed 9th abdominal dorsum, and adults have a ridged frons which can disappear medially. These taxa should be associated with the Physorhinini, possibly as a new tribe. The Agriotini proper are closely related to the Elaterini as the larvae have no tubercles or spines and the adults have no frontal ridge. Becker (1956), however, associated all of the above in a common monophyletic grouping, and with this I disagree.

KEY TO THE TRIBES OF ELATERINAE

- 1. Claws strongly serrate **Adrastini**
 - Claws simple or with basal tooth 2
 - 2 (1). Fourth tarsal segment never lobed, at least 3rd segment with membranous lobe;⁸ frontal carina complete 3
 - Fourth tarsal segment lobed or simple, if 3rd segment lobed, 4th is either lobed or very short; frontal carina variable 5
-
8. Rare exceptions: (1) if all segments are simple but metacoxal plates are greatly expanded and 1st metatarsal segment elongate, the specimen may be in Physorhinini (*Anchastus* LeConte); (2) if all segments are lobed and frontal carina is projecting and more nearly straight across, the specimen may be in Dicrepidiini (*Blauta* LeConte).

- 3 (2). Tarsal segments 1 to 3 or 2 and 3 with membranous lobe beneath 4
 Tarsal segment 3 only with membranous lobe beneath **Physorhinini**
- 4 (3). Claws of ♂ bifid, of ♀ normally acuminate; only 2nd and 3rd tarsal segments lobed; prosternal
 lobe truncate or straight in front **Odontonychini**
 Claws of both sexes normally acuminate; tarsal segments variously lobed; prosternal lobe nor-
 mally arcuate anteriorly **Dicrepidiini**
- 5 (2). Frons carinate above antennae, carina complete between eyes 6
 Frons, if carinate, not complete between eyes 8
- 6 (5). Carina of frons well developed and usually straight across (moderately to feebly arcuate at
 times) and well separate from labrum; prothorax usually broader anteriorly **Pomachiliini**
 Carina of frons arcuate, approaching or often meeting labrum; prothorax not broadened,
 generally more or less narrowed anteriorly 7
- 7 (6). Procoxal cavities broadly open behind and wide anteriorly; prosternal process flat between
 procoxae; elytral apex entire **Ampedini**
 Procoxal cavities partly closed behind by projection of proepisternum, *or* anterior margin more
 or less angulate; prosternal process more or less grooved between procoxae; elytral apex
 truncate, scalloped or at least serrate or spinose **Megapenthini**
- 8 (5). Second antennal segment more than ½ length of 3rd; prosternal sutures usually double, if
 single then frontal carina directed towards meson, frontal carina otherwise rarely directed
 to labrum **Agriotini**
 Second antennal segment ½ or shorter than ½ length of 3rd, or both 2nd and 3rd segments,
 than 4th; prosternal sutures usually single; frontal carina directed downwards to labrum
 **Elaterini**

Tribe DICREPIDIINI Candèze

Dicrepidiites Candèze, 1859.

Adult. Head capsule oval, deflexed, mouthparts inferior, frontal carina complete, usually projecting, antennae 11-segmented, serrate or occasionally flabellate in ♂; prosternum normally arcuate anteriorly, prosternal sutures double, often excavated at apices; scutellum shield-shaped, not cordate; mesocoxae open to both mesepimeron and mesepisternum; meso- and metasternum distinct, joined by a definite suture; tarsi with segments 1 to 3 or 2 and 3 or (rarely), 1 to 4 lobed beneath (*Blauta* LeConte); claws simple or dentate, without basal setae.

This is a moderately sized tribe which at the latest count contained 40 genera. The only recent detailed work on the group is an unpublished microfilm by Clark (1963) revising the North American species.

Tribe ODONTONYCHINI Girard

Odontonychini Girard, 1972.

Adult. Head capsule oval, deflexed, mouthparts inferior, frontal carina complete, usually projecting; antennae 11-segmented, strongly serrate; prosternal lobe truncate or straight in front, prosternal sutures double, varying from largely excavate to closed; scutellum shield-shaped, not cordate; mesocoxae open to both mesepimeron and mesepisternum; meso- and metasternum distinct, joined by a definite suture; tarsi with 2nd and 3rd segments lobed beneath; claws of ♂ bifid, of ♀ normally acuminate, without basal setae.

This small tribe containing 3 genera with a total of 13 species, mostly in *Odontonychus* Candèze, was recently erected by Girard (1972). Girard did not treat *Odontonychus* in detail, except to list the species and name 2 new ones. The Odontonychini are presently known only from Africa.

Tribe AMPEDINI Fleutiaux

Ampedinae Fleutiaux, 1947.

Adult. Head capsule oval, deflexed, mouthparts inferior, frontal carina complete, arcuate, bending down between antennae to meet or at least close towards labrum; antennae 11-segmented, serrate; prothorax more or less normally narrowed anteriorly, prosternal sutures entire or excavated in front, double or single, surface of prosternal process flat between procoxae, procoxal cavities broadly open behind and wide anteriorly; scutellum shield-shaped, never cordate; mesocoxae open to both mesepimeron and mesepisternum; meso- and metasternum distinct, joined by a definite suture; apex of elytra entire; tarsi simple; claws simple, without basal setae.

A large tribe of 27 genera. Some species are well known, but most of the taxa have not been studied in any detail. *Ampedus* Dejean is the best known and largest genus. In the past it has been placed under *Elater* Linnaeus and this has caused some confusion in the literature.

Tribe MEGAPENTHINI Gurjeva

Megapenthini Gurjeva, 1973.

Adult. Head capsule oval, deflexed, mouthparts inferior, frontal carina complete, arcuate, bending down between antennae to meet or at least close towards labrum; antennae 11-segmented, serrate; prothorax more or less normally narrowed anteriorly, prosternal suture entire or excavated in front, double or single, surface of prosternal process more or less grooved between procoxae, procoxal cavities partly closed behind by a projection of the proepisternum, or anterior margin more or less angulate; scutellum shield-shaped, never cordate; mesocoxae open to both mesepimeron and mesepisternum; meso- and metasternum distinct, joined by a definite suture; elytral apex scalloped, truncate or at least serrate or spinose; tarsi simple; claws simple, without basal setae.

A tribe of 13 genera recently erected by Gurjeva (1973). I have added the genus *Simodactylus* Candèze as the adults fit the particulars given in the present key and description. It is quite possible that other genera at present listed under the Ampedini will also be found to belong here. Ôhira (1970b) discussed the Japanese species of this tribe under the designation *Megapenthes*-group (Ampedinae).

Tribe PHYSORHININI Candèze

Physorhinites Candèze, 1859.

Adult. Head capsule oval, deflexed, mouthparts inferior, frontal carina complete, usually projecting, antennae 11-segmented, serrate; prosternum normally arcuate anteriorly, prosternal sutures excavated in front, double; scutellum shield-shaped, never cordate; mesocoxae open to both mesepimeron and mesepisternum; meso- and metasternum distinct, joined by a definite suture; tarsi with 3rd segment only lobed, 4th very small; claws simple, without basal setae.

The tribe contains 9 genera with fewer than 200 species, more than ½ of which are in the genus *Anchastus* LeConte. Some recent work has been done by Schaaf (1970) on the genus *Physorhinus* Eschscholtz from the Americas, but he points out that analysis of generic differences between *Physorhinus* and *Anchastus* is not complete, and *Anchastus* may well be divided into several more genera.

Tribe ADRASTINI Candèze

Adrastites Candèze, 1863.

Synaptina Jacobson, 1913.

Adult. Head capsule oval, deflexed, mouthparts inferior, frontal carina complete or incomplete, but characteristically as an elevated rim over the antennal bases which may or may not meet in the middle in front of the labrum to which it may or may not be connected by a ridge, antennae 11-segmented, serrate; prosternum normally arcuate anteriorly, prosternal sutures double, excavated in front; scutellum shield-shaped, never cordate; mesocoxae open to both mesepimeron and mesepisternum; meso- and metasternum distinct, joined by a definite suture; tarsi simple or 3rd or 4th segment lobed; claws strongly serrate, without basal setae.

There are 8 genera and over 150 species of which more than $\frac{1}{2}$ are in *Glyphonx* Candèze in the tribe. Little else is known about these insects.

Tribe POMACHILIINI Candèze

Pomachilites Candèze, 1859.

Adult. Head capsule oval, deflexed, mouthparts inferior, frontal carina complete, well separated from labrum, moderately to feebly arcuate, antennae 11-segmented, filiform to serrate; prosternum normally arcuate anteriorly, prosternal sutures double, closed or excavate anteriorly; scutellum truncate anteriorly, never cordate; mesocoxae open to both mesepimeron and mesepisternum; meso- and metasternum distinct, joined by a definite suture; tarsi simple; or with 4th broadened and cordate or 4th very small and 3rd broadened or lobed, 1st hind tarsal segment nearly as long as next 2 or 3 following segments; claws simple, without basal setae.

The above definition is a modified version as presented in my *Leptoschema* Horn paper (Stibick 1970). There are 23 genera and probably 200 or more species, about $\frac{1}{2}$ in the genus *Pomachilius* Eschscholtz.

Tribe AGRIOTINI Champion

Agriotini Champion, 1894.

Adult. Head capsule oval, deflexed, mouthparts inferior, frontal carina arcuate, more or less interrupted in middle, either directed towards meson (and seemingly complete) or rarely directed downward and obviously incomplete; antennae 11-segmented, filiform to serrate; prosternum normally arcuate anteriorly, prosternal sutures entire or excavated in front, usually double, rarely single; scutellum shield-shaped, never cordate; mesocoxae open to both mesepimeron and mesepisternum; meso- and metasternum distinct, joined by a definite suture; tarsi simple; claws simple or with basal tooth.

There are 10 genera and perhaps nearly 300 described species. The majority of species (200+) seem to belong to *Agriotes* Eschscholtz. Becker (1956) reviewed the North American species of *Agriotes* and also discussed the taxonomic history, status, phylogeny and other aspects of the tribe.

Tribe ELATERINI Leach

Adult. Head capsule oval, deflexed, mouthparts inferior, frontal carina arcuate, directed downward and projecting towards labrum, absent in middle, or as a large, thick pad between eyes, with trough, antennae 11-segmented, filiform to usually serrate; prosternum normally arcuate anteriorly, prosternal sutures entire or excavated in front, usually single, rarely double; scutellum shield-shaped, never cordate;

mesocoxae open to both mesepimeron and mesepisternum; meso- and metasternum distinct, joined by a definite suture; tarsi simple; claws simple.

This is a large group with 36 genera. There are perhaps 500 species. The largest genus is *Agonischius* Candèze with about $\frac{1}{3}$ of the species. The North American species of the tribe were monographed by Roache (1960).

Hyslop (1917) originally placed 2 subtribes in the Steatoderini, the Steatoderina and the Sericosomina, based on *Sericosomus* Dejean only. The genus *Steatoderus* Dejean is now a synonym of *Elater* Linnaeus and *Sericosomus* is a junior isogenotypic synonym of *Sericus* Eschscholtz (Hyslop 1921). Gurjeva (1974) correctly recognized the former synonym when she listed Elaterina and Sericosomina under Elaterini, but not the latter. Although Gurjeva listed these subtribes without comment, I have chosen to relegate the Sericosomina to synonymy under the Elaterini. This is done for several reasons. First, Hyslop's citation of several larval characters (convex head, pentatuberculate mandibles, single sense process on the 2nd antennal segment) does not seem sufficient to me when so many larval forms are still unknown. Second, it will be necessary (under Recommendation 40A) to establish a new name for the subtribe, based on the senior synonym available, in which case a thorough study of the Elaterini would be proper.

Dolin (1975a) established the tribe Dolerosomini, listing the genera *Dolerosomus* Motschulsky, *Sericus* Eschscholtz, *Sericoderma* ?author and *Campylomorphus* Duval. However, *Dolerosomus* is a subjunctive synonym of *Sericus* and its type-species *Dolerosomus flavipennis* Motschulsky is a subjective synonym of *Sericus silaceus* Say (cf Roache 1960). Consequently, use of the name Dolerosomini is not acceptable. The Sericosomina of the preceding paragraph is based on the type-species of *Sericus*, *S. brunneus* Linnaeus and is likewise unacceptable. It would be necessary to raise a new name, based on *Sericus*, but taking the date 1917 [Article 39A(i)] if it is intended to establish a tribal grouping as listed by Dolin. As stated above, such action will require extensive study of the Elaterini and the only move taken in the present paper is to relegate the Dolerosomini to synonymy under the Elaterini.

Candèze (1863) established the tribes Hypodesites and Cardiorhinites, both based on single genera. Champion (1894) in his study of the Elateridae of Central America followed Candèze without comment, but Hyslop (1917) stated that these 2 tribes cannot be placed until the larvae are available. The characters Hyslop cited for the Hypodesini, plus examination of specimens of *Hypodesis* Latreille agree with keys and descriptions leading to the Elaterini as presented in the present work. Consequently, *Hypodesis* is placed here and Hypodesites becomes a synonym of Elaterini. The Cardiorhini likewise agree in all respects with the relevant keys and descriptions. The bilobed labrum, as characterized by Hyslop, is not actually bilobed, but simply deeply impressed in the middle. This impression varies from specimen to specimen. *Cardiorhinus* Eschscholtz is consequently listed here, and Cardiorhini becomes a synonym of Elaterini.

VIII. APLASTINAE, **new subfamily**

Adult. Body depressed, parallel-sided, head capsule oval, deflexed, mouthparts inferior, frons without ridge between antennae, with or without short oblique ridge above antennal insertions, antennae of various lengths; thorax subquadrate or quadrilateral (rarely convex in front of middle); prosternum truncate, exposing labrium, prosternal sutures single, straight or curved, sometimes excavated in front; scutellum shield-shaped, never cordate; mesocoxae open to both mesepimeron and mesepisternum or (apparently) just closed to mesepisternum; mesosternal coxae approximate to contiguous, metasternum pointed to nearly obsolete between coxae; meso- and metasternum distinct, joined by a definite suture; tarsi simple; claws simple.

Larva. Nasule present, head corrugated transversely on dorsum, galea of 2 segments, mandibles greatly produced externally, postmentum subrectangular; prosternum greatly produced, covering mouthparts; laterotergite incompletely separated from mediotergite; spiracle more or less well developed, embedded in mediotergite; 9th segment simple, without ornamentation or other structures present.

Crowson (1972) moved the family-group name *Plastocerinae* to the *Cantharidea* and raised it to full family status (*Plastoceridae*), pointing out that it was based on a misidentified type genus, whose type-species, *Plastocerus angulosus* (Germar), from Asia Minor, appears to be a primitive *Canathanoidea*. This action left the remaining forms, comprising a number of genera, without a family-group name of their own, although Crowson did say that these latter insects had clear affinities with the elateroid *Cebrionidae*.

Examination of larvae of *Aplastus* and *Euthysanius* revealed that these forms are very close to those of the *Elaterini* (as defined in this paper), particularly in the shape of the 9th abdominal segment. Major modifications are the produced prosternum and mandibles and transverse ridges on the dorsum of the head. This approaches the larvae of *Cebrionidae*, which, however, possess a large eversible cervical membrane (Boving & Craighead 1931, Hyslop 1923). The adults have a truncate prosternum (as do *Oestodinae*), but this is not shortened, as in the *Cebrionidae*. Certain characters listed by Hyslop (1923) for distinguishing *Cebrionidae* from *Elateridae* are sometimes compromised; i.e., mandibles not strongly protuberant, mesocoxae distinctly separated, tibial spurs lacking or very feeble, and 5 visible abdominal segments in both sexes (*Elateridae*) versus mandibles protuberant, mesocoxae approximate, tibial spurs well to feebly developed, and 6 visible abdominal segments in male (*Cebrionidae*). So far as is known the anterior tibiae of *Elateridae* seem not to be expanded at the apex as are those of the *Cebrionidae*. Another character, the prosternal mucro, is abruptly incurved in the *Cebrionidae* but more gradually incurved than straight in the *Aplastinae*.

The foregoing illustrates the very close relationships between the *Cebrionidae* and *Aplastinae*, and it seems evident that the *Aplastinae* represent a link between the *Elateridae* and the *Cebrionidae*. The *Cebrionidae*, indeed, were only considered a separate family in this century and there are considerable grounds for including them as a subfamily within the *Elateridae* as given in this paper. Such a move would take in the *Aplastini* and *Pleonomini* as separate tribes within such a proposed group-
ing, along with the nominate tribe. At present I feel it better to let the matter rest

until the relationships of the Elateroidea in general are more clearly understood than at present.

Seventeen genera and 65 species grouped in 2 tribes are included in this new taxon. The genera are listed under their respective tribes.

KEY TO THE TRIBES OF APLASTINAE

1. Prosternal sutures straight and closed **Pleonomini**
 Prosternal sutures curved, more or less excavated in front **Aplastini, n. tribe**

APLASTINI, **new tribe**

Adult. Body depressed, parallel-sided, head capsule oval, deflexed, mouthparts inferior, frons without ridge between and above antennae; antennae reaching only to behind elytral bases; thorax subquadrate or quadrilateral; prosternum truncate, exposing labium, prosternal sutures single, curved and more or less excavated; scutellum shield-shaped, never cordate; mesocoxae open to both mesepimeron and mesepisternum, mesosternal coxae approximate to contiguous, metasternum pointed to nearly obsolete between coxae; meso- and metasternum distinct, joined by a definite suture; tarsi simple; claws simple.

Eight genera and some 42 species are contained in this tribe. Until relatively recently it was considered a separate family, the Plastoceridae, and listed as such by Schenkling (1927). It has since been sunk into synonymy with the Oestodinae by various authors. With Crowson's (1972) removal of *Plastocerus* and the consequent establishment of the Aplastinae in this paper, the inclusion of the Pleonomini necessitates the erection of a tribe for members of the nominate grouping.

All species known are from the Americas or Madagascar (including Mauritius). A single species listed from SE Asia (Tonkin), *Plastocerus thoracicus* Fleutiaux, is congeneric with *Plastocerus angulosus* (Germar). This was recognized by Fleutiaux (1940) when he transferred *P. thoracicus* to *Ceroplastus*, which contained only *P. angulosus* and is now synonymous with *Plastocerus*.

The tribe stands in need of revision, especially at the specific level. Van Dyke (1932) has provided keys to the then recognized North American species and Fleutiaux (1929) gave keys to the Madagascar species.

Included genera: *Aplastus* LeConte, 1859 (= *Anamesus* LeConte, 1866); *Diplophoenicus* Candèze, 1895 [= *Paradoxon* Fleutiaux, 1903, = *Paradoxon* Fleutiaux, 1929 (error)]; *Didymolophus* Fairmaire, 1904; *Pyrapractus* Fairmaire, 1884; *Practapyrus* Fleutiaux, 1929; *Euthysanius* LeConte, 1853; *Dodecacius* Schwarz, 1902; *Octinodes* Candèze, 1863 [= *Plastocerus* LeConte, 1853 (nec Schaum, 1852, Plastoceridae)].

Tribe PLEONOMINI Semenov-Tian-Shanskij & Pjatakova

Pleonomini Semenov-Tian-Shanskij & Pjatakova, 1936.

Adult. Body depressed, parallel-sided; head capsule oval, deflexed, mouthparts inferior, frons without ridge between antennae but with a short oblique ridge above antennal insertions, antennae often very long, much longer than $\frac{1}{2}$ the body in the δ ; thorax subquadrate or quadrilateral (rarely convex front of middle); prosternum truncate, exposing labium, prosternal sutures single, straight, closed; scutellum shield-shaped, never cordate; mesocoxae open to both mesepimeron and mesepisternum or (apparently)

just closed to mesepisternum, mesosternal coxae approximate, metasternum pointed; meso- and metasternum distinct, joined by a definite suture; tarsi simple; claws simple.

This is a small tribe with 9 genera and 24 species. Laurent's 1966 work covers most of this group, which he designated as a subfamily. The particulars given in this diagnosis lead me to refer this taxa to the Aplastinae very close to the Aplastini, and I suspect these 2 groups have very little to separate them. The chief distinguishing features are the straight and closed prosternal sutures, long antennae and oblique ridge over the antennae of Pleonomini versus the curved and excavated prosternal sutures, normally short antennae and absence of a ridge above the antennae in the Plastocerini.

Semenov-Tian-Shanskij & Pjatakova's 1936 work contains the earliest reference to Pleonomini which I can find, and they cite it as a tribe of Denticollinae related to the Nyctorini and Cardiophorini, which were also considered to be in that subfamily. These authors included the genera *Pleonomus* Mentrès and *Clon* Semenov. By implication, an earlier unnamed author is responsible for the tribal name, but such a paper (if it exists) has not been located to date.

Included genera: *Pleonomoides* Schwarz, 1907; *Alyctelater* Laurent, 1966; *Promopleus* Laurent, 1966; *Nothoscus* Laurent, 1966; *Mopleonus* Fleutiaux, 1935; *Pleonomus* Mentrès, 1849 (= *Ictis* Candèze, 1863, = *Serropalpus* Falderman, 1835); *Lomopheus* Gurjeva, 1976; *Nomopleus* Candèze, 1891; *Clon* Semenov, 1900.

IX. Subfamily OESTODINAE Hyslop

Oestodini Hyslop, 1917.

Hemiopsinae Fleutiaux, 1940. **New synonymy.**

Adult. Head capsule oval, deflexed, mouthparts inferior, frons without ridge between and above antennae or carinate only above antennal insertions; prosternum truncate, exposing labium; scutellum various, never cordate; mesocoxae open to both mesepimeron and mesepisternum; meso- and metasternum distinct, joined by a definite suture; tarsi without pads; claws simple, without basal setae.

Larva. Nasule absent or vestigial, galea of 2 segments, mandibles simple, with teeth, postmentum subrectangular; laterotergite incompletely separated from mediotergite at most; spiracle more or less well developed, embedded in mediotergite; 9th abdominal segment flattened in caudal ½, with prongs and small caudal notch.

This particular subfamily is admittedly diverse and probably will have to be divided when research is able to show the proper placement of the 3 tribes that are at present included here. The only tribe that can be placed with confidence in the Oestodinae is the Oestodini, whose larva is described above. The larva of *Geranus lineicollis* White was described by Hudson (1934) but the description omits some important details, which make a reexamination of the larva necessary. Very likely Laurent's Athoormorphini (Laurent 1966) will be included in the subfamily also, for there is little real difference in the adult forms, save for the shape of the front. The Sphaenelaterini seem more like typical elaters in shape.

The Phyllocerinae Reitter, 1905 (nec Heyden, 1906) should be included if one

follows Fleutiaux (1940). However, study shows that in the Phyllocerinae the frons is eucnemid-like, as Fleutiaux admits. This is one of the basic characters separating the Eucnemidae from the Elateridae. Therefore, until the relationship between these 2 families is better understood, this character should not be compromised. Hence the Phyllocerinae are regarded as Eucnemidae in this paper.

Recently, Gurjeva (1974) and Dolin (1975a) included the tribe Drapetini Gurjeva, 1974 (nec Dolin, 1975a) with the single genus *Drapetes* Dejean. Previously this genus had been regarded by most authorities as belonging to the Throscidae, subfamily Lissominae. Since *Drapetes* has a lobed, not a truncate prosternum, I feel it better to leave it in the Throscidae until the relationships and limits of the Elateridae, Throscidae and Eucnemidae are more clearly understood.

KEY TO THE TRIBES OF OESTODINAE

1. Front strongly declivous, gently rounded **Anthoomorphini, n. status**
 Front contracted, not convex anteriorly 2
- 2 (1). Pronotum normally wide and flat; body somewhat depressed and broadened
 **Sphaenelaterini, n. tribe**
 Pronotum either short and evenly convex or even globular or elongate and subcylindrical, never
 wide and flattened; body cylindrical, not depressed **Oestodini**

Tribe OESTODINI Hyslop, 1917

Adult. Body normally shell-shaped, head capsule oval, deflexed, mouthparts inferior, frons without ridge between and above antennae; antennae of normal length, i.e., reaching beyond elytral bases; thorax normally arcuate on sides and convex or globular dorsally to elongate, narrow and subcylindrical; prosternum truncate, exposing labium, prosternal sutures concave and double or secondarily closed (excavated line present) and straight; scutellum shield-shaped, never cordate; mesocoxae open to both mesepimeron and mesepisternum, mesosternal coxae more or less approximate, metasternum more or less pointed; meso- and metasternum distinct, joined by a definite suture; tarsi simple or with lobe on 1 or more segments; claws simple.

At present the tribe comprises 5 genera with 35 species. *Hemiops* LaPorte is newly included in this tribe, as on examination its species were found to possess the distinguishing characters given above. This places the Hemiopsinae as a subjective junior synonym of the Oestodinae. *Anaspasis* Candèze is also placed here in accordance with von Hayek (1973) who associated this genus with *Protelater* Sharp.

Tribe ATHOOMORPHINI Laurent, **new status**

Athoomorphinae Laurent, 1966.

Adult. Body normally shell-shaped, head capsule oval, deflexed, mouthparts inferior, frons without ridge between and above antennae but here strongly declivous and convex anteriorly; antennae of normal length, i.e., reaching beyond elytral bases; thorax short, about as long as wide but normally arcuate on sides, convex dorsally; prosternum truncate, exposing labium, prosternal sutures concave and double; scutellum shield-shaped, never cordate; mesocoxae open to both mesepimeron and mesepisternum, mesosternal coxae approximate, metasternum pointed; meso- and metasternum distinct, joined by a definite suture; tarsi simple; claws simple.

The tribe contains 1 genus and 1 species only. The Athoomorphini were the 2nd of 2 subfamilies established by Laurent (1966), who separated it from the Oestodinae on the grounds that the genera *Athoomorphus* Schwarz and *Oestodes* LeConte differ in the form of the frons, the shape of the last segment of the palpus and in the type of genitalia, which differ significantly. I am not sure about the value of the last palpal segment as a tribal (or subfamilial) character and have not included it in the tribal diagnosis.

SPHAENELATERINI, new tribe

Adult. Body normally shell-shaped but depressed, normally arcuate on sides; head capsule oval, deflexed, mouthparts inferior, frons without ridge between and above antennae, antennae scarcely reaching to elytral bases; thorax wide and flat, normally arcuate on sides; prosternum truncate, exposing labium, prosternal sutures single, straight and closed or partly open; scutellum shield-shaped, never cordate; mesocoxae open to both mesepimeron and mesepisternum, mesosternal coxae well separated, metasternum truncate; meso- and metasternum distinctly joined by a definite suture; tarsi simple; claws simple.

The new tribe is based on *Sphaenelater* Schwarz (New Zealand) with 4 species; also included are *Tetraraphes* Yablokov (fossil, Lower Oligocene) with 1 species and *Anthracoptyx* Horn (United States) with 1 species. This is an ancient group which probably predates the other, more specialized tribes. Although *Tetraraphes* is known from the Oligocene, the group itself is surely much older than that. It is remarkable that the extant relicts still survive.

X. Subfamily MELANOTINAE Candèze

Melanotites Candèze, 1859.

Adult. Head capsule oval, deflexed, mouthparts inferior, frons ridged above and between antennae (may be obsolete in middle); prosternum normally arcuate anteriorly; scutellum various, never cordate, may be slightly excavate anteriorly; mesocoxae open to mesepimeron but closed to mesepisternum; meso- and metasternum distinct, joined by a definite suture; tarsi simple, without pads, but rarely 3rd segment broadened to receive 4th; claws prominently pectinate and without basal setae.

Larva. Nasule present, galea of 2 segments, postmentum subrectangular; laterotergite incompletely separated from mediotergite at most; spiracle generally well developed, embedded in mediotergite; 9th abdominal segment flattened in caudal $\frac{1}{2}$, no prongs or caudal notch but platelike and scalloped.

A small, rather homogenous subfamily with 8 genera and perhaps 300 species, mostly in the genus *Melanotus* Eschscholtz. Study of the group has been hindered by difficulties in separating the various species on external morphological grounds, making genitalia examination imperative in many cases. For this reason there are probably many named synonyms and perhaps more undescribed species. The North American species have recently been monographed (all in *Melanotus* Eschscholtz) by Quate & Thompson (1967).

XI. Subfamily NEGAstriINAE Nakane & Kishii

Negastrinae Nakane & Kishii, 1956.

Adult. Head capsule flattened, mouthparts more or less prognathous, flattened, frons ridged above and between antennae; prosternum usually wider in middle, sometimes parallel-sided, sutures usually

arcuate, prosternum usually prominent anteriorly, may be truncate, exposing mouthparts, prosternal process elongate; mesepimeron and mesepisternum cut off from mesocoxal cavity by meso- and metasternum, mesepimeron reduced in size; meso- and metasternum distinct, joined by a definite suture; scutellum oval; tarsi variable, simple, or 3rd and 4th lobed or lamellate or 4th only lobed or lamellate; claws simple, feebly toothed or flanged.

Larva. Head depressed, nasule present, galea 1-segmented, mandibles simple with teeth and denticles; laterotergite of only 1 sclerite; spiracle small, fitting within concavity of laterotergite, no spiracular sclerite; abdomen normally segmented and with caudal notch on 9th segment.

A large subfamily which has not been well studied at the specific level. Probably $\frac{1}{2}$ or more of the specimens presently in collections belong to species yet to be described. Only the European fauna is well known.

The subfamily is well defined and a recent generic revision by Stibick (1971) has clarified the status of the genera [excluding 2 fossil genera recently added by Dolin (1976)]. It may eventually be necessary to group the genera into tribal units. This is not advisable until the majority of species has been described and assigned to appropriate genera.

The genus *Tropihypnus* Reitter was moved by Dolin (1975a) to the Athoini (Athouina of this paper) on grounds of larval and wing morphology. This removes an apparently discontinuous genus within the Negastrinae. The closed mesocoxae will still raise queries, but it should be pointed out that the mesepimeron of *Tropihypnus* is not reduced as in the negastrines or cardiophorines, a fact which is utilized in the subfamily keys. Since simple open or closed mesocoxae occur elsewhere within other groups (i.e., Pyrophorinae), it appears that this development occurred independently a number of times and has no relationship to the well developed and modified plates surrounding the mesocoxae of negastrines and cardiophorines.

XII. Subfamily CARDIOPHORINAE Candèze

Cardiophorites Candèze, 1860.

Dicronychidae Schwarz, 1897.

Aptopina Jacobson, 1913.

Esthesopinae Fleutiaux, 1919.

Adult. Head capsule usually oval, deflexed, but may be somewhat depressed, mouthparts inferior, frons ridged between and above antennae; prosternum variable, usually straight on sides, sometimes broad, usually prominent, sometimes emarginate or truncate in front, exposing mouthparts, prosternal process short, truncate; mesepimeron and mesepisternum cut off from mesocoxal cavity by meso- and metasternum, mesepimeron reduced in size; meso- and metasternum distinct, joined by definite suture; scutellum usually cordate, sometimes shield-shaped or oblong; tarsi various, simple, or 4th or 3rd and 4th lobed or 4th cordate; claws variable, simple, bicuspidate, dentate or pectinate.

Larva. Head depressed, elongate, nasule present, galea 2-segmented, mandibles deeply cleft into dorsal and ventral branches; laterotergite separate, entire, continuous over pseudosegments; spiracle small, more or less fitting within concavity of laterotergite with lateral ambulatory papilla, no spiracular sclerite; abdomen thread-like, with nodulated pseudosegmentation; 9th segment with anal lobes.

This is a fairly large subfamily with 38 genera and perhaps 1000 species. The principal genus is *Cardiophorus* Eschscholtz, which was listed in 1925 by Schenkling

with 472 species. Further species were listed in Schenkling's addenda (1927b) and in Lanchester (1971).

As a group, the Cardiophorinae are little known and in great need of revision. I recognize 2 tribes, the Cardiophorini and the Nyctorini, as does Gurjeva (1974). However, the status of the monogeneric Nyctorini needs to be closely reappraised. Gurjeva (1974) also placed the Hemiopsini here, but in my opinion, the characters of the Hemiopsini, especially of the thorax and arrangement of the sternal plates, necessitate placing this group in synonymy under the Oestodini.

The Dicronychidae, listed as a separate family by various authors (e.g., Schenkling 1927b) is listed here as a synonym. Arnett (1962) also listed Dicronychidae as a synonym under Cardiophorinae as did Leseigneur (1972), the latter following Jeannel (1955).

KEY TO THE TRIBES OF CARDIOPHORINAE

Prosternum normally arcuate or emarginate in front **Cardiophorini**
 Prosternum truncate, prosternal lobe completely absent **Nyctorini**

Tribe CARDIOPHORINI Candèze

Adult. Head capsule usually oval, deflexed, but may be somewhat depressed, mouthparts inferior, frons ridged between and above antennae; prosternum variable, usually straight on sides, sometimes broad, usually prominent, sometimes emarginate in front, exposing mouthparts, prosternal process short, truncate; mesepimeron and mesepisternum cut off from mesocoxal cavity by meso- and metasternum, mesepimeron reduced in size; meso- and metasternum distinct, joined by definite suture; scutellum usually cordate, sometimes shield-shaped or oblong; tarsi various, simple, or 4th or 3rd and 4th lobed or 4th cordate; claws variable, simple, bicuspidate, dentate or pectinate.

This tribe is a heterogeneous assemblage of 35 genera from which the Nyctorini are rather doubtfully separated. A thorough generic and specific study could eventuate in a number of new tribal or subtribal taxa being established. The only studies on the tribe to date have been of a regional nature. Two recent papers, Leseigneur (1972) and Lanchester (1971) deal with the specific level only.

Tribe NYCTORINI Semenov-Tian-Shanskij & Pjatakova

Nyctorini Semenov-Tian-Shanskij & Pjatakova, 1936.

Adult. Head capsule oval, deflexed, mouthparts inferior, frons ridged between and above antennae; prosternum straight on sides, truncate anteriorly due to absence of lobe, prosternal process short, truncate; mesepimeron and mesepisternum cut off from mesocoxal cavity by meso- and metasternum, mesepimeron reduced in size; meso- and metasternum distinct, joined by definite suture; scutellum subpentagonal, almost subcordiform; tarsi simple, narrow; claws simple, slender and elongate.

The tribe contains 1 genus, *Nyctor*, and 1 species, *N. expallidus* Semenov-Tien-Shanskij & Pjatakova, only. The original description of the tribe singled out the following 3 characters to separate it from the Cardiophorini: (1) absence of a prosternal lobe; (2) enlarged eyes; and (3) well pronounced sexual dimorphism of the antennae and prothorax. Only the 1st character is listed herein, as the latter 2 are suspect. Both

large and normal eyes may occur in some species within the same genus (certain New Zealand Hypnoidinae for example) and sexual dimorphism is quite pronounced or at least evident in many species scattered throughout the family. I have not checked for the absence of the prosternal lobe in all the genera listed under the Cardiophorini, but some contain species which do have an emarginate prosternum.

It should be noted that Gurjeva (1974) retains this tribe, but that Dolin (1975a) disagreed and sunk it into synonymy under the Cardiophorini.

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LIST OF FAMILY-GROUP TAXA

One hundred and twenty-three family-group names are listed alphabetically, with the number of the pertinent subfamily following in Roman numerals. Subfamilies recognized in this paper are in CAPS, all synonyms are in *italics*, and new taxa are in **boldface**; the original spelling of certain taxa are in brackets.

<i>Adelocerini</i> III	CARDIOPHORINAE.XII	Elaterini VII
Adrastini VII	Cardiophorini XII	(Elaterites) VII
(Adrastites) VII	(Cardiophorites) XII	<i>Esthesopinae</i> XII
Agriotini VII	<i>Cardiorhinites</i> VII	<i>Eudactylites</i> VI
(Agrypnides) III	<i>Cavicoxumidae</i> III	Euplinthina III
Agrypnini III	(Chalcolepidiides) III	Hapsodrilina III
<i>Alaites</i> III	Chalcolepidiini III	Heligmina III
<i>Allotriites</i> VI	Compsoplinthina III	Heligmini III
(Ampedinae) VII	Conoderini III	Hemicrepidina VI
Ampedini VII	<i>Corymbitites</i> VI	(Hemicrepidini) VI
Anischina VI	Crepidomenina VI	<i>Hemiopsinae</i> IX
(Anischinae) VI	(Crepidomenites) VI	(Hemirhipides) III
APLASTINAE VIII	<i>Cryptohypnites</i> V	Hemirhipini III
Aplastini VIII	(Ctenicerinae) VI	HYPNOIDINAE V
<i>Aptopina</i> XII	Ctenicerini VI	(Hypnoidini) V
<i>Asaphites</i> VI	Denticollina VI	Hypnoidini V
(Athoites) VI	DENTICOLLINAE VI	<i>Hypodesites</i> VII
(Athoomorphinae) IX	(Denticollini) VI	<i>Hypolithinae</i> V
Athoomorphini IX	Denticollini VI	<i>Laconini</i> III
Athouina VI	Dicrepidini VII	<i>Lepturoidini</i> VI
<i>Beliophorina</i> VI	(Dicrepidites) VII	<i>Limoniina</i> VI
(Campsosterninae) I	<i>Dicronychidae</i> XII	<i>Ludiides</i> VII
Campsosternini I	Dimina VI	Megapenthini VII
<i>Campylides</i> VI	(Dimites) VI	(Melanactides) IV
Campyloxenini III	ELATERINAE VII	MELANACTINAE IV

MELANOTINAE X	<i>Phyllophoridae</i> III	Pyrophorini III
(Melanotites) X	Physodactylina VI	(Rostricephalinae) II
<i>Monocrepidiites</i> III	(Physodactylini) VI	Rostricephalini II
NEGASTRIINAE XI	Physorhinini VII	<i>Semiotinae</i> I
Nyctophyxina III	(Physorhinites) VII	Senodoniina VI
Nyctorini XII	Piezophyllina III	(Senodoniinae) VI
<i>Octocryptites</i> III	PITYOBIINAE II	<i>Sericosomina</i> VII
Odontonychini VII	Pityobiini II	Sphaenelaterini IX
OESTODINAE IX	Pleonomini VIII	<i>Steatoderini</i> VII
(Oestodini) IX	(Pomachiliites) VII	<i>Synaptina</i> VII
Oestodini IX	Pomachiliini VII	<i>Taxognatini</i> VI
(Oxynopterides) I	Prisahypini V	Tetralobina III
OXYNOPTERINAE I	Protagyrypnini III	Tetralobini III
Oxynopterini I	Pseudomelanactini III	(Tetralobites) III
(Pachyderinae) VI	Pyrophorina III	<i>Toxognathinae</i> VI
Pachyderini VI	PYROPHORINAE III	
Pectocerini II	(Pyrophorites) III	

FAMILY-GROUP TAXA NOT INCLUDED IN THE ELATERIDAE

- Drapetini (Throscidae), see IX
 Phyllocerinae (Eucnemidae), see IX
 Plastocerinae (Plastoceridae), see VIII