SYSTEMATICS OF THE AUSTRALIAN CRYPTOCEPHALINAE (COLEOPTERA: CHRYSOMELIDAE)

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DECLARATION

This thesis does not contain any material which has been submitted for the award of any degree or diploma at any university. The research reported in this thesis was conducted by me and all the sources used have been acknowledged.

Christopher Athol McEwan Reid
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phthisis n. progressive wasting disease

Oxford English Dictionary

Abstract

The morphology of the larvae, pupae and adults of Camptosomata (Cryptocephalinae and sister-group Lamprosomatinae) is reviewed, with special reference to the Australian fauna. Terminology for the larval structures is redefined and a special study is made of the adult female oviposition structures. The morphological data base is studied with the phylogenetic analysis program PAUP and the variation of characters and taxa examined further with the program MACCLADE.

The morphological data and the phylogenetic analyses based on these data are applied to the redefinition of the Camptosomata and constituent taxa using a cladistic methodology. The Camptosomata are redefined and their possible sister-groups discussed. The Camptosomata are shown to be a monophyletic group and to exclude both Megascelidini (a tribe of Eumolpinae) and Synetinae. The Camptosomata comprise two subfamilies, Lamprosomatinae and Cryptocephalinae. Four tribes of Cryptocephalinae are recognised and redefined. One of these, the Cryptocephalini, with a high proportion of Australian taxa, is divided into five subtribes of 1, 3, 3, 5 and 11 genera.

The following nomenclatural changes are proposed (ignoring changes of rank) : Platycolaspina subtribe nov., Coenobiina subtribe nov., Ditropidina subtribe nov. and synonymy of Monachina (a homonym) and Cryptocephalina. New genera or subgenera proposed are : *Semelvillea* (in Platycolaspina), *Ditropidella* (in Ditropidina) and *Melatia* (in Cryptocephalina), and the subgenera *Aorocarpon* and *Cadmoides* in *Cadmus* Erichson (Cryptocephalina). The following generic synonymy is proposed (senior synonym first) : *Leasia* Jacoby (= *Agetinella* Jacoby); *Aprionota* Maulik (= *Cephalocryptus* Gressitt, *Pycnophthalma* Maulik); *Ditropidus* Erichson (= *Bucharis* Baly, *Elaphodes* Suffrian, *Euditropidus* Lea, *Pleomorphus* Chapuis, *Polyachus* Chapuis, *Prasonotus* Suffrian, *Tappesia* Baly); *Scaphodius* Chapuis (= *Nyetra* Baly); *Cryptocephalus* Geoffroy (= *Jaxartiolus* Jacobsen and *Bassareus* Haldeman); *Aporocera* Saunders (= *Chariderma* Baly, *Chloroplisma* Saunders, *Cyphodera* Baly, *Loxopleurus* Suffrian, *Melinobius* Jacoby, *Rhombosternus* Suffrian, *Schizosternus*

Chapuis). New combinations of genera in tribes and subtribes are *Mylassa* Stål reinstated as a valid genus in Pachybrachini, *Platycolaspis* Jacoby and *Leasia* Jacoby in Cryptocephalini (Platycolaspina) and *Arnomus* Sharp and *Atenesus* Weise in Platycolaspina. As a result of the above new generic synonymy, several new species combinations are made. The new genus *Semelvillea* ,with eight species, is monographed.

Types of three-quarters of the described species of New Zealand and Australian Cryptocephalinae were examined and the following new species synonymy is made (senior synonym first) : *Chlamisus aterrimus* (Lea) (= *C. australis* Bryant); *Arnomus curtipes* Broun (= *A. impressus* Broun, = *A. viridicollis* Broun); *Arnomus signatus* Broun (= *A. fulvus* Broun, = *A. vicinus* Broun); *Ditropidus anthracinus* Erichson (= *D. punctivarius* Lea); *Ditropidus aurichalceus* Suffrian (= *D. oblongipennis* Lea); *Ditropidus carbonarius* Baly (= *D. subsimilis* Lea); *Ditropidus festivus* (Suffrian) (= *D. suffriani* Chapuis); *Ditropidus maculicollis* Chapuis (= *D. erythroderes* (Lea), = *D. niger* (Lea), = *D. maculicollis* (Weise)); *Ditropidus ornatus* Baly (= *D. alphabeticus* Lea); *Ditropidus pallidipennis* Chapuis (= *D. dolichognathus* (Lea)); *Ditropidus ruficollis* Saunders (= *D. elegantulus* Baly, = *D. rufipes* Saunders); *Ditropidus saundersi* (Baly) (= *D. multimaculatus* (Lea)); *Ditropidus variiceps* Lea (= *D. marginipennis* Lea); *Aporocera albogularis* (Chapuis) (= *A. coccineus* (Chapuis), = *A. delicatulus* (Lea)); *Aporocera apicalis* Saunders (= *A. bicolor* Saunders); *Aporocera argentata* (Chapuis) (= *A. fasciata* (Weise)); *Aporocera aurantiaca* (Chapuis) (= *A. monticola* (Blackburn)); *Aporocera australis* (Saunders) (= *A. erosa* (Saunders), = *A. larinus* (Lea)); *Aporocera cicatricosa* (Chapuis) (= *A. calomeloides* (Lea)); *Aporocera gibba* (Chapuis) (= *A. lugubris* (Lea)); *Aporocera iridipennis* (Chapuis) (= ***A. decens*** (Weise)); *Aporocera libertina* (Suffrian) (= *A. castor* (Lea)); *Aporocera nigrolineata* (Chapuis) (= *A. castigatus* (Lea)); *Aporocera parenthetica* (Suffrian) (= *A. melanopa* (Lea)); *Aporocera paupercula* (Germar) (= *A. rufescens* (Boheman)); *Aporocera ringens* (Chapuis) (= *A. clypealis* (Lea)); *Aporocera tasmanica* (Saunders) (= *A. impressicollis* (Boheman)); *Aporocera viridipennis* (Saunders) (= *A. t-nigrum* (Lea));

Aporocera viridis (Saunders) (= *A. aereus* (Suffrian)); *Aporocera analis* (Chapuis) (= *A. foveiventris* (Lea)); *Cadmus crucicollis* (Boisduval) (= *C. canaliculatus* Chapuis, = *C. rugosus* Suffrian); *Cadmus litigiosus* Boheman (= *C. vibrans* Suffrian); *Cadmus cariosus* Chapuis (= *C. minor* (Blackburn)); *Cadmus pauxillus* Chapuis (= *C. perlatus* Lea); *Cadmus braccatus* (Klug) (= *C. saundersi* Baly); *Cadmus breweri* (Baly) (= *C. duboulai* Baly).

Representation of Cryptocephalinae in Australia is shown to be as follows (number of genera in brackets) : Chlamisini (1), Clytrini (1), Pachybrachini (1, introduced), Platycolaspina (4), Coenobiina (1), Ditropidina (2) and Cryptocephalina (4). Larvae and adults of the genera and subgenera in Australia and the south-western Pacific are diagnosed and keys are provided for the identification of these taxa at both life stages. The entire Camptosomatan fauna of Australia and the south-western Pacific is catalogued.

The only truth lies in learning to free ourselves from insane passion for the truth.

William of Baskerville, 1327 (in Eco 1983).

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Arthur Lea, 1904.

Chapter 1 : The systematics of Australian Cryptocephalinae

1.1 Introduction

The Chrysomelidae is one of the larger families of polyphagan Coleoptera and is distributed in all major zoogeographic regions of the world. Within the Chrysomelidae a distinct, closely related group of subfamilies, collectively known as the Camptosomata, has long been recognised (Crowson 1967). The present study is primarily concerned with Australian members of one of these subfamilies, the Cryptocephalinae, but the results significantly affect the classification of the Camptosomata as a whole. The new nomenclature proposed for all familial and generic taxa in the Camptosomata is compared in Table 1 with the classification available from the standard checklist (Seeno and Wilcox 1982). This new nomenclature is used throughout the following text so that there is no confusion of names between the introductory discussions and the derivation of the new classification (Chapter **8**). Where necessary the older name is given in square brackets. Two former subfamilies, Chlamisinae and Clytrinae, are reduced to tribal rank within the Cryptocephalinae. Within the informal but traditional designation Camptosomata two subfamilies are recognised, Lamprosomatinae and Cryptocephalinae. Maintenance of the term Camptosomata is perhaps unfortunate. For the present it is justified for the following reasons : this term is well understood within the Chrysomelidae; there is no available rank between family and subfamily; given the closeness of certain Eumolpinae and the Synetinae to Lamprosomatinae it seems unwise to elevate the Camptosomata to familial status; and the differences between Lamprosomatinae and Cryptocephalinae warrant their separate subfamilial status. Some previous treatments of Camptosomata have united the Lamprosomatinae, Chlamisini, Clytrini and Cryptocephalini together with Megascelidini as one subfamily (Crowson 1967), or excluded the Lamprosomatinae on plesiomorphic evidence (Jolivet 1957; Medvedev 1971).

It has been necessary to designate subtribes for the recognition of monophyletic groups of genera within tribes. The Code gives no recommendation for subtribal

Table 1. Summary of nomenclature used here compared with that of Seeno and Wilcox (1982). This list includes all suprageneric taxa mentioned in the text, all Australian genera of Cryptocephalinae and all genera, worldwide, of Cryptocephalini. Genera present in Australia are indicated with an asterisk.

This work	Seeno and Wilcox 1982
Eumolpinae	Eumolpinae
Megascelidini	Megascelinae
Synetinae	Synetinae
Lamprosomatinae	Lamprosomatinae
Sphaerocharitini	Sphaerocharini and Neochlamisini
Lamprosomatini	Lamprosomatini
Cryptocephalinae	Cryptocephalinae, Chlamisinae and Clytrinae
Chlamisini	Chlamisinae
**Chlamisus*	*Chlamisus*
Clytrini	Clytrinae
Clytrina	Clytrini
**Aetheomorpha*	*Aetheomorpha*
Megalostomina	Megalostomini
Babiina	Babiini, Arateini and Ischiopachini
Eoclytrina	Eoclytrini
Pachybrachini	Pachybrachini (in Cryptocephalinae)
Mylassa	*Cryptocephalus* (partim)
**Metallactus*	*Metallactus*

Achenopini	Achenopini
Cryptocephalini	Cryptocephalinae
Stylosomina	Stylosomini
Stylosomus	_Stylosomus_
Platycolaspina	(in Colaspini, Eumolpinae)
*_Platycolaspis_	_Platycolaspis_ (in Eumolpinae)
*_Leasia_	_Leasia_ (non-Chrysomelidae) and _Agetinella_ (in Eumolpinae)
*_Atenesus_	_Atenesus_ (in Stylosomini)
Arnomus	_Arnomus_ (in Stylosomini)
*_Semelvillea_	-
Coenobiina	Monachini (partim)
Coenobius	_Coenobius_
Isnus	_Isnus_
*_Aprionota_	_Ditropidus_ (partim), _Cephalocryptus_ and _Pycnophthalma_
Ditropidina	Monachini (partim)
Adiscus	_Adiscus_
*_Ditropidus_	_Bucharis, Ditropidus, Elaphodes, Euditropidus, Pleomorphus, Polyachus, Prasonotus_ and _Tappesia_ (in Cryptocephalini)
*_Ditropidella_	_Ditropidus_ (partim)
Scaphodius	_Scaphodius_ and _Nyetra_
Cryptocephalina	Cryptocephalini and Monachini (partim)

Cryptocephalus	*Cryptocephalus*, *Jaxartiolus* and *Bassareus*
Heptarthrius	*Heptarthrius* (Monachini)
Lexiphanes	*Lexiphanes* (Monachini)
Stegnocephala	*Stegnocephala* (Monachini)
Protinocephalus	*Protinocephalus*
Lophistomus	*Lophistomus*
Melixanthus	*Melixanthus*
**Diachus*	*Diachus*
Triachus	*Triachus*
**Aporocera* s. str.	*Aporocera*, *Chariderma*, *Chloroplisma*, *Cryptocephalus* (partim), *Cyphodera* (sg. of *Cadmus*), *Loxopleurus*, *Melinobius*, *Rhombosternus*, *Schizosternus*,
sg. **Diandichus*	*Diandichus* (in Pachybrachini)
**Cadmus* s. str.	*Cadmus* and *Prionopleura* (sg.)
sg. **Brachycaulus*	*Brachycaulus*
sg. **Lachnabothra*	*Lachnabothra*
sg. **Cadmoides*	*Cadmus* s. str.(partim)
sg. **Aorocarpon*	*Brachycaulus*, *Cadmus*, *Cryptocephalus* and *Loxopleurus* (all partim)
**Melatia*	*Cadmus* (partim) and *Lachnabothra* (partim)

names and two suffices are in current use in entomological works. The plural suffix -iti, as used by Miller (1988), avoids the confusion with generic names (for example *Procrisina* Aslam) shown by the more commonly used -ina suffix (Seeno and Wilcox 1982). Names using -iti are close to those proposed by Chapuis (1874), using -ites, a suffix which is no longer considered valid (Art. 11f). Nevertheless, the suffix -ina is used here because it has precedent in Chrysomelidae, it should not be confused with italicised generic names and it is much less ugly.

In Australia the Camptosomata consists almost entirely of Cryptocephalini; there are no Lamprosomatinae or Pachybrachini, and I know of only two native species of each of Chlamisini and Clytrini. At the start of this study 537 names were available for Australian Cryptocephalini. I have included all of the Camptosomata in Australia because of the small size of the non-cryptocephaline subfamilies.

The approximately 3500 species of Cryptocephalini, as recently arranged (Seeno and Wilcox 1982), were placed in 49 genera in five tribes. This classification of tribes and genera remained essentially unchanged from its original inception (Chapuis 1874). Twenty-one of these genera were understood to be endemic to Australia or Australia plus New Guinea. This is a remarkable proportion of the world fauna for a regional fauna with no known gondwanan elements, and in a subfamily which is considered to be recently derived (Kasap and Crowson 1976). The Australian Cryptocephalini were described in the Stylosomini, Pachybrachini, 'Monachini' and Cryptocephalini, especially the last two tribes which included 99% of the species (Clavareau 1913; Lea 1920a). The fifth tribe, Achenopini was based on a single genus with few species, confined to southern Africa.

It is quite clear from even a cursory glance at the literature that the generic nomenclature of the Australian fauna is very unstable, and that the so-called endemism should be treated circumspectly. Several authors have drawn attention to the generic instability; notable is Lea's *crie de coeur* quoted above (frontispiece). The problem is particularly acute in the Cryptocephalina where there are several monotypic genera and where the presence of genuine *Cryptocephalus* Geoffroy has been contentious.

Several Australian genera have been synonymised by some authors (Seeno and Wilcox 1982) with *Cryptocephalus* which is a vast genus of approximately 1800 species worldwide in seven subgenera, although only the nominate subgenus has been recognised from Australia. The last keys to Australian genera were published in 1904 (Cryptocephalina : Lea 1904) and 1920 (Ditropidina : Lea 1920a), but these are not workable and exclude many taxa.

Nomenclatural instability has also been created by the misapplication of species names to genera, especially to the genus *Cryptocephalus*. Many unnecessary *nomina nova* have been created for homonyms based on misidentifications of the parent genus. Fortunately many other temporary homonyms have never been acted upon.

This project sets out to resolve three aspects of the classification of Australian Cryptocephalinae :

(1) to determine the phylogeny of the Australian species and consequently to establish a new generic framework,

(2) to determine the relationship between the Australian and other faunae,

(3) to provide detailed descriptions of the genera and present keys for their identification.

In practice these studies have considerable overlap and each is dependent on the others.

The approach to this project is strictly morphological but makes extensive use of adult and larval structure. The study of larvae is deliberately restricted to the first instar for two reasons. First, to avoid rearing problems, since successive instars have an increasing risk of mortality and, in some non-Australian species at least, take two years to develop (Medvedev and Zaitsev 1978). No Australian Camptosomata have been reared from egg to adult. Second, the first instar may be phylogenetically more useful at supra-specific levels, being a more conservative expression of the larval phenotype (Kimoto 1962a; Goulet 1979), and also having a few characters concerned with eclosion not present in later instars (Cox 1988). In later instars of Cryptocephalinae the presence of numerous secondary setae confuses the discernable setal patterns (for example see Medvedev and Zaitsev 1978; LeSage 1982). The use of first instars in phylogenetic analyses of Coleoptera is deservedly becoming more widespread, for example in Carabidae (Bousquet and Goulet 1984), Dytiscidae (Nilsson 1987) and Chrysomelidae of the subfamily Chrysomelinae (Kimoto 1962a, b, c; Reid 1983) and tribe Galerucini (Takizawa 1972).

1.2 History of the Australian Camptosomata

1.2.1 Cryptocephalini

The first described species, *Cryptocephalus didyma* Fabricius (1775), is now known to belong to the Eumolpinae (Radford 1981). For the next 65 years all described species were placed in the genus *Cryptocephalus*. There was a peak of nomenclatorial activity in the 1840s as the fauna came to be considered sufficiently different to warrant the creation of new genera or subgenera : *Ditropidus*, *Cadmus* (Erichson 1842); *Aporocera*, *Dicenopsis*, *Mitocera* (Saunders 1842a,b); *Brachycaulus* (Fairmaire 1843a); *Ochrosopsis*, *Anodonta*, *Idiocephala* (Saunders 1843a, b, c); *Odontoderes*, *Prionopleura*, *Onchosoma* (Saunders 1846a, b); *Chloroplisma*, *Lachnabothra*, *Pleomorpha* (Saunders 1847a, b); *Cataplus* (Gistel 1848). Three of these names were *nomina nuda* coined by Chevrolat in Dejean's catalogues of the 1830s (Chevrolat 1837). By 1847 descriptions or specimens of 61 species had been available to Saunders. The review of the Australian species by Suffrian (1859) has probably been the most influential work on the Australian fauna, as subsequent authors have generally followed his concepts. He described the genera *Elaphodes*, *Prasonotus*, *Loxopleurus*, and *Rhombosternus*, and was able to recognise 97 species. Suffrian acknowledged the genus *Cryptocephalus* in Australia.

The next phase of activity was promoted by a world review of chrysomelid genera (Chapuis 1874), in which the treatment of Cryptocephalini closely followed Suffrian's studies. By this time much new Australian material was available and the two leading rival chrysomelid workers, Baly and Chapuis, were describing many new genera (and species) : *Diandichus*, *Pleomorphus* (Chapuis 1874); *Polyachus* (Chapuis 1875a); *Schizosternus* (Chapuis 1876c); *Chariderma*, *Cyphodera*, *Paracephala*, *Euphyma*, *Paracadmus*, *Tappesia* (Baly 1877a, b, c). *Coenobius* Suffrian (1857) and *Bucharis* Baly (1865) were noted as Australian (Chapuis 1877; Baly 1878), having been originally described from Africa and south-east Asia respectively. Baly considered the Australian fauna of Cryptocephalina to be autochthonous and did not recognise any species of *Cryptocephalus*. Masters (1887), in his catalogue of Australian Coleoptera, listed 22 genera and 293 species as valid, but made some attempt to rationalise the plethora of names by synonymising several genera.

The most recent phase of taxonomic activity was at the beginning of this century when both Lea and Weise described new taxa, again from very different viewpoints. Lea, an Australian, had a more comprehensive collection to work from than any other worker and he attempted reviews of the Australian Cryptocephalini based on the material before him, without reference to types (Lea 1903a, 1904, 1920a, b, 1921a, b, c, 1926). He was conservative in seeking to preserve the existing classification (of Chapuis), although clearly finding it inadequate. He described just one new genus, *Euditropidus* (Lea 1920a), but provided keys and descriptions for most taxa and his nomenclature has been the system used throughout Australia to date. Weise worked on expeditionary material in Germany, without reference to other collections, and described many new species which have been ignored by Australian workers (Weise 1908, 1916, 1923). He erected the genus *Atenesus* (Weise 1923). The last taxonomic work on Australian Cryptocephalini described one new species (Oke 1932). I have recently noted the American species *Diachus auratus* (F.) in Australia (Reid 1988).

1.2.2 Pachybrachini

The genus *Diandichus*, described in Pachybrachini by Chapuis (1874), was correctly placed in the Cryptocephalini by Baly (1877a). There are no native Pachybrachini in Australia.

1.2.3 Clytrini

Only two species have been described, both in the early nineteenth century (Fabricius 1801; Lacordaire 1848). These are currently placed in *Aetheomorpha* Lacordaire. Neither species has been commented upon by Australian workers. *Leasia* Jacoby was described as a putative megalostomine in Clytrini (Jacoby 1907), and its status as a clytrine was endorsed by Crowson (1967). Here it is placed in Cryptocephalini.

1.2.4 Chlamisini

Only one species has been described, in the tropicopolitan genus *Chlamisus* Rafinesque (Bryant 1956).

1.2.5 Lamprosomatinae

There is no evidence for the existence of this subfamily in Australia despite assertions to the contrary (Seeno and Wilcox 1982; Kimoto 1988).

1.3 History of the non-Australian Camptosomata

1.3.1 Cryptocephalini

In most other areas of the world the generic and tribal systems of Suffrian (Asia : 1855, 1860; Africa : 1857; South America : 1863, 1866) and Chapuis (1874) have been retained. From an Australian perspective there have been two important more recent developments : (i), comprehensive faunal revisions of much of south-east Asia and the western Pacific islands and, (ii), the attempted subdivision of *Cryptocephalus* in the Palaearctic, especially central and western Asia. Also important is the lack of any modern treatment of the potentially related South American and African faunae.

In the West Pacific genera endemic to New Caledonia (*Scaphodius* Chapuis, *Nyetra* Baly), New Zealand (*Arnomus* Sharp), and Samoa/Fiji (*Aprionota* Maulik, *Pycnophthalma* Maulik) were listed by Seeno and Wilcox (1982). Conversely, many

Australian genera have been recognised in New Guinea (Gressitt 1965) and Fiji (Bryant and Gressitt 1957).

In the period 1950-1980 the subgenera of *Cryptocephalus*, which were all founded on Palaearctic species, were revised and nine new taxa added, largely based on male attributes of south European and western Asian species (Burlini 1955; Medvedev 1963; Lopatin 1965; Burlini 1969; Berti and Rapilly 1973; Lopatin 1977; Tomov 1979). However recently two of the authors involved have conceded that at least part of the new subgeneric system is unworkable (Berti and Rapilly 1979).

1.3.2 Pachybrachini

This tribe of nine genera is distributed throughout Africa, the Americas and Asia. The genera *Pachybrachis* (Holarctic) and *Griburius* (American) are particularly large. There are no modern revisions but the genus *Mylassa* Stål was studied by Monrós (1949b) who suggested a relationship with Australian Cryptocephalina.

1.3.3 Clytrini

The tribe is most diverse in the Neotropics and this fauna has been revised by Monrós (1953b) and Moldenke (1981). The Old World fauna is also large, but there have been no comprehensive revisions, the most complete treatments being those of Jacoby (1908b) for the Indian subcontinent, and Gressitt and Kimoto (1961) for China. Genera are still being added piecemeal.

1.3.4 Chlamisini

This small tribe is also most diverse in the Neotropics (Monrós 1951a; Karren 1972), the remaining species being generally restricted to the genus *Chlamisus* in south-east Asia (Gressitt and Kimoto 1961).

1.3.5 Lamprosomatinae

This is another small assemblage of species with a Neotropical centre of diversity. The world genera were revised by Monrós (1956a).

1.4 Diagnosis and biology of Camptosomata

A precise definition of the Camptosomata is not considered here but is given after discussion of the phylogenetic analyses (Chapter 9).

The Camptosomata are most obviously defined by their biology which has recently been reviewed, albeit from a eurocentric perspective (Erber 1988). They are plant feeders as both adults and larvae. All Camptosomata lay each egg with an individual coat of faecal matter plus glandular secretion, and this sac-like coat (scatoshell) is maintained by the larva and pupa. The larva has a characteristic C-shape, as a consequence of the need to bring the anus to the only exit from the scatoshell, and is bereft of well defined sclerites. In Australia the larvae most commonly feed on dead plant material, but may attack tree seedlings.

The adults are relatively unremarkable 'higher' Chrysomelidae, but usually comparatively compact and cylindrical. They are variable in size, 1-12mm long, and usually brightly coloured if large and metallic or black if small. The males have apical setae on the aedeagal median lobe and the females have at least some slight differentiation of the dorsal and ventral rectal surfaces which is used in creation of the scatoshell. Published definitions of the adult Camptosomata do not satisfactorily separate them from Eumolpinae and this lack of resolution is the reason for the controversial position of such groups as *Leasia*, Megascelidini and Lamprosomatinae. Adults feed on a wide variety of plants, particularly *Eucalyptus* and *Acacia* in Australia, and on both flowers and leaves. Flower feeding species may ingest pollen (Erber 1988; pers. obs.) but do not digest the grains, and the adults lack a mandibular mola.

In Australia, Chlamisini and Clytrini are confined to the wet tropical zone of the north but Cryptocephalini are found throughout.

1.5 Outline of study

For each life-stage studied there is a chapter giving an account of the material and the methods used to study it, an exposition of the basic external anatomy, the characters used and their states in tabular form, discussion of derivation of states and their polarity, and finally phylogenetic analysis of the character set using the computer based packages PAUP and MACCLADE. These chapters are followed by an analysis of all the data in combination and then a comparison of this data set and its analyses with data from other sources, primarily from literature and species not included in the analyses. The last sections are a classification with keys and descriptions of all supraspecific taxa, based on the analyses, and a discussion of various aspects of the biology of the Australian Camptosomata.

The format of this thesis is therefore as follows :

Chapter **2** : brief discussion of the material and methods used.

Chapter **3** : the camptosomatan egg and scatoshell and their contribution to phylogeny.

Chapter **4** : first-instar larvae, their structure and rôle in phylogenetic reconstruction.

Chapter **5** : brief review of the scant pupal data.

Chapter **6** : adult morphology and its contribution to camptosomatan phylogeny.

Chapter **7** : numerical analyses of combined life-stage data.

Chapter **8** : comparison of the morphological variation and numerical analyses described in Chapters **3-7**, together with additional taxa and characters, to provide a systematic phylogeny of the Camptosomata.

Chapter **9** : classification of the Australian Camptosomata with keys and descriptions for all named supraspecific taxa, based on the conclusions of Chapter **8**.

The appendices are : **A**, a list of all specimens examined in detail; **B**, a complete catalogue of Australian Camptosomata with notes on nomenclatural changes; **C**, the full data matrices for eggs, larvae, pupae and adults based on the material in **A**.

The tradition of all the dead generations weighs like a nightmare on the brain of the living

Marx, Karl (1848)

Application of parsimony algorithms to particular data sets can only be as good as those data allow. The open question, then, is not so much how best to analyse a data matrix, but how best to represent organismic variation in the matrix

Platnick, Norm (1987)

Chapter 2 : Materials and methods ; apologia

This essentially phylogenetic study was based on determination of the variation of characters in dead specimens. The characters were therefore the fundamental units. The choice of characters was limited by available material, methods used for studying morphology and methods of character analysis.

Details of collection, rearing and preparation are given in the individual life-stage chapters.

2.1 Choice of material

I have used species as the fundamental building blocks of this attempted classification. Ideally this study should have been based upon the examination of adults and larvae of all type species of all world cryptocephaline genera, plus those species expressing a wide range of character diversity within those taxa, plus undescribed forms with morphology lying outside the range of known genera. In practice these aims were attained for the adults of the Australian fauna and for the larvae of approximately a quarter of the Australian species, including two-thirds of the type species. Adults of nine of the 49 world genera were not examined, but adequate descriptions of these exist. Larvae of only four non-Australian cryptocephaline genera were available materially or as detailed published descriptions. A few adults and larvae of outgroup taxa and non-Australian Camptosomata from institutions in Australia and elsewhere were used to complete the data set.

This study of phylogeny was based on analyses of morphological variation between species of supposedly different genera. To provide some understanding of typical ranges of variation between and within genera, the range of variation of characters within well-defined monophyletic species groups (genera) was examined in three apparently (*a priori*) unrelated groups of Cryptocephalini. These groups were : (i) *Atenesus*, *Leasia*, *Platycolaspis*, *Semelvillea* and *Arnomus*; (ii) *Diandichus*; (iii) *Lachnabothra*.

Crowson (1970) has advocated an extreme form of analytical approach to higher taxonomy in which group relationships are examined from the top ranks downwards without necessarily examining individual *species*. He proposed this in opposition to a synthetic approach, for example beginning with a generic revision and working upwards through the ranks. Crowson's suggestion seems to involve too many *a priori* assumptions about the phylogenetic expression of characters, and ignores the fact that the basic unit in any classification of this kind is ultimately the species.

2.1.1 Adults

All material studied is listed in Appendix A.

The major aims of this study concerned the Australian supraspecific taxa of Cryptocephalini. Therefore all material available in the larger Australian collections was examined. Lea was the only significant Australian reviser of the fauna so I concentrated on the specimens seen by him, scattered through institutions in Hobart, Melbourne, Canberra, Sydney, Adelaide and Brisbane. The examination of types of Australian species was completed by visits to London, Oxford, Brussels and Berlin and loans from Halle, Copenhagen and Stockholm. This examination of described Australian taxa allowed assessment of the status of all genera and erection of new combinations and synonymies where necessary. Complete assessment of the status of all described species was not possible because this would have required, for example, critical dissection of almost all of the 250+ *Ditropidus* species, designation of hundreds of lectotypes (none of the describers of Australian cryptocephalines designated holotypes), and so on. From the outset it was likely that undescribed supraspecific taxa were present in collections and extensive loans were made of unsorted material from most Australian institutions and from the British Museum (Natural History) in London.

Fieldwork allowed the accumulation of further adult material, some of which was maintained alive to obtain eggs and then larvae (see below).

I intended to ascertain the relationships of the Australian cryptocephaline fauna to others. Therefore specimens of 21 non-Australian genera, from a variety of sources, were studied. In most cases the type species was included, or was known to be insignificantly different from the species studied. However in the case of *Achenops* Suffrian the species borrowed was not the type and appears to belong to *Acolastus* Gerstaecker. In view of the supposed intermediacy of *Achenops* between *Lexiphanes* Gistl and *Stylosomus* Suffrian (Chapuis 1874) this may have been a critical omission for the phylogenetic analyses. Non-Australian taxa were studied from a small synoptic collection at Australian National Insect Collection in Canberra, and the loans of south-west Pacific material from Hawaii and Brussels, and of other taxa from London and Harvard.

2.1.2 Eggs, larvae and pupae

No adult-associated immature stages of Australian taxa were available, therefore the Australian material used was reared for this study. Adults were collected by beating or hand-picking (the latter more successful on hot days) and placed with several shoots of host-plant in cylindrical clear-plastic containers with tight fitting screw-top lids. These containers varied in diameter and height between about 4.5 x 4.5 to 6.5 x 9 cm and the lids of most had the central 3-4 cm. diameter disc cut out and replaced with fine metal gauze which was fixed by applying heat to the overlap with the plastic. Commercially available glass vials, 5 x 2.5 cm., with gauze tops, were also used. Specimens from tropical or high rainfall areas were kept in unmodified tubs otherwise they suffered high mortality from desiccation. Generally, some effort was made to procure both sexes of a species. On summer field trips the temperature inside a vehicle sometimes reached 51°C. so living material was kept cool in an esky.

Mated females collected in the field usually laid eggs readily within the first two days of capture, even if they refused the available food-plant foliage. Since only first-instar larvae were required the process of rearing was very easy: simply keeping the eggs until they hatched.

Some Asian species take two years to reach maturity (Medvedev and Zaitsev 1978) and therefore I did not plan to rear pupae nor to use them in my work. Nevertheless, in the course of this project a few specimens were taken with definite adult association and the data from these have been incorporated in this study.

Larvae of two species of Chlamisini were borrowed from institutions in Queensland and non-Australian larvae of Cryptocephalini, Clytrini and Lamprosomatinae were borrowed from London.

In principle I was loth to use published descriptions in the analyses because so many character states were unrecorded. However, I used published larval descriptions for the critical genera *Stylosomus* and *Pachybrachis* Chevrolat, and published pupal descriptions for several taxa.

Appendix A includes names and data for all immature material studied.

2.1.3 Sources of loaned material

Material was borrowed from the following institutions:

AMS = Australian Museum, Sydney
ANIC = Australian National Insect Collection, Canberra
BCRI = Biological and Chemical Research Institute, New South Wales Department of Agriculture, Rydalmere
BPBM = Bernice P. Bishop Museum, Hawaii
BMNH = British Museum (Natural History), London
CIE = Commonwealth Agricultural Bureau, Institute of Entomology, London
DPIB = Department of Primary Industry, Brisbane
DPIM = Department of Primary Industry, Mareeba
DSIR = Department of Scientific and Industrial Research, Wellington
HDOU = Hope Department, Oxford University, Oxford
MCZ = Museum of Comparative Zoology, Harvard
MLUH = Martin Luther Universität, Halle
MMSU = Macleay Museum, Sydney University, Sydney

MRHN = Museum Royale d'Histoire Naturelle, Brussels

MVM = Museum of Victoria, Melbourne

RMS = Riksmuseet, Stockholm

SAM = South Australian Museum, Adelaide

TDAH = Tasmanian Department of Agriculture, Hobart

TMH = Tasmanian Museum, Hobart

UQIC = University of Queensland Insect Collection, Brisbane

USNM = United States National Museum, Washington

WADA = Western Australian Department of Agriculture, Perth

WAM = Western Australian Museum, Perth

ZMB = Zoologische Museum, Berlin

2.2 Technical methods

Examination and illustration of material was based on a combination of light and electron microscopy. These techniques for viewing morphology were essentially complementary, in that some characters could be better seen with one microscope rather than the other. For example larval sensilla were more clearly visible in light microscope preparations whereas electron microscopy was more useful for discriminating larval setal types. Illustrations are of paramount importance in taxonomy. Photographs have a much more immediate effect on the viewer than line drawings and in an ideal world this thesis would have been illustrated by several thousand photographs together with supplementary drawings of transparent features.

The light microscopes were a Wild M8 binocular and an Olympus BH2 compound, both with drawing attachments. Dissected and cleared material was examined in 70% ethanol in cavity blocks, or in glycerol in cavity slides, depending on the size of the structure.

Scanning electron microscopy (SEM) was performed on a Jeol JSM 35C at the Division of Entomology, CSIRO. The facility at CSIRO Entomology allowed specimens to be mounted on points which were then placed in a small rotatable and tiltable vice. Specimens could be viewed from several angles with a distant (therefore dark) background, unlike the usual stub-mounting procedure.

Drawings and photographs are separately presented in life-stage sequence from egg to adult. Larval and adult stage illustrations are mostly presented in a morphological sequence from head to abdomen, with exceptions for particular studies of individual taxa. No attempt has been made to arrange figure numbers according to sequence of text citation. Furthermore, scale bars are not provided because I believe that it is sufficient to know in a morphological study that a species is small or large (sizes of material are given in Appendix A). Similar structures are drawn at similar size. The drawings are somewhat stylised in the use of outlines and block shading. The larval head capsule, pronotum and kotpresse are obviously symmetrical structures but have been drawn as seen. Numerous illustrations are included because it is important to show lack of morphological variation in taxa as well as the full range of diversity.

Details of the methods for preservation and examination of each life stage are given in each life-stage chapter.

2.3 Choice of characters

A character is defined as some anatomical structure or a derived ratio, and all of its transformed states, from the initiation of that character to its morphological endpoint. Ratios are justified as characters because they are descriptors of shape. The use of ratios has been severely criticized (*vide* Atchley and Anderson 1978), although this criticism was primarily applied to their use in phenetic analyses in which only isometric variation is permitted. Any character with states of the form short/long, wide/narrow, or longer than/shorter than, involves a ratio. The main problem with use of such ratios is that discrimination of their states is likely to be made *a posteriori*.

Initiation and endpoint of the character states do not have to be defined beyond the particular clade being studied. For example the form of the male tegmen in all states recognised for the study taxa is apomorphic relative to many other Chrysomelidae. A few characters had well defined discrete states but most had states which were difficult to discriminate for at least a few taxa. Most multistate characters were considered to have ordered states, and these characters were obviously much more useful for phylogenetic construction than their unordered counterparts. Multistate characters with unordered states were usually found to be character complexes.

Colless (1982) has criticised cladists for not distinguishing between simple and complex characters, and thereby not giving the latter sufficient weight. It is more likely that cladists do not have to "choose between them" (Colless 1982, p.103) because they realise that even the most complex structure can be dismantled to a group of simple characters. For example, in this study the complex organ of egg-coating manufacture (kotpresse) provided 18 characters, at least initially.

The characters used in this study were from the external and, to a lesser extent, internal anatomy. Although I have used egg, larval, pupal and adult morphology the bulk of the study concerned first-instar larvae and adults. As much Australian material as possible was examined initially to acquaint myself with the gross variation within this group. Adult and larval specimens of at least each type species were disarticulated and all relevant literature was scanned to search for as many diverse characters as possible. Almost all of the larval material had to be reared for this study, therefore the larval analysis was largely based on Australian taxa. In contrast, a much wider sweep of world taxa was possible for adult morphology, so the adult data were more useful for the identification of relationships between Australian and other groups. Thus, in this study, analysis of the larval material is supplementary to the adult material although the two data sets are morphologically (but not genetically) independent (Goulet 1979).

The choice of characters is perhaps the most important part of any phylogenetic analysis. I wanted to include, at least initially, all of the relatively few 'traditional' characters discriminating supraspecific taxa. To these were added all characters which appeared to provide apomorphic states defining at least two species. Some of these characters were later rejected when it became obvious that they provided autapomorphies for single taxa, were universal, or that their states were not accurately determinable. I intended to use characters with discrete and mutually exclusive states, so several characters were rejected from the initial list because too many indeterminate states were present (e.g. mouthpart setae) or because possession of more than one state was possible (e.g. secondary sexual characters). In some cases it was found that mutually exclusive states of the morphological variation of a feature were not necessarily states of the same character. Note that indeterminate states are not an analytical problem for the methods of analysis used, that is, for PAUP and MACCLADE.

The characters and their states were not checked meticulously for the elimination of all covarying characters. Covarying characters may be of two types.
(i) Those which are essentially duplications of a single character artificially inflate the importance of these single characters, for example size and mensural characters (not used) and character repetition (a possible example being the number of tarsal segments on each leg). Further examples of duplicatory covariation are the presence of the same homologous structural state in different life stages (e.g. some features of pupae and adults), or the more indirect creation of special features in one life-stage due to the action of the previous stage. This last applies particularly to the possibility that eggshell shape is due to ovipositor shape. All duplicate characters were avoided.
(ii) Some characters covary because they have become contemporaneously modified in the derivation of some structure, or because of coincidence. These were not eliminated for two reasons: (a) to do so would immediately have led to extremely subjective assessments of what was genuinely an independent character and what was not, with consequent operator bias in the data; (b) removal of covariant characters would have destroyed the importance of character complexes. For example, a group of taxa may be divisible into two different subgroups on type of ovipositor or dorsal vestiture (setae/no setae) and ovipositor structure may be a covarying complex of six characters. I would use all six characters rather than one for the ovipositor, otherwise the ovipositor structure would be given equal rank to vestiture.

The stricture concerning character independence is usually applied to size and is particularly a criticism of phenetic dependence on mensural characters. Direct measurement of size of any feature or of the whole animal was avoided because size is not discrete and all measurements are a function of body size. However I did use ratios of one measurement to another where these ratios seemed to be genuinely discrete or with few intermediates. The character 'body size' compares with biological characters such as habitat, host plant or behaviour. It is perhaps better and more interesting to leave them out of the analyses altogether, to be compared against classifications derived from other characters.

Determination of character or state is a problem with missing characters. For example the visible part of the adult mesoscutellum may be absent or present with various modifications, or a larval mandibular tooth may be absent or present in various sizes. In general I have chosen to deal with absent characters by making the absence/presence combination a separate character from the various states of the character when present. This was done particularly when the state 'absence' could not be identified as part of an ordered sequence of states coding for variations of presence. For example, in the adult mesoscutellum the scutellar lobe may be absent altogether but it is impossible to identify one particular state of scutellar lobe shape from which absence could be derived. In a few cases, such as the larval mandibular tooth, absence of a feature seemed part of a logical procession involving reduction and finally loss and absence was treated as a state in the reduction series.

2.4 Morphology and phylogeny - analytic method

2.4.1 General discussion

The analysis of character and taxon variation provides or aids in the construction of a classification that has as much predictive content as possible, for any particular aspect of biology or palaeontology. The distribution of traits in organisms, genetically controlled, can be used to map the organisms' relationships. Relationships are recognised by assuming that close similarity is due to genealogy. Knowledge of relationships allows predictions to be made about morphology and other aspects but even if the phylogeny is 'correct' predictions for new taxa cannot be a hundred percent accurate because allowance must always be made for peculiarly derived features in an individual taxon, or autapomorphies. Certain character changes, usually involving complete loss of a feature, may be considered irreversible, at least within the homology of that character. Because all morphological characters of an organism are evolving in different ways, perhaps not necessarily independently but at different rates and with slightly different genetic control, the study of evolution of taxa through their character changes becomes very complex. Especially in larger data sets, reversals, homoplasies and differential rates of evolution are all likely to obscure the true pathway.

In this study numerical cladistics has been used to provide a guide to the probable relationships of the genera of Cryptocephalini and the relationship of these to other Camptosomata. Cladistics is so widely used in biology now that it should not need an apologia. Nevertheless, the method has not been used convincingly in Chrysomelidae. The simple 'cladograms' of Kasap and Crowson (1976), Mann and Crowson (1981), Cox (1982) and Suzuki (1988) include unrooted 'clades', with terminal taxa often defined by symplesiomorphy. Outside the Chrysomelidae there are many useful studies of insect taxa using cladistics in which the methodology is discussed, for example in Diptera (Munroe 1974), Coleoptera (Ashe 1984; Smetana 1986), Hymenoptera (Carpenter 1987), Lepidoptera (Kitching 1985; Miller 1988) and Phthiraptera (Lyal 1985). In these studies the methods of analysis may vary and there may be slight variation in the definition and application of terms but the basic principle is constant, that is, relationship should be defined by genealogy, as determined by shared derived states. Cladistics is the only suitable method for the comparison of different life-stage data sets, as in this study, because it is based on genealogy. For example, larvae and adults share the same genealogy but are subject to different evolutionary pressures. One subgroup of taxa may be extremely conservative in larval morphology, but extremely divergent in adult morphology in contrast to a different conservative subgroup. The true phylogenies of the two stages are identical although in practice there may be less resolution of the morphologically conservative taxa. Phenetic analyses, not being based on any biological principle, would not be able to compare the two stages.

Numerical cladistics was used because of the difficulties in handling large numbers of taxa and characters and because a suitable program, PAUP, was readily available. The adoption of as many potentially useful characters as possible in up to 96 taxa gave comparatively large data matrices. Lyal (1985) has shown that it is not necessary to use computers to resolve large matrices (351 species and 187 characters), by use of a strictly Hennigian method of analysis initiated by identification of obvious synapomorphically defined groups of taxa. The result is an array which may make reasonable morphological and evolutionary sense but which may not be the most parsimonious tree. The law of parsimony "states that no more causes should be assumed than are necessary to account for the facts" (O. E. D.), that is, that problem resolution should follow the least number of steps. Conflict of data due to homoplasy or poor understanding of characters seems inevitable in large data sets and the law of parsimony has been regarded as the only sound theoretical basis for resolving such problems (Sober 1983). Parsimony is integral to numerically cladistic programs such as PAUP (Swofford 1985).

For this study computer-based analyses were required to indicate robustness of groups of taxa, to isolate problem taxa for further study, and to provide a general picture of likely phylogenies, based on the shortest or most parsimonious trees. The program PAUP, version 2.4, developed by Swofford (1985) was very useful for these aims because it handles large data matrices, gives branch-lengths and lists of character changes at nodes on the cladogram, and is based on the principle of maximum parsimony using a Wagner algorithm.

The program PHYLIP (Felsenstein 1986) was not used, as it was only available towards the end of my study. It has limitations with matrix size (not appropriate for more than 20 x 20) and character states, all characters having to be binary.

The Macintosh personal computer program MACCLADE, version 2.1 (Maddison and Maddison 1987), was used for smaller data sets (eg. pupae), and for the study of character change and taxon phylogeny amongst the robust groups of taxa identified by PAUP. MACCLADE does not have the powerful parsimony based algorithms of PAUP.

Matrices contained up to 96 taxa and 317 characters. Analysis started with large matrices of non-sanitized data, that is, including poorly defined, dubiously homologous, or highly homoplasious character states. Preliminary analyses were run using PAUP on these matrices. The data were progressively 'cleansed' to remove nonsensical phylogenies, by removal of some characters, fusion of states and creation of new characters where necessary.

Characters were removed because of high subjectivity in state determination or extremely low consistency index (CI). The CI for a character is the ratio of the minimum possible number of changes to the actual number of changes for that character (Swofford 1985). The CI value is therefore an indicator of the compatibility of pattern of variation in any character with any particular tree. PAUP provides the CI for each character for any given tree. PAUP and MACCLADE also provide a CI for each tree, which is the ratio of the sum of the minimum possible number of changes of state to the sum of the actual number of changes. Obviously, for a set of taxa, as more characters are included the CI will decrease.

It seemed fairly clear from studies of the larval and adult data sets with PAUP that certain groups of taxa were almost always monophyletic despite various data treatments, whereas other, generally monotypic, taxa were variably placed. Furthermore the PAUP analyses of large data sets gave no consistent patterns of relationship between the clusters of taxa. PAUP was used on these large matrices to make the analysis relatively non-subjective with maximal information content. An alternative analytic method was to abandon objectivity and pick only those characters which defined clades. This is the familiar 'chicken and egg' story, except that here the clades were roughly defined for me by the PAUP analyses.

Analyses of these 'hand-picked' characters were performed on MACCLADE. The adult and larval data matrices used in PAUP were carefully examined for suitable characters. In some cases the number of states was reduced to simplify analysis or remove autapomorphies. The resultant considerably reduced data sets were used for analyses of larvae (AL (v)), adults (AA(x-xi)) and both adults and larvae (ALA(iv)). These data sets were also used for testing my own subjective phylogenies.

In PAUP binary state characters are very easily dealt with, since the program decides for itself the apomorphic states, given an outgroup for comparison. Whether a state is (0) or (1) is arbitrary to the program as long as the appellation is consistent. Designation of the direction of a transformation series (characters with more than two, ordered, states) is also arbitrary to the program, as long as the states are placed in a morphologically logical sequence. However I have tried to determine and indicate these polarities from outgroup and/or ingroup information to make these numerals have consistent meaning, at least in terms of my initial ideas about the character evolution. Missing characters were coded as ambivalent ('9' in PAUP, '?' in MACCLADE) when states defining some morphological attribute were required.

In the PAUP analyses I used both the default setting without character weighting, and the setting WEIGHTS = 1. The latter equilibrates all *characters* to a value of one rather than equilibrating all *character states* as with the default. Using WEIGHTS seems more logical for two reasons : (i) characters are emphasised rather than states (states were emphasised in the old systems of Chapuis and others); (ii) multistate characters are often those with loosely defined states which intergrade, and my preference would be to demote rather than promote these states in relative importance.

PAUP does not allow characters to be set either as irreversible or due to a single evolutionary step. Irreversibility is potentially important in a group such as the Camptosomata in which many features are lost or fused, for example fusion of sternites VI and VII. Fixing a character change as a single evolutionary event (which may be reversed) may be justified for complex features, such as derivation of the subcubital fleck. Such a designation would be difficult to justify without *a priori* evidence that the feature has been lost rather than separately evolved and also that it is not just a plesiomorphic state for the whole group. For any most parsimonious PAUP tree for a large data set there are likely to be apparently nonsensical character changes. These can be checked by using the CHANGELIST option, but the changes cannot be prevented unless they are weighted very highly. This leads to subjective problems, such as how much a character should be weighted. The program MACCLADE allows both irreversible and 'Dollo' (only in the sense of single evolutionary origin) settings for characters and is therefore more practical for producing clades with sensible information content. However it does not have a quick means of finding shortest trees and is therefore best used after finding the basic robust groups and problem areas using PAUP. MACCLADE and PAUP clades are not strictly comparable unless the character transformation types are made identical by avoiding use of the irreversible and Dollo settings in MACCLADE.

2.4.2 Subjectivity - choice of taxa and characters

In order to be valuable to all users, hierarchical classifications should be objective (and observer neutral) rather than subjective. Classification by phyletic sequencing from a phylogeny is an example of objective method (Lyal 1985). If classifications based on phylogeny are to be objective it follows that the methods used to derive the phylogenies should also be objective. For example, 'intuitive' reasoning for the weighting of characters should be disallowed. Similarly, claims of recognition of new generic taxa before phylogenetic analysis of generic relationships are premature to say the least.

Subjectivity itself is of course unacceptable in systematics and acolytes are exhorted to use as many characters as possible with as many techniques as possible in order to remove any vestige of it. I have tried to avoid subjectivity too, having come to the subject with few preconceptions of cryptocephaline relationships and by using many characters of both larvae and adults. Nevertheless, some subjectivity is inevitable. In this study it occurs in : choice of representative taxa of both ingroup and outgroup; choice of characters; determination of character expression (ordered states and so on) and states; choice of analytic method; choice of preferred trees; and choice of rank for classification.

2.5 Choice of outgroup

To derive phylogeny from morphology some means of detecting plesiomorphic and apomorphic states is required. In this study polarisation of the character states is based on outgroup analysis (Stevens 1980; Patterson 1982; Maddison, Donoghue and Maddison 1984). Plesiomorphic states are likely to be widespread in other taxa outside the study group and apomorphic states are likely to be restricted to the study group. Therefore, the most sensible and practical approach is to attempt to identify the character states likely to have been held by the shared ancestor of the group being studied (ingroup), and its closest relative(s) (outgroup, in this sense sister group). This method begs the question: how to determine the sister group? Some paraphyletic range of taxa may have to be chosen if the sister group is unclear.

One pitfall in use of outgroups with uncertain affinity to the ingroup is to keep extending the analysis outside the ever increasing nested set of taxa and eventually be confronted with a huge data matrix in which the group of interest is swamped. For example, Maddison *et al.* (1984) suggest that the phylogeny of the outgroup taxa should also be resolved. The most likely outgroup for Cryptocephalini was considered to be the Clytrini. However the relationships of Cryptocephalini, Pachybrachini, Achenopini, Clytrini and Chlamisini are not universally agreed, and the position of the Lamprosomatinae is also debatable, therefore I felt justified in going beyond the Camptosomata for an outgroup. Fortunately it is not "elephants all the way down" (Colless 1982, p.103, a singularly inappropriate metaphor) to the outgroup.

Outgroup choice was confounded by conflicting information available from the literature. The sister taxa to the Camptosomata have variously been the Megalopodinae and Megascelidini (Chen 1940b; Mann and Crowson 1981), the Megalopodinae alone

(Crowson 1946; Monrós 1954, 1959; Jolivet 1959), the Megascelidini alone (Monrós 1960a), the Eumolpinae and Megascelidini (Medvedev 1971), and the Cassidinae and Hispinae (Suzuki 1988 - not seen at time of outgroup choice). The Camptosomata themselves have at times included (according to proposed phylogenies) the Eumolpinae and Megascelidini (Jolivet 1959), Eumolpinae, Cassidinae and Hispinae (Chen 1940b), or Eumolpinae (Chen 1985). I found no reason to evoke a relationship between Camptosomata and any other subfamily of Chrysomelidae besides those listed above.

I rejected the Hispinae (*sensu lato*, Lawrence and Britton in press) largely because of their larval attributes : the paronychial appendix of the leg and annular spiracles are shared apomorphies with Chrysomelinae and Galerucinae, and the larval head and mouthparts are also very similar in all three groups (Böving and Craighead 1931). In the adult the wing venation (Jolivet 1957), mandible morphology (Sakai 1983), and the derived form of the ovipositor (Kasap and Crowson 1985) are quite different from Camptosomata which also do not have the bifid tarsal setae found in Hispinae (Mann and Crowson 1981). Although females of the latter may also use an excremental shell to protect the eggs they do not have a kotpresse (Erber 1968; I have examined *Uroplata* spp.), but the eggs may be attached to plants by stalks as in Chlamisini (Buzzi 1988). The male soft-part genitalia are remarkably similar in the two groups (Mann and Crowson 1983; Suzuki 1988), although this is partly due to the sperm pump which is convergently derived in many Chrysomelidae and partly to the reduction in size of the accessory gland. Suzuki (1988) greatly exaggerates the importance of these features.

I could find almost no reasons for the consideration of Megalopodinae as an outgroup. General similarity of body shape and antennae does not stand up to detailed scrutiny. The male and female genitalia are completely different, as are the larvae and wing venation (Monrós 1954b; Jolivet 1957; Kuschel and May, in press). Shared features such as the mesonotal stridulatory file (also present in Clytrini; Monrós 1953b) could easily be convergent and other similarities, such as tibial spurs, are plesiomorphies. One feature which has been considered important for the association of Camptosomata and Megalopodinae (and also Megascelidini) is the overlap of basal abdominal lobes against the metathorax (Mann and Crowson 1981). As shown below (Chapter 6) the conjunction of the abdomen and thorax is a complex character-suite, this type of juncture is poorly defined, and it is reasonable to assume that such a system may be convergently derived.

The other subfamilies could not be dismissed so easily, so for this analysis I used material of the Eumolpinae (several tribes including both primitive and modern forms but not Aulacoscelini *sensu* Monrós 1953a) and Megascelidini as outgroup taxa. I also included the Synetinae (*Syneta*) as the subfamily shows no clear association with any of the higher chrysomelids, but the female has similar external abdominal morphology to that of Camptosomata (Mann and Crowson 1981). Details of the species used are given in Appendix A.

Chapter 3 : Eggs

3.1 Introduction

Eggs of Megascelidini, Synetinae, and primitive Eumolpinae are unknown. The eggs of all Camptosomata are completely enclosed by an adult-secreted scatoshell (Erber 1968, 1969, 1988; Hinton 1981). Other Chrysomelidae lay exposed eggs on leaves (Alticinae, Chrysomelinae), insert eggs into plant tissue (Alticinae, Chrysomelinae, Donaciinae, Eumolpinae, Megalopodinae), oviposit in soil (Eumolpinae), or attach one or more eggs to a plant surface and secrete a protective shell on top (Criocerinae, Eumolpinae, Hispinae, Megalopodinae, Sagrinae). Oviposition in Camptosomata has recently been reviewed by Erber (1988).

Kitching (1985) found the structure of danaiine butterfly egg-chorion useful for phylogenetic analysis at the ranks of tribe and genus. Very little information is available for any Chrysomelidae and what there is suggests remarkable uniformity in expression of this character. The chrysomelid chorion has been illustrated for Galerucinae (Houston 1982; Krysan 1987), Bruchinae (*sensu* Lawrence and Britton, in press; Wightman and Southgate 1982; Pfaffenberg1985), and *Cryptocephalus* in Camptosomata (LeSage1986). However, no pattern was discernible in my few attempts made to see the structure of the chorion by SEM. As the egg surface is protected in all Camptosomata, the chorion might be expected to be extremely conservative in structure and therefore of little help for analysis compared to the input required for its study. Furthermore, from the available literature the amount of chorionic variation within Chrysomelidae appears to be very limited, providing few characters. I would expect it to be useful in leaf-ovipositing groups, such as Chrysomelinae and Galerucinae. Efforts to use the surface sculpture of the egg for phylogenetic analysis were therefore abandoned. One chorionic structure has been used here : in several taxa the apex of the egg is drawn out into a long chorionic stalk which is attached to a substrate. This stalk has been erroneously described as part of the scatoshell, but it actually passes through the scatoshell wall (Fig. 171).

The structure of the scatoshell is more obviously useful for analysis, although there is a possible problem of character correlation with the structure of the female abdomen. Characters of the scatoshell have been used to characterise various ranks of Camptosomata from species to subfamily and have been extensively figured (Fiebrig 1910; Spruyt 1925; van Emden 1932; Monrós 1949a, 1953b; Medvedev 1962b; Erber 1969, 1988; Lawson 1976; Medvedev and Zaitsev 1978; Hinton 1981; LeSage 1982, 1984a, 1984b, 1985, 1986). In this study the surface sculpture and shape had great diversity in all the taxa but this variability was generally graded.

Egg and scatoshell morphology was not used as a single independent character suite for analysis of all taxa individually because not enough characters were available. Instead, these characters were used as a supplement to the analyses of larvae and adults. Only taxa for which larval material was available were considered.

Scatoshell morphology is created by the behaviour and anal structure of the ovipositing female and this suite of characters is therefore not independent of the female anatomy and is a component of the adult genome. It does provide additional characters to a strictly morphological study, and the anal structure and scatoshell can be examined for correlating traits. Scatoshell morphology will be discussed further under the analysis of adult characters (Chapter 6). The present chapter is merely concerned with isolation and description of discrete character states.

3.2 Material and methods

'Eggs' (ie. scatoshell + egg) were obtained from females collected in the field. Often scatoshells were not produced unless females were fed with fresh correct food-plant, and the uncoated eggs quickly shrivelled. Scatoshells were simply allowed to dry and were examined in this condition. A few were critical point dried and gold-coated for SEM work (details given under larvae, Chapter 4). The taxa for which eggs were examined are listed in Appendix A.

Published descriptions of the scatoshells of Chlamisinae (LeSage 1984a) and *Pachybrachis* (LeSage 1985) were used to supplement this study.

3.3 Scatoshell morphology

I have taken some liberty in treating the act of enclosure of the eggs in outgroup and ingroup as homologous (Character E1), even though the glandular and rectal structure of the female abdomen is very different in Eumolpinae and Cryptocephalinae (Erber 1968; Suzuki 1988). No other characters of the egg-case (not a scatoshell because not scattered) of Eumolpinae were scored, because of this difference.

Details of the construction and structure of scatoshells are given by Erber (1968). The scatoshell can be described as having head and tail ends separated by the cylindrical body. Although the scatoshell serves only to protect the egg there is a wide variety of form displayed (Erber 1988). For the purposes of this study many of these could be dismissed as single taxon autapomorphs and the variation is essentially prescribed by : stalked/ unstalked; body unstructured/structured; texture coarse/fine; head end simple/modified; tail end simple/modified.

Altogether eight characters (E1-8 in data matrix) were used for the eggs available.

(E1). Homology of the 'scatoshells' of Eumolpinae and Camptosomata is questionable, although they are similar in appearance. Camptosomatan scatoshells seem to include much more coarse fibre, but the nature of this fibre has not been analysed, and the shell of the eumolpine is smooth and unstructured. The shell of the eumolpine *Edusella* encloses several eggs together on their site of attachment (state 0, not illustrated) : a plant or even barbed wire (label data in ANIC). All ingroup taxa secrete the scatoshell around individual eggs and attach them to plants by a stalk (1; Fig.171) or drop them (2). The three states are considered to represent a behavioural progression. This polarity may be justified by the wide distribution of attachment of eggs to plants in Chrysomelidae, and by the logical progression from partial to complete covering of egg by scatoshell.

(E2-6). Surface sculpture of the scatoshells was diverse but difficult to discretely categorize. The following characters were discriminated : (E2) unridged (0; Figs 171), evenly ridged in approximately spiral rows (1; Fig. 172), irregularly ridged (2; Fig.178); (E3, if unridged) rough fibrous (0), shiny smooth (1), rough, chunky (2); (E4, even ridges present) very fine ridges, broad flat interspaces (0; Fig. 172), fine or coarse, concave between (1; Fig. 175); (E5, irregular ridges) ridges fine and narrow (0), coarse and chunky (1; Fig.178); (E6, ridges present) broad flat blades (0; Fig.1), ridges without blades (1; Fig.172), long thin pointed blades (2; Fig.2).

The fibrous type without ridges is also illustrated by LeSage (1982, 1984a). Otherwise the surface may be organised in a shallow spiral of small overlapping scales (which may be acutely or coarsely ridged, the ridges occupying the whole scale or very narrow), and these may be reduced and obscured by the smoothness and thickness of the bonding secretion. Described like this the surface sculpture apparently has an ordered sequence of states, but since any one state can be derived from any other the character states were unordered.

(E7-8). One end of the scatoshell is blunter and this pole is where the larval head will emerge. The profile of the head end (E7) may be truncate, or concavely hollowed with an inner chamber (0; Figs 171, 174), or merely less acuminate than the opposite pole (1; Figs 173, 175). Application of the scales of scatoshell at this end (E8) is usually similar to the rest of the shell (1), but the scales may be overlapped in a spiral twist like a sweet wrapper (2, Fig. 172, also illustrated by LeSage, 1985), or produced around the rim to form a hollow chamber (0; Figs 174, 177, 180).

Features not used in the analysis because they were autapomorphies, include the shape of the hollow chamber-mouth (compare Figs 177 and 180), the development of elongate scales posteriorly (autapomorphy for *D. antennarius*, Fig. 174) and the presence of cross-ribs between the spiral ridges (autapomorphy for *Aprionota* Fig. 173). Further features are represented in published works, summarised and re-drawn by Erber (1988).

3.4 Results

A character matrix was constructed for 72 taxa (Appendix C). This matrix was obviously not analysable on its own because there were so many unscored states and because many of the identical groups of taxa were autapomorphically related to each other. With PAUP it was only used in combination with the first instar larval matrix in some analyses. The following trends were apparent :

Character **E1**. The outgroup taxon *Edusella* is the only member of the study group to attach its eggs directly to a substrate. Only stalked eggs occur in Chlamisini (Fig. 171) and Lamprosomatinae, both stalked and unstalked in Clytrini, but only unstalked in Pachybrachini and Cryptocephalini (Figs 172-180).

Character **E2**. Only unridged scatoshells were found in Lamprosomatinae and Chlamisini (Fig. 171), but both ridged and unridged in the other groups. Most of the Cryptocephalina had irregular ridges (Fig. 178) and most of the Ditropidina regular ridges (Fig. 175) and both groups also had unridged scatoshells (Figs 174, 177, 180). Scatoshells of the Platycolaspina (Figs 175) and *Aprionota* (Fig. 173) were regularly ridged.

Character **E3**. For scatoshells without ridges (number of taxa in brackets) the surface was rough and fibrous in Lamprosomatinae and Chlamisini, shiny and even in Clytrini (1), Ditropidina (2) and Cryptocephalina (1), and rough and chunky in Ditropidina (1) and Cryptocephalina (4).

Character **E4**. The nature of ridges and interspaces was poorly defined and the states difficult to distinguish. No clear trend was discernible.

Character **E5**. For scatoshells with irregular ridges (number of taxa in brackets), the ridges were fine and narrow in Ditropidina (5) and Cryptocephalina (3) and coarse and chunky only in Cryptocephalina (25; Figs 178-179).

Character **E6**. For scatoshells with ridges, broad flat blades were confined to *Semelvillea acaciae* (Fig. 1), and long thin pointed blades were confined to the two species of *Aporocera* (*Diandichus*) (Fig. 2). All other taxa had simply ridged scatoshells (Fig. 172).

Character **E7**. It was not always easy to distinguish the two states of the head-end profile and I think that many Cryptocephalina were mis-scored because shape of the scatoshell was obscured by the rough texture. Taxa with apparently truncate scatoshells included all Lamprosomatinae, Chlamisini (Fig. 171), Clytrini and most Ditropidina (Figs 174, 175, 177), and rounded scatoshells were found in Platycolaspina (Fig. 172) and most Cryptocephalina (Figs 178-179). The scatoshells of *Pachybrachis*, *Ditropidus* [*Prasonotus*] *submetallicus* (Fig. 176) and *D.* [*Pleomorphus*] sp. 522 were indeterminate.

Character **E8**. Formation of a hollow chamber was confined to *Ditropidus antennarius* (Fig. 174), *D.* [*Elaphodes*] *cervinus* (Fig.177) and *Cadmus litigiosus* (Fig. 180), and formation of a twist to *Platycolaspis* (Fig. 172) and *Pachybrachis*.

3.5 Discussion

Eight characters were identified for the egg plus scatoshell and one of these (E4) was subsequently rejected as indefinable. Therefore seven characters were distributed across 72 taxa. From this limited information alone it is difficult to be objective because homoplasies are concealed by lack of counter evidence. Furthermore the sample sizes of some groups are too small so that generalisations made from this data set do not compare well with available literature (Erber 1988), the character states are only poorly discriminated and the outgroup Eumolpinae is of no use in deriving polarities.

A full discussion of the significance of scatoshell morphology will be given under the discussion of character variation compared with phylogeny (Chapter **8**).

Chapter 4 : First-instar larvae

4.1 Introduction

Larvae of Megascelidini and 'primitive' Eumolpinae are unknown, and relatively few descriptions are available for the rest of Eumolpinae (Lysaght 1930; Böving and Craighead 1931; Gardner 1935; van Emden 1946; Peterson 1951; Gilyarov and Kurcheva 1956; Broodryk 1965; Crowson 1967; Gressitt 1967; Kurcheva 1967; Oglobin and Medvedev 1971; Medvedev and Zaitsev 1978; Cox 1988), Synetinae (Kurcheva 1967), and Camptosomata (Dugès 1876, 1880; Reineck 1913a; Moreira 1913; Böving and Craighead 1931; Paterson 1931; van Emden 1932, 1946; Fiori 1948, 1951, 1957; Monrós 1949a, 1951a, 1953b; Peterson 1951; Masutti 1960; Medvedev 1962b; Oglobin and Medvedev 1965, 1971; Steinhausen 1966, 1978; Erber 1969; Kasap and Crowson 1976; Lawson 1976; Medvedev and Zaitsev 1978; LeSage 1982, 1984a, 1984b, 1985, 1986; Root and Messina 1983). The only description of an Australian species of Camptosomata is not associated with an adult (Kasap and Crowson 1976). Almost all the material discussed here was reared for this study.

Larval biology has recently been reviewed by Erber (1988). Camptosomatan first-instar larvae hatch within the scatoshell, bite through one pole, and then retain the shell which is progressively enlarged. Retention of the scatoshell is unique to camptosomatan larvae. The method of enlargement of the case is not really relevant here as later instars were not studied, but it is interesting to note that two separate methods seem to be used. In *Chlamisus* the original scatoshell may remain almost unaltered as an appendage or nipple at the apex of the larval case (Erber 1988), the case being enlarged only at the entrance. In *Cryptocephalus* (Erber 1969) and Australian Cryptocephalini the scatoshell is enlarged by the larva periodically eating out a longitudinal slit along the floor of the case and adding material to the sides of this, eventually almost obliterating external evidence of the original scatoshell. Larvae from eggs with a chorionic stalk emerge through the opposite end to the stalk, then bite through the stalk (Goidanich 1956).

Most camptosomatan larvae live on the forest floor, where they eat fallen leaves and decorticate twigs and fruit, but a few attack living foliage either habitually or facultatively (Erber 1988; pers. obs.) and others feed on living bark (Monrós 1949). Living foliage may be necessary in the diet before ecdysis (Erber 1988).

The eumolpine larvae included here bite through the enclosing shell and drop to the ground where they burrow into soil to attack plant roots. All other known eumolpine larvae and the larvae of *Syneta* are also soil dwelling (for example : Lysaght 1930; Broodryk 1965; Kurcheva 1967; Medvedev and Zaitsev 1978; Isono 1988).

4.2 Material and methods

4.2.1 Sources of material

The larval characters analysed below were obtained from three sources: larvae reared from field-collected adults, larvae loaned from institutions, or from published descriptions. The collection data and names of larvae used in the construction of matrices are listed in Appendix A.

Almost all of the material included in this analysis was derived from females captured in the field. After production of eggs, the females were preserved, and later identified where possible (unidentified species were coded), but the eggs were left in vials for up to a month to allow hatching. Frequently, especially in species from hotter climes, the hatched larvae died before breaking the surrounding scatoshell. This was not important as I merely required the first instar. On long field-trips hatched larvae were preserved in KAA to prevent damage to the scatoshell and larva. Generally, however, larvae were allowed to dry out. First-instar larvae of approximately three-quarters of the Australian camptosomatan "genera" and two-thirds of their type species were collected personally on field-trips in south-east Australia, south-west Australia and the areas around Adelaide and Brisbane. Altogether first instars of about 150 species were collected although only a portion of these was examined in detail. Specimens used in analyses are listed in Appendix A. The Eumolpinae were represented by specimens of *Edusella* Chapuis (Eumolpini), *Geloptera* Baly

(Eumolpini) and *Tomyris* Chapuis (Adoxini) which are all 'higher' eumolpine genera. Only larvae of *Edusella* were used in analyses but larvae of the other eumolpine genera were identical to these for all characters. All larvae collected for this study are to be deposited in ANIC.

The field collection was supplemented to some extent by material from three institutions. Fresh larvae of two species of *Chlamisus* Rafinesque were obtained from DPIB. Further larval material was available from ANIC, but was generally not used because of the lack of adult associations (most larvae came from various leaf-litter extraction methods). I used a little of this material to check keys and descriptions. One first-instar specimen of a Neotropical cryptocephaline was also utilised from this collection. I incorporated this specimen in the study (Cryptocephaline A) because it showed a unique combination of character states which made it apparently intermediate between *Ditropidus* and *Pachybrachis* (LeSage 1985). It is now evident that this is a pachybrachine. Finally, all of the available camptosomatan larvae in BMNH were made available to me. Although relatively small in extent this collection included useful non-Australian comparative material, of the genera *Oomorphus* Curtis, *Labidostomis* Germar, *Smaragdina* Chevrolat and *Cryptocephalus*. Specimens from the last two institutions had been preserved in ethanol.

The published descriptions of seven species were also used, although it was not possible to derive scores for all characters. These taxa were the North American species *Neochlamisus eubati* (Brown) (LeSage 1984a), *Pachybrachis peccans* Suffrian (LeSage 1985), *Lexiphanes saponatus* (Fabricius) (LeSage 1984b) and *Cryptocephalus venustus* Fabricius (LeSage 1986) and the Palaearctic *Cryptocephalus frenatus* Leach (Fiori 1951), *Syneta betulae* (F.) (Kurcheva 1967) and *Stylosomus sinensis* Lopatin (Medvedev and Zaitsev 1978).

4.2.2 Methods

Dried specimens were resurrected either by immersion for *c.* 24 hours in a dilute detergent solution (Decon® 90), or for *c.* 2 hours in 10% KOH, then water.

Either treatment was usually sufficient to produce rehydrated, expanded larvae with minimal body contents. With the first method further clearance was achieved by adding immersion in KOH, followed by water, to the sequence. Specimens preserved in KAA or ethanol were taken through dilute alcohols to water then soaked in 10% KOH for 12-24 hours, before washing in water.

Larvae were examined with both compound light and scanning electron microscopes.

LeSage (1984) described an elaborate procedure for permanently slide-mounting camposomatan larvae using six different foci on the slide for head, pronotum, legs, and abdomen. Although at first his method was followed, three things mitigated against its continued use. The size of the animals in this study was consistently small; generally LeSage studied the more easily dissected later instars which can be treated quickly. LeSage's method does not allow manipulation of the mounted specimens, which may be critically important if only a few are available. Lastly, the whole fixed-mount procedure is relatively time consuming especially when dealing with a large number of very small animals.

Goulet (1977) described a much more practical, if impermanent, method of mounting carabid larvae, using glycerol as the mounting medium. He showed that glycerol allowed easy access to the specimens, while preserving them for at least 2-10 years.

In this study I have followed Goulet in using glycerol, but have substituted cavity slides for slides plus rings. The majority of specimens studied here were transferred directly from water to a small drop of glycerol on a washed cavity slide. Under the high power of a dissecting microscope the head capsules of three larvae (if available) were removed by tearing the surrounding integument with fine pins, and the ventrally placed mouthparts removed from at least one capsule. The labio-maxillary complex was removed by inserting a pin in the mouth cavity and pulling gently backwards. The mandibles were then splayed apart or removed. One foreleg was freed from each body, otherwise the bodies were left intact. The slide was then labelled and temporarily stored in a slide cabinet. These specimens may eventually be placed in sealed vials with glycerol and mounted on the same pin as the female parent.

One advantage of this method of preparation is that the specimens can be easily manipulated on the slide and viewed from any angle. A disadvantage is that the specimens do move around fairly easily in the glycerol, especially when breathed on, causing problems with drawing. Another is that the slides may accumulate dust and dead booklice (*Liposcelis bostrychophilus* Badonnel).

Specimens for examination in the SEM were taken from either fixed or rehydrated material. In either case the larvae were dehydrated through a series of alcohols to amyl acetate, critical-point dried and mounted on a card point prior to coating with gold.

4.3 Larval morphology

Camptosomatan larvae have been the subject of a few recent morphological studies, although these have generally not dealt in detail with the first instar. There is therefore some consensus available for the description of general structures. First-instar larvae have been described in some detail (usually head capsule) for *Oomorphus* in Lamprosomatinae (Kasap and Crowson 1976), *Diplacaspis* Jacobson (van Emden 1932), *Exema* Lacordaire (LeSage 1982) and *Neochlamisus* Karren (LeSage 1984a) in Chlamisini, *Lachnaia* Chevrolat (Fiori 1948), *Cheilotoma* Chevrolat, *Labidostomis* and *Smaragdina* (all Medvedev 1962) in Clytrini, and *Pachybrachis* (LeSage 1985), *Lexiphanes* Gistel (LeSage 1984b), *Stylosomus* (Medvedev and Zaitsev 1978), *Suffrianus* Weise (Medvedev and Zaitsev 1978; usually a subgenus of *Cryptocephalus*), *Cryptocephalus* (Fiori 1951; Masutti 1960; Oglobin and Medvedev 1965, 1971; LeSage 1986) and genus unknown (Kasap and Crowson 1976) in Cryptocephalini. Details of the eggbursters have recently been given for Eumolpinae and Camptosomata (Cox 1988). Apart from setae, the larvae generally lack variable structures so the focus of this study has been on setae, particularly the establishment of setal homologies between rather diverse taxa.

The larvae are white and weakly sclerotised except for the legs, head capsule and, in some taxa, pronotal sclerite. The free larvae of Eumolpinae and *Syneta* are straight (Fig. 3) (C-curved when killed in alcohol) with a prognathous head capsule. Camptosomatan larvae are enclosed in a portable case with a narrow entrance and are strongly C-curved (Figs 4-8). The hypognathous head of these larvae is strongly sclerotised and may be similar in appearance to the gastropod operculum (Fig. 2), like a flattened plug. The following description is intended to include both Camptosomata and Eumolpinae but applies particularly to the former.

4.3.1 Head (see Figs 181-188 for labelled parts)

The head is divided by the anterior arms of the ecdysial suture (frontal sutures) into two major areas: anterior and posterior. The anterior area is the frons and clypeus combined. Terminology of the posterior area has not been consistent. The term vertex refers to an 'upper' area only : traditionally the cranium above and behind the frons and stemmata. In beetle larvae the whole area posterior to the frontal sutures has usually been referred to as the epicranium, although some authors have used epicranium for the vertex and others have used epicranium for the entire head capsule (Snodgrass 1935; Mackerras 1970). Snodgrass preferred the synonymy of vertex and epicranium, because this more closely adheres to the Greek meaning of the latter word. For this study I have followed the prevailing view amongst coleopterists and used epicranium for the whole area posterior to the frontal sutures. Laterally the frontal sutures divide the six stemmata on the vertex from the antenna inserted on the side margin of the frons. The edges of the basal stem of the ecdysial suture (epicranial suture) are infolded basally (internal keel) which makes this part of the suture wider (a feature thought to be diagnostic for Chlamisini by LeSage (1984) but actually present throughout the taxa considered here). In Eumolpinae the line of the epicranial suture is continued apically as an internal keel (the endocarina) down the frons. Near the lower, anterior margin of the epicranium lie from nought to six stemmata, usually in two groups, the upper of four (St1-4) and the lower of two (St5-6). The latter are at the base of the mandible, anterior to the antenna. The head capsule has a fairly stable number of setae and sensilla in various dispositions, the nomenclature of which is discussed below. The cephalic foramen has a broad smooth border, divided from the vertex by a keel which curves from the epicranial suture to the acetabulum for reception of the mandible. This feature showed no systematic value. The frons and clypeus are fused and not distinguishable except that internal keels suggest their lateral demarcation. The antenna is inserted in a groove at the lower margin of the frons and vertex and has from one to three segments as well as a sensorium on the apex of segment two. The sensorium can be distinguished by its lack of sensilla and setae, and its uniformly weak sclerotisation.

The labrum is fused or free. The mandible is strongly sclerotised, roughly triangular and apically variably toothed, but without a mola. At its base, towards the outer margin, there is a semicircular articulating condyle which fits into a hollow on the ventral margin of the mouth. The number of mandibular teeth seems to be primitively five in 'higher' Chrysomelidae (if it is accepted that these are monophyletic), as seen in Alticinae, Cassidinae, Chrysomelinae, Criocerinae, Galerucinae (Böving and Craighead 1931), although it may be an autapomorphy for this clade of subfamilies. From three to five teeth were present in the sample. The homology of the teeth can be deduced if it is assumed that the most prominent, apical tooth in all taxa is tooth 3. This results in the constancy of the origin of the apex of the internal straight edge (basal projection) in the Camptosomata, that is, it is not a tooth.

The labio-maxillary complex is elongate (especially stipes and mentum) and forms a flat floor to the head capsule in Camptosomata, but is more transverse, convex and normally proportioned in other chrysomelids. The maxilla consists of a relatively small basal cardo, and large stipes to which the palp, galea and reduced lacinia are attached. The maxillary palp comprises four segments, the palpifer and segments 1-3. Maxillary palp segment 3 always has a single digitiform sensillum in a groove on its outer face. The galea is a broad oval lobe internal and dorsal to the palp and is internally armed with spinuliform setae. The lacinia lies internal to the galea, is apparently fused to the stipes and is reduced to an inconspicuous narrow lobe armed with two spinuliform setae. The postmentum (*sensu* Snodgrass 1935; mentum *sensu* Kasap and Crowson 1976) occupies the space between the stipes. This structure has been named both pre- and post- mentum by LeSage, but, according to Cox's study of the larva of the phylogenetically more plesiotypic chrysomelid *Orsodacne* (Orsodacninae; Cox 1981), it is the submentum and mentum combined which is the postmentum of Snodgrass. At its apex lies the compact foreshortened cluster of the labial palpi, of one to two segments, inserted on the narrow, poorly defined prementum, and dorsal to these the ligula. Occasionally the narrow bases of the paramental sclerites (which arch into the buccal cavity) are visible between the apex of the mentum and the stipes. Visibility of the paramental sclerites was considered to be of phylogenetic importance by Kasap and Crowson (1976), but LeSage (1985) proved that they are universally present in the Camptosomata although easily overlooked. In this study very little use was made of the labio-maxillary complex because of its small size in the first instar and its great conservatism in structure. For example, in numbers and distribution of setae and sensilla, and in structure, the labio-maxillary complex is almost identical to that of *Orsodacne* (Cox 1981), Galerucinae (Houston 1982) and the Paropsina (Reid 1983).

4.3.2 Thorax and abdomen (see Figs 239, 240, 242 and 270 for labelling of structures)

A complicated nomenclatural system exists for the setiferous thoracic and abdominal sclerites of larval Chrysomelinae, derived for the study of phylogeny of this difficult group (Kimoto 1962a, 1962b, 1962c). This system has been applied to the morphologically similar Galerucinae (Takizawa 1972), which *sensu lato* are probably the sister-group of Chrysomelinae, and lately applied to the Chrysomelidae *in toto* in a comparison of eggbursters (Cox 1988). The externally feeding larvae of Chrysomelinae and Galerucinae have distinct, prominent and usually strongly pigmented, sclerites, which have variable numbers of setae (*vide* Kimoto, 1962a, for the rationale behind a sclerite-based nomenclature rather than seta-based). This is certainly not true in the taxa considered here in which a sclerite system is largely absent and the setae appear to be relatively invariable in both number and position. Because of this absence of sclerites, and the small size of first-instar larvae and many of their setae, I have refrained from systematically labelling the setae on the basis of their supposed sclerites. The few sclerites present are mentioned individually below.

The prothorax is distinguished from the other thoracic segments by the presence of a large pronotal sclerite (Figs 3-8, 51, 239) which may be thickened and therefore darkened. This sclerite covers the entire dorsum of the prothorax and represents the D-DL-EP of Kimoto's system. Below this are the sclerites associated with the legs : fixed, quadrate sclerites corresponding to the trochantin and sclerite P of Kimoto.

The meso- and metathorax differ from each other only in the presence of a large spiracle in the anterior of the mesothorax and, apart from this, the following description applies to both. In the Camptosomata both thoracic segments have a large rectangular sclerite (Figs 4-8, , 51, 239) dorsal to the trochantin (Tr of Kimoto) and P. This sclerite appears to be derived from the fusion of sclerites EP and DLe of Kimoto, and is here named EP-DLe. The mesothoracic spiracle lies immediately anterior to it. Above EP-DLe and slightly posterior to it lies a small or very small sclerite armed with a minute posteriorly directed tooth, the eggburster. This sclerite appears to correspond to sclerite DLpi of Kimoto, and has been described as such by Cox (1988) who indicates the homology of this structure throughout the Chrysomelidae. The egg-burster is very small in all the taxa considered here, and possibly all larvae eat one of the poles to emerge from the egg, as described for *Cryptocephalus* (Paterson 1931). There are no further sclerites on the thoracic segments.

The legs (Fig. 240) are identical in structure on each thoracic segment and comprised of : large, elongate coxa; short triangular trochanter fused to elongate femur; elongate narrow tibia; pointed and curved tarsungulus. The base of the tarsungulus is unsclerotised. In the Camptosomata the legs are comparatively long and slender, especially the forelegs. A paronychial appendix, characteristic of Chrysomelinae and Galerucinae, is absent.

Well defined sclerites are not generally discernible on the abdominal segments of Camptosomata or Eumolpinae, nor are there any appendages or ambulatory ampullae (Figs 3, 4, 51, 270). In a few taxa there is a minute eggburster on abdominal segment I (Fig. 52), and even II in Eumolpinae (Cox 1988), which is so small that it may be overlooked, in the position of sclerite DLpi. A pair of spiracles is present on each of segments I-VIII, at about the lateral midline. The anus is apical, and its surrounds were not investigated in the present study.

Spiracles are present on the mesothorax and abdominal segments I-VIII (Figs 239, 270). They are quite complicated structures on and below the surface of the animals, and their study requires both light microscopy and SEM. With light microscopy a cellular plate is visible at the surface with an internal orifice leading to the trachea (Fig. 270). The trachea is also connected to the plate by a thin sclerite for muscle attachment which acts to control the width of the orifice. Internal to this sclerite the trachea subdivides. These features seem to be universal in the larvae studied here. However the cellular construction of the spiracle plate is variable (Figs 264-272). The 'cells' are seen to be spherical air spaces with SEM (Figs 55-60). In bicameral spiracles (Kasap and Crowson 1976; Crowson 1981) the cells are arranged in two vertical columns connected only at the base, where the tracheal orifice lies (Fig. 264). SEM shows that bicameral cells are almost entirely hidden from external view (Figs 55-56). In cribriform spiracles (Kasap and Crowson 1976; described as uniforous by LeSage) the cells are evenly spread in an oval disc and every cell is exposed to the air (Figs 57, 58, 239, 267). This type of spiracle is apparently especially found in soil inhabiting beetle larvae for the prevention of waterlogging (Crowson 1981). The cells are partly covered by mushroom-shaped pillars of chitin arising from the intercellular spaces. Cell number is variable between taxa, individuals, thorax and abdomen, and between abdominal spiracles (anterior usually largest). The tracheal orifice lies at or near the base of the plate (Fig. 239). In Camptosomata there is a modification of the cribriform type, in which the central field of cells is missing and the sides have come together forming an elongate vertical strap two cells wide, which is here named moniliform type (Figs 59, 60, 270, 272). Apart from its shape the moniliform spiracle is structured as in the cribriform. Cribriform and moniliform spiracles have been illustrated for *Cryptocephalus* (Oglobin and Medvedev 1965; Medvedev and Zaitsev 1978).

In some taxa the spiracles of later instars may be of different construction, usually annular (Kurcheva 1967; LeSage 1984a).

4.3.3 Chaetotaxy, and arrangement of campaniform sensilla

Few studies have been made of chaetotaxy and sensilla in larval Coleoptera and these have mostly concentrated on two ends of the family tree, the Adephaga and the Phytophaga. The nomenclature used for these two groups is completely different although the Coleoptera are of course monophyletic. Examination of the chaetotaxy of the carabid head capsule (Bousquet and Goulet 1984) and of the dytiscid leg (Nilsson 1988) certainly suggests much homology with the chaetotaxy of Phytophaga. Here the chaetotaxy of the Camptosomata is considered only within the confines of the Phytophaga.

4.3.3.1 History of chaetotaxy of camptosomatan larvae

The following discussion is only concerned with the head, since only crude nomenclatural systems exist for other parts, and since I have concentrated my own studies on the head.

In this study the basic assumption is that because the Chrysomelidae are monophyletic the larval setal patterns are all derived from a single original system. Determination of this fundamental pattern will therefore help to identify homologous setae. A scan of chrysomelid larval literature certainly suggests that the number of setae on the various regions of the head is reasonably constant, but the size and position of setae are variable and most workers have studied later instars in which the setal pattern is often quite different from that of the first instar (for example, Chrysomelinae (Cox 1982); Galerucinae (Takizawa 1972); Eumolpinae (Kurcheva 1972)). Problems also arise if the head capsules are uniformly multi-setose (*Chrysolina* , Takizawa 1971; Anthribidae, Lee and Morimoto 1987), or show considerable intra-specific variation (*Chrysophtharta*; Reid 1983). Few have attempted to devise or make use of setal homologies. There have been two approaches : one looking for a common, widespread pattern across the gamut of subfamilies, and the other applying an already available pattern from the Curculionidae. The justification of this latter appproach is that the Curculionoidea and Chrysomeloidea are sister groups (Lawrence and Newton 1982).

Medvedev and Zaitsev (1978, p.9) have pointed out that "the homology of the setae... has not been studied at all" in the subfamilies of Chrysomelidae. This is slightly unfair to Cox who appears to have studied the homology of cephalic setae in Chrysomelidae although the basic premise of his work remains in a relatively inaccessible form (Cox 1976). Cox studied the British fauna and came to the conclusion that there was a basic setal pattern, followed or adapted by the various larval forms. However his determination of individual setae seems to be a matter of intuition in much the same way that Saether (1988) has argued for 'underlying synapomorphy'. For example 'extra' setae are ignored in the nomenclature because they do not conform to the chosen pattern. In his two published papers (Cox 1981, 1982), the determination of setae is not explained and the figures are frequently at variance with the text, as in figures of *Orsodacne* and *Phaedon* where it is not at all clear what is and what is not a vertical or genal seta (head capsule setae are divided into vertical, genal, frontal, and postclypeal).

Cox's system was primarily derived from the early works of Paterson (1931) and Hennig (1939) which appear to be the source of the setal nomenclature used by Medvedev and Zaitsev (1978). Paterson was perhaps the first to recognise the importance of the disposition of cephalic setae in chrysomelid larvae. She divided the head capsule into vertex, frons and postclypeus. In individual descriptions of larvae the vertex was further subdivided into vertical, gular and ocellar subregions, but a means of distinguishing these setae was not given. Hennig derived his system from Paterson but applied it to Chrysomelinae only and ignored the setae near the external margin of the vertex and the stemmata. Medvedev and Zaitsev (1978) used a setal nomenclature but quite openly admitted to this being for practical purposes only.

A second system of setal nomenclature in current use is that derived from the work of Anderson (1947) for Curculionidae. Its leading proponents are LeSage, who in a series of papers has described various larval North American Camptosomata (LeSage 1982, 1984a, 1984b, 1985, 1986), and May (1978, 1981), who has primarily described Curculionidae. LeSage considered that Anderson's system "could be adapted readily for chrysomelid larvae, the basic pattern of both groups being the same" (LeSage 1982, p.318).

Anderson (1947) based his setal system upon the late instar larva of *Pissodes*, a typical curculionid with reduced frons and only a single pair of stemmata. For the epicranium he described (p.126) four "moderately easily defined groups" of setae, membership of these groups being defined by relative position (dorsal, lateral, ventral and posterior epicranial setae). Anderson also claimed the relative constancy in Curculionidae of five pairs of frontal setae, two pairs of clypeal setae and two pairs of labral setae.

Perhaps the major problem with using curculionid larval morphology to describe Chrysomelidae is that although the two families belong to sister superfamilies, they are far from basal within their respective lineages. Given that the sister group to the Curculionoidea-Chrysomeloidea is unknown (Lawrence and Newton 1982) it would be more useful to base a setal classification upon a basal ingroup such as the Nemonychidae, Anthribidae, Disteniidae, or even Megalopodinae (sensu Kasap and May (in press). Another problem is that the distribution of the various epicranial setal groups in a curculionid becomes less clear when six stemmata and a foreshortened epicranium occur, as in most Chrysomelidae. Thus, although in each paper LeSage claimed to follow Anderson, his nomenclature of the cephalic setae has not been consistent. For example, the seta between the four dorsal stemmata and the frontal suture was variously named OS2, SS1 and DES5, the seta on the lower part of the frons changed from CS1 to FS4, the outer dorsal epicranial seta changed from DES2 to LS1 and so on, and these changes were not referred to in the texts (LeSage 1982, 1984a, 1984b). The system employed by LeSage is now stable (LeSage 1984b, 1985, 1986) but differs significantly from Anderson's original plan. Hereafter I refer to his most recent nomenclature when comparing my system with LeSage's.

Anderson's system has also been adopted by May, originally in descriptions of New Zealand Curculionidae (May 1978, 1981), but recently in a description of a late instar Australian megalopodine (Kuschel and May, in press). The head capsule setae of the megalopodine larva and curculionid larvae are generally similar which certainly supports the idea of an homologous setal pattern for the curculionoid-chrysomeloid assemblage. The nomenclature May has used is similar to that of LeSage's earliest paper (LeSage 1982) and of course Anderson, but the identity of clypeal setae remains conjectural. The determination of clypeal setae is problematical because in all of these beetle larvae the clypeus and frons are fused, and the frontoclypeal suture visible on the lower margin of the frons is due to an internal thickening of the head capsule between the base of the mandibles (Crowson 1981), not necessarily at the junction of the frons and clypeus. 'Clypeal' and 'frontal' setae are often found on the edge of this frontoclypeal suture.

Detailed resolution of this problem of setal homology and therefore nomenclature for the curculionoid-chrysomeloid assemblage requires a separate study of their more basally derived groups. Here I am interested in a group of 'higher' Chrysomelidae (Eumolpinae + Camptosomata) for which evidence of setal homology can generally be derived by in-group analysis with a little help from other taxa. I have however altered the nomenclature where the Anderson system is inappropriate (for example anterior-epicranial for dorsal-epicranial).

The outgroup used here for Camptosomata is Eumolpinae but for the study of larvae this is a doubly unfortunate 'choice'. Eumolpine larvae are root feeders and therefore relatively derived in a negative way, having lost taxonomically useful features including stemmata and probably setae. They are also very poorly studied, especially in the first instar, and larvae of the basal groups of Eumolpinae remain to be described.

4.3.3.2 Setal nomenclature of head and associated appendages (see Figs 181-188 for labelled setae)

Numbering of groups of setae always follows the two sequences basal to apical, and internal to external. Two nomenclatures are given: first the one used in this study, and second the nomenclature used by LeSage (1986).

The row of four setae at the back of the epicranium (postero-dorsal epicranial setae, Pdes = Pes,1-4) is universally present, although the setae are often considerably reduced. No systematic significance was attached to them or to their associated sensillum (Pdesm = Pesm,1). The anterior of the epicranium between stemmata and epicranial suture generally has a row of setae and interpolated sensilla, with one or two setae on the disc of the epicranium behind this. The size and setal nomenclature of members of the anterior row depends on additional insertions from behind, the degree to which the anterior margin is keeled, and the presence of stemmata. I recognise a basic row of five anterior setae (Aes = Des,1-5), although the fourth and fifth are closely associated with the stemmata and the first may be much more posteriorly placed (Fig. 181). Aes4 usually occupies a position just above and slightly forward of the most dorsal stemma. Aes5 usually occupies a position just below and anterior to the most anterior stemma. Behind this row on the central disc of the epicranium there is normally a solitary seta (Des = Les,1) and nearby sensillum. This seta may be advanced, in taxa with an operculate head capsule, to mid-way between Aes2 and Aes3 within the anterior setal row of the epicranium (Fig. 17). There could be some argument for considering Aes1 as a dorso-epicranial seta , but for the Camptosomata this name is not so appropriate. Between the dorsal stemmata (St1-4), Aes3, and the posterior margin of the head capsule, lie three latero-epicranial setae (Les1-3 = Les2-4) in elongate triangular or linear configuration (see Figs 9-22). These setae vary little in structure or position in the first instars and were not used in the following analysis. A group of three further setae (ventro-epicranial, Ves = Ss, 1-3) are located below (or anterior to) the dorsal stemmata (St1-4) and behind the antennal insertion, the most ventral (or anterior) of which (Ves3) is close to the base of the mandible. Ves2 is frequently hidden by the antenna in anterior view. These setae also show little variation and were not included in analyses.

The frons and clypeus are fused in all the taxa considered here, therefore correct resolution of setae as frontal or clypeal is not certain. In this study six pairs of frontal setae (Fs1-6) are recognised and one pair of clypeal (Cs1), in conformity with previous studies. The central disc of the frons is occupied by two or three pairs of setae (Fs1-3) whose configuration is phylogenetically important. The three remaining frontal setae (Fs4-6) generally form a transverse row along the presumed fronto-clypeal junction. Fs6 may be displaced posteriorly to lie in line with Fs3. Morphologically Fs1-6 are usually very similar. In contrast the clypeal seta (Cs1), which may be difficult to recognise by position alone, is often structurally different from the frontal setae. This seta lies close to the midline, anterior to Fs4 and usually closely associated with a sensillum (Csm1). The labrum, whether fused or free, has three or four pairs of external setae (Lbs1-4) and, dorsally at the apex in most Camptosomata, four to eight pairs of epipharyngeal setae (Eps = Ss1-8). These setae are certainly epipharyngeal in origin but most or all migrate to the dorsal surface in Cryptocephalinae. One or more pairs may be absent or overlooked. The epipharyngeal setae were confusingly labelled Pes, Es or Ss by LeSage (1986). The number and positions of epipharyngeal setae were not used in analysis because of the problem of identification.

The three or four antennal setae were ignored in this study. The mandible constantly has two pairs of setae (Ms1-2), inserted towards the base of the outer face (Fig. 187).

The setae of the labio-maxillary complex (Figs 188) appear to be almost constant in position and shape and were not used, but they are described below. The cardo bears one seta (Cos1) which may be absent or overlooked. The stipes has three setae, two externally (Ess1-2) and one internally (Iss1). The maxillary palpifer has two setae (Mps1-2), and palp segment two has one or two setae (the internal may be overlooked). The galea bears an internal row of spiniform setae, of which the basal members are usually obscured. The lacinia is constantly represented by two spiniform setae which are often obscured. Of the labium, there are three pairs of setae on the mentum (Mes1-3), one pair on the prementum at the base of the palpi (Pms1), and two pairs at the apex of the ligula, one dorsal, one ventral. The palpi are unarmed.

4.3.3.3 Leg setal nomenclature (Fig. 253)

The setae of the leg from tarsungulus to trochanter are described below. However, only the tibia and tarsungulus of the foreleg was used in the analysis, for three reasons : the other legs are essentially identical in pattern, differing only in the relative lengths of setae; the size and position of the trochantral and femoral setae showed little variation; and, some of the coxal setae are very small and difficult to identify. The nomenclature used here applies primarily to Camptosomata and is based on setal position. Quite probably it would not function for the ancestor of the whole group of taxa included here, or its closest derivative. However the setal pattern described below is not so different from that seen in first-instars of Chrysomelinae or Alticinae.

The tarsungulus is always ventrally armed with a single, spiniform tarsungular seta (Ts), which usually curves up towards the tip of the tarsungulus from at least half way towards the base. The tibia usually has nine setae, considered in three groups when viewed from the side, but in Chlamisini there are additional ventral setae and the setal homology is unclear (Fig. 240). Towards the middle and base of the dorsal surface there are three dorsal tibial setae approximately in a row from base to apex (Dts1-3), of which Dts3 is more laterally placed. Along the ventral surface there are four setae, usually arranged in pairs obliquely across the midline, the ventral tibial setae (Vts1-4). Near the apex of the tibia there are two setae, dorsally at the tip the dorso-apical (Dats1) and laterally and short of the apex, the latero-apical (Lats1). The femur has eight setae, which may be divided into anterior and posterior dorso-apical, anterior and posterior ventro-apical, anterior and posterior mid-ventral, and post-ventral and post-dorsal. There are five trochanter setae : dorsal, anterior and posterior lateral, anterio-ventral, post-ventral.

4.3.3.4. Thoracic and abdominal setae (see Figs 239, 242 and 264-272)

These were not specifically used in this study because of small setal size, problems of homology in the taxa with missing setae, and intra-specific variability in position. However they do provide potential characters and are therefore briefly described below.

An initial study of the pronotal setae (Figs 239, 241-248) suggested that there was no phylogenetic significance in the absence of setae, but rather, frequent mis-observation especially of the minute setae of the posterior row. One or two setae were apparently absent in *Leasia minuta*, *Platycolaspis australis*, *Aprionota inconstans*, *Semelvillea nothofagi*, *Ditropidus concolor*, *Cadmus* (*Lachnabothra*) *braccata*, and *Chlamisus mimosae*. All dorsal setae were clearly present in *Ditropidus cervinus*, *D. submetallicus*, and *Cryptocephalus venustus*.

There are at least two different numerical systems available for the identification of pronotal setae of chrysomelid larvae (Cox 1981; LeSage 1986), one of which has been applied to Camptosomata. Both are inadequate because both fail to name setae which are constant throughout this group, and these systems are therefore ignored here. The pronotum has constantly seven setae along the anterior border of each half and from six to eight irregularly dispersed in the posterior half. In contrast to Cox's supposition for all Chrysomelidae (1981), the seven anterior setae are primary setae, in being always present in the first instar, and therefore should be labelled as such (Anterior pronotal setae, Aps1-7) (Fig. 242). Aps5 and Aps7 are almost always enlarged and Aps6 reduced. The posterior pronotal setae are much more irregularly distributed, and often very small or even absent. I refrain from naming them here pending a more thorough investigation of their dispersion in other chrysomelid subfamilies.

The remaining body setae were not studied in detail across taxa within the Camptosomata. This was mainly because of the small size of many setae and the ease with which they could be overlooked amongst the integumental tubercles. I also ignored these setae from *a priori* reasoning : such setae are enclosed in the same scatoshell in all Camptosomata, probably have identical function and therefore are unlikely to convey much phylogenetic information for a study within the Camptosomata. All members of the Camptosomata seemed to have a similar distribution of setae dorsal to the spiracles on each side of segments II-VIII: two to four usually short, widely spaced, anterior setae, and four equally spaced posterior setae, the most lateral of which lay close to the spiracle. In the Camptosomata the only abdominal setae to show obvious variation are the dorsal setae of segments VI and VII, where one or more posterior pairs are very much longer than the others and posteriorly curved.

In contrast the body setae of Eumolpinae are fairly conspicuous, and rendered more so by flattening the larvae dorso-ventrally on a slide. These larvae have the same dorsal abdominal setal configuration as Camptosomata, except that the most lateral seta of the posterior row is anterior to the remainder and immediately dorsal to the spiracle.

4.3.3.5 Structure of setae

Four structurally different kinds of setae were present in the material studied and this encompassed the range of variation known for Camptosomata and Eumolpinae.

(i) Simple pointed setae (eg. Figs 181, 185) were found throughout the taxa in all body areas.

(ii) Papillate setae were found on the head capsule of many taxa and rarely on the pronotal shield. Papillate setae were expanded apically, flattened, with one face slightly hollowed almost to the base and covered in basiconic sensilla. In outline they were crenulate. *Narrow* papillate setae were those in which the apical expansion was due to crenulation only, the narrowest part of the papillate face equalling the basal stalk in width (Figs 45, 47, 189, 192). In *broad* papillate setae the apical expansion was much broader than the basal stalk (Figs 48, 211, 222).

(iii) Clavate setae (Figs 46, 186, 204) were found on the head capsule of two taxa and were taken to be homologous although rather different in shape. In clavate setae the apex was expanded and rough-edged, but not papillate.

(iv) Spatulate setae (Figs 240, 257, 258) were found on the ventral surface of the tibia in a few taxa. These setae were somewhat longer than the other ventral setae and curved at the apex, which was flattened in a narrow oval shape.

4.3.3.6 Distribution of campaniform sensilla (see Figs 181, 185, 186 and 253 for labelled sensilla)

A campaniform sensillum is a small circular cavity in the cuticle connected to the surface by a minute pore (Snodgrass 1935). These are the 'pores' of Adephaga workers (Bousquet and Goulet 1984; Nilsson 1988). The campaniform sensilla are best seen using compound light microscopy in which they appear as small circles, rather than with SEM in which only the smaller pore is visible (Chan, Baker and Ellsbury 1988; an antennal sensillum is clearly visible in Fig. 44). The detailed cellular structure has been described for Elateridae and Scarabaeidae in which they are almost certainly homologous (Zacharuk 1971; Zacharuk, Albert and Bellamy 1977)

The usefulness of campaniform sensilla to phylogeny should be similar to setae, although there are fewer sensilla, they are more conservatively distributed and are more easily overlooked. LeSage (1982, 1984ab, 1985, 1986) is the only worker to have used the distribution of campaniform sensilla in the taxonomy of Camptosomata, but they have been utilised in studies of other groups, notably Dytiscidae (Nilsson 1988) and Carabidae (Bousquet and Goulet 1984). For this study I have included the sensilla of the head capsule and legs and have adopted in part the nomenclature developed by LeSage. However, as with the setae, LeSage has not been consistent in his nomenclature. Not all the head capsule sensilla were used in the present analysis and most are named in agreement with LeSage's study of *Pachybrachis* (1985). The epicranial sensilla have been renamed to be consistent with the setal nomenclature given above and leg sensilla are named for the first time.

On the epicranium (Figs 181, 185, 186) I recognise three sensilla (Aesm = Desm,1-3) from the epicranial suture to the stemmata, fairly close to the frontal suture. Other epicranial sensilla are more posteriorly or ventrally placed (near the cephalic foramen) and were not used. On the frons there are one or two pairs of frontal sensilla, centrally placed (Fsm1-2). In Camptosomata the clypeo-labral area has two pairs of dorsal sensilla the more central of which has been named the clypeal (Csm1), and the outer the labral (Lbsm1) by LeSage. This designation may be supported by the distribution of sensilla on the eumolpine larva, in which there is a pair on the fronto-clypeal juncture and two pairs (the outer pair very small) on the free labrum. The distribution of sensilla on the antennae and mouthparts was almost constant, very difficult to determine in some cases and was therefore not used in the analysis. Typical distribution was as follows : first antennal segment (2); mandible (3, one large median, 2 small lateral); stipes (1, near Ess2); palpiger (1); maxillary palp segments 1 (2), 2 (1), 3 (1); mentum (1 apical pair); post-mentum (1 pair); ligula (1 pair); apical labial palp segment (1).

The leg sensilla are few and almost constant in position. Two are present on the tibia (Fig. 253) : at the extreme apex of the dorsal surface the apical tibial sensillum (Atsm1), and slightly basal to this the preapical tibial sensillum (Ptsm1). The femur has a single apical sensillum (Afsm1) in similar position to Ptsm1 and the trochanter has three or four sensilla, usually appearing as an oblique row. Distribution of the sensilla on the rest of the body was not determined.

4.4 Larval characters used in analysis

The following gives an account of the characters (L1-80), their states and their gross distribution amongst the study taxa. All taxa used for analyses are listed in Appendix A and the full matrix is given in Appendix C.

4.4.1 Head, L1-61, 80

4.4.1.1 Mandible, L1-9, L59

There were basically four different types of mandible in the sample with minor overlap of state distributions : (i) narrow triangular with three apical teeth and without internal basal projection (Fig. 182); (ii) triangular with three apical teeth and internal basal projection (Fig. 224); (iii) broad triangular with one tooth overlapping internal basal projection (eg. Figs 225, 227, 233-238); (iv) broad triangular with teeth separated from internal basal projection by a concavity (eg. 226, 228-232). The positions of teeth 3 and 5 in types (iii) and (iv) are shown in Figs 232-233. 10 characters were derived to prescribe the morphological variation.

(L1). The number of mandibular teeth was five (state 0; Fig. 209), four (1; Figs 225-228, 230-238) or three (2; Fig. 224), and treated as an ordered sequence. State (0) was autapomorphic for *Aprionota inconstans* and state (2) was limited to *Edusella*, *Oomorphus*, *Arnomus*, *Semelvillea* and *Aporocera bihamatus*. Scores for *Pachybrachis*, *Stylosomus* and *Cryptocephalus frenatus* were not determined.

(L2). The gap between tooth 5 and the rest of the internal edge was described as follows : shallow concavity (0; Figs 238, 231, 232), deep concavity before basal piece (1; Figs 226, 229-230), overlap with basal piece (2; Figs 225, 227, 233-238), tooth 5 and/or internal edge not distinguishable (3; Fig. 224). The sequence was not obvious so this character was treated as unordered. State (0) was confined to eight Ditropidina and *Syneta*, state (1) was confined to the remaining Ditropidina and all other taxa showed state (2), except *Edusella*, *Oomorphus*, *Arnomus* and *Semelvillea* (3). Scores for *Pachybrachis*, *Stylosomus* and *Cryptocephalus frenatus* were not determined.

(L3). The basal projection was either present (1) or absent (0; Figs 182, 219, 221). The projection was absent in *Edusella*, *Syneta*, and the two species of *Ditropidella*. *Pachybrachis* and *Stylosomus* were not scored.

(L4). Tooth 5 was either smaller (0; Type (iii)) or larger (1; Type (iv)) than tooth 4. State (1) was an autapomorphy for the Ditropidina and Cryptocephaline A. Scores for *Pachybrachis*, *Stylosomus* and *Cryptocephalus frenatus* were not determined.

(L5). The gap between teeth 3 and 4 was either deeply concave (0; Type (iii)), shallow (1; Type (iv)), or else tooth 4 was absent (2; Fig. 224). This was assumed to be an ordered sequence. State (1) was an autapomorphy for the Ditropidina and Cryptocephaline A. State (2) was an autapomorphy for *Oomorphus*. Scores for *Pachybrachis* and *Stylosomus* were not determined.

(L6). The mandible varies in shape from solidly pyramidal to flatter and deeply hollowed on the internal surface. The base of this hollow may vary in position : either almost reaching the mandibular base (0; Figs 233-238), or terminating well short of the base at the basal projection if present (1; Figs 228-232). State (1) was found in *Oomorphus*, and all Ditropidina except a *Ditropidella* (sp. 724). Scores for *Pachybrachis*, *Stylosomus* and *Cryptocephalus frenatus* were not determined.

(L7). Tooth 1 was either present (0; Fig. 209) or absent (1). The tooth was only present in *Platycolaspis* and *Aprionota*. *Stylosomus* and *C. frenatus* were not scored.

(L8). This character described the position of the basal projection, whether closer to tooth 3 or the apex than the base (0; Types (ii-iii)), or closer to the base than tooth 3 or the apex (1; Type (iv)). State (1) was an autapomorphy for the Ditropidina and Cryptocephaline A. Scores for *Pachybrachis*, *Stylosomus* and *Cryptocephalus frenatus* and taxa lacking the basal projection were not determined.

(L9). Seta Ms1 was either simple (0) or papillate (1; Fig. 226, also LeSage, 1985, Fig. 21). State (1) was confined to *Pachybrachis* and Cryptocephaline A. The state for *Stylosomus* was not determined.

(L59). Relative position of Ms1-2 was either lateral (0; Figs 182, 224), or longitudinal (1) on the mandible. State (0) was confined to *Edusella*, *Oomorphus* and *Aporocera* sp.1049. The state for *Stylosomus* was not determined.

4.4.1.2 Epicranium and frons, L10-23, 25-48, 55

(L10). The endocarina was either present throughout the middle of the frons (0; Fig. 181) or absent from the frons (1). State (0) was confined to *Edusella* and *Syneta.*

(L11-13, 15). These are epicranial ridge characters The development of an epicranial ridge and its related setae was apparently progressive. However there were at least three types of ridge (L11 states (2), (3), and L15) as well as a simply planar face at an angle to the epicranium (L11 state (1)). In all these states the head may be described as operculate. States (2) and (3) of L11 may be reversed. The ridge, associated setae and frontal sutures may show different relationships to each other (L12 and L13).

(L11). The dorsal arc of epicranium between stemmata was described as smoothly rounded (0; Figs 9-11), smoothly angulate (1; Figs 12-16, 20), ridged by stemmata only (2; Fig. 18), or ridged throughout (3; Figs 17, 19, 21-22). These states were thought to represent an ordered sequence. State (0) was shown by *Edusella*, *Syneta*, *Oomorphus*, Chlamisini, Clytrini, *Pachybrachis*, *Leasia*, *Platycolaspis*, *Atenesus*, *Stylosomus*, all Ditropidina (except *D. submetallicus*), *Aprionota*, *Lexiphanes*, *Aporocera* (*Diandichus*) sp.4, and *A. flaviventris*. State (1) was present in two species of *Semelvillea*, *D. submetallicus*, and many species of both Holarctic and Australian Cryptocephalina. State (2) was present in *Arnomus*, Cryptocephaline A, and all six species of *Cadmus s. str.* State (3) was shown by *Semelvillea acaciae*, and many species of both Holarctic and Australian Cryptocephalina.

(L12). If the ridge was present (L11 states 2-3) it either lay dorsal to setae Aes 1-3, enclosing them (1; Fig. 40), or lay across the line of setae, incorporating them (0; Fig. 39). State (1) was confined to Cryptocephaline A, and all *Cryptocephalus.*

(L13). If the ridge was present (L11 states 2-3) it was either approximately parallel with the frontal sutures (0; Figs 33, 39), or the frontal sutures diverged from the ridge towards the midline (1; Figs 35, 40). State (1) was confined to *Arnomus*, Cryptocephaline A, and all *Cryptocephalus*.

(L15). If the ridge was present (L11 states 2-3) it was either even (0; Figs 33, 35, 40), or crenulate (1; Fig. 39). State (1) was present in all ridged Australian Cryptocephalina only.

(L14, L16-20). These characters describe the surface sculpture of the frons and epicranium This varied greatly between taxa and also between areas of the head capsule. In most taxa the five separate areas identified were either completely atuberculate or with round hemispherical microtubercles. Similar microtubercles are widespread in Paropsina, Chrysomelinae (Reid 1983). In one taxon acutely pointed tubercles were present on the epicranium (Fig. 17), in one taxon the upper frons was transversely grooved (Fig. 189), and in many taxa the upper epicranium was pitted. The surface sculpture of the epicranium seemed to be naturally divided into three regions (L18-20), in each of which three states could be defined. The logical sequence (reversible) for these states was from pitted to smooth to tuberculate.

(L14). If microtubercles were present adjacent to the frontal sutures, they were on the frons only (0; Fig. 215), on both sides (1; Fig.), or on epicranium only (2; Fig. 31). In some taxa the frontal suture was associated with the adjacent development or retention of tubercles on either the epicranium or frons. This series of states was considered a logical ordered sequence. State (1) was found in *Stylosomus*, *Arnomus*, *Semelvillea*, two large *Ditropidus* spp., *Cryptocephalus*, most Australian Cryptocephalina and Cryptocephaline A. State (0) was present in four species of Ditropidina and a few Australian Cryptocephalina. State (2) was autapomorphic for *Platycolaspis*, and the remaining taxa were scored (9). *Pachybrachis*, *Lexiphanes*, *C. venustus* and *C. frenatus* were not scored.

(L16). Microtuberculation was absent from the frons (0; Figs 29-30), present throughout the area above setae Fs4-6 (1; Figs 35-40), or confined to the vicinity of the sutures (2; Fig. 193). The states were unordered , although there could be some argument for ordering them in the sequence given. State (1) was widespread in Ditropidina, and in all Cryptocephalina except *Aporocera viridis*, Cryptocephaline A, *Stylosomus*, *Arnomus* and *Semelvillea* except *S. nothofagi*. State (2) was confined to *S. nothofagi* and *A.viridis*. *Pachybrachis*, *Lexiphanes*, *C. venustus* and *C. frenatus* were not scored.

(L17). If L16 (1), then the microtubercles were very weak (0; Figs 27-28), or strong and prominent (1; Figs 33-40). The two states of L17 were fairly well defined. However there was no clear pattern of distribution amongst the taxa, although in the larger groups most Ditropidina showed (0) and most Australian Cryptocephalina showed (1).

(L18)-(L20). These three characters describe the surface sculpture of : the upper epicranium between Des1 and the epicranial suture, or behind Aes1 in those taxa with Des1 anteriorly placed **(L18)**; the middle epicranium between Des1, Les1 and the cephalic foramen **(L19)**; and the lower epicranium between Les2, the labium and the stemmata **(L20)**. In L18-20 the sculpture was either rough, with microtubercles (0; Fig. 17), smooth (1; Figs 12-15), or rough, with irregular rows of pits (2; Figs 11, 21-22). These sequences were considered ordered. In L20 state (2) was absent. State (0) of L18 was restricted to *Stylosomus*, *Arnomus*, *S. acaciae*, and *D. submetallicus* and state (2) was found in two species of Holarctic *Cryptocephalus* and many Australian Cryptocephalina. L19 state (0) was confined to *Stylosomus*, *Arnomus*, *S. acaciae* and Cryptocephaline A, and state (2) was present in the Clytrini, *Cryptocephalus*, and many Australian Cryptocephalina. L20 state (1) was present in *Edusella*, *Syneta*, *Oomorphus* and the Chlamisini. *Pachybrachis*, *Lexiphanes*, *C. venustus* and *C. frenatus* were not scored for all three characters.

(L21). Seta Des1 was positioned well behind Aes2-4 (0; Figs 9-18, 22), or slightly behind the line formed by Aes2-4 (1; Figs 19-20), or within that line (2; Figs 21, 222). States (1) and (2) were confined to several taxa of Australian Cryptocephalina, state (2) being more frequent.

(L22-23, 25-48). These characters describe the size, shape and position of epicranium and frons setae and sensilla. The characters and their states are mostly self-explanatory. For these characters there were occasional indeterminate states which were scored (9).

(L22). Character L22 is an umbrella character, scoring presence or absence of any modified setae. It therefore overlaps with other characters scoring individual setae (L25, 27, 29, 31, 32, 40-45 and 49), coding for either absence of modified setae (0), presence of at least one pair of papillate setae (1), or presence of at least one pair of clavate setae (2). States (1) and (2) were found to be mutually exclusive. State (2) was confined to *C. mimosae* and *Atenesus*, while (1) was present for all other taxa except *Edusella*, *Syneta*, *Oomorphus* and *Neochlamisus*.

(L23, 25, 27, 29, 31, 32, 40-45). These characters describe the structure of individual setae, respectively Des1, Aes1, Aes2, Aes3, Aes4, Aes5 and Fs1-6. Setae were either simple (0), or papillate or clavate, but narrow (1), or papillate or clavate and broad (2), and the states were considered ordered. **L23** (seta Des1) : state (1) (Figs 37-38) was confined to seven Australian Cryptocephalina, and (2) (Fig. 222) was present in *Aprionota*, *C. venustus*, and 21 Australian Cryptocephalina. **L25** (seta Aes1) : state (1) (Fig. 212) was present in *Pachybrachis*, two Platycolaspina, *Stylosomus*, four *Ditropidus*, and two Australian Cryptocephalina, and state (2) (Fig. 193) was found in *Platycolaspis*, *Arnomus*, *Semelvillea*, *Aprionota*, *Lexiphanes*, Cryptocephaline A and all Cryptocephalina except those with state (1). **L27** (seta Aes2) : state (1) (Figs 189, 218, 220) was limited to *Smaragdina*, both species of *Ditropidella*, *Ditropidus* sp. 522, and four Australian Cryptocephalina, and (2) (Figs 208, 222) was more widely distributed, amongst *S. acaciae*, *Aprionota*, *Lexiphanes*, *C. venustus*, and all Australian Cryptocephalina except those with state (1). **L29** (seta Aes3) : state (1) (Fig. 192,) was found in *Labidostomis*, *Atenesus*, *Stylosomus*, most Ditropidina and *Cadmus crucicollis*, and (2) (Fig. 222) in *Pachybrachis*, *Platycolaspis*, *L. minuta*, *Arnomus*, *Semelvillea*, *Prasonotus*, *D. antennarius*, *Aprionota*, *Lexiphanes*, Cryptocephaline A and all Cryptocephalina except *C. crucicollis*. **L31** (seta Aes4) : the distribution of states was very similar to L29, with state (1) in *Leasia* sp.2, *Atenesus*, *Stylosomus*, half Ditropidina and *C. crucicollis*, and (2) in the same pattern as L29, except not *S. nothofagi*. **L32** (seta Aes5) : this character had almost identical distribution of states to L31, except *Smaragdina* with (1), and all Ditropidina either (1) or (2). *Syneta* was not scored. **L40-2** (Fs1-3) : all states in these characters were identically distributed, (1) (Figs 189, 192) in Clytrini, *Atenesus*, *Stylosomus*, all *Ditropidus* [*Elaphodes*], and two other *Ditropidus* spp, and (2) in *C. mimosae*, *Pachybrachis*, and the remaining Ditropidina, *Lexiphanes*, Cryptocephaline A and Cryptocephalina. **L43** (Fs4) : distribution of states was similar to L40-2 but with reduction of scores in *C. mimosae* (0), *L. minuta* (1), *Ditropidus* sp. 865 (1), *D. semicrudus* (1), *Aporocera* sp nr *inconstans* (0) and *A castus* (0). **L44** (Fs5): the distribution of states was similar to L43 but with a reduction of (1) and (2) scores, *Labidostomis* (0), *Leasia* sp. 2 (1), *Atenesus* (0), *Arnomus* (1), *Ditropidus* sp. 522 (1), *A. flaviventris* (1) and *C. crucicollis* (1), and state (2) in *A.* nr *inconstans* and *A. castus*. **L45** (Fs6) : similar to L44 but with reduction of states in *Pachybrachis* (1), *Platycolaspis* (0), two *Semelvillea* (0), three *Cryptocephalus* (1) and elevation of states in *Ditropidus* sp. 522 (2) and *A. flaviventris* (2). *Syneta* was not scored for L40-45.

(L80). The amount of papillation on the most papillate seta (the amount of papillation was almost constant in the setae of any given species) was assessed as either confined to the apical third or at least half (0; Fig. 211), or more or less reaching the base of the seta (1; Fig. 48). This character showed gradation but all taxa were scored. State (1) was characteristic of all *Semelvillea*, Cryptocephaline A, *Cryptocephalus coryli* and many Australian Cryptocephalina.

(L26, 28, 30). these characters describe the relative sizes of setae, repectively Aes1 and Aes4, Aes2 and Aes1, Aes3 to Aes1 or Aes4. Setae were considered of the same length if within a 25% range. Generally, size differences were very obvious.

(L26). The relative size of Aes1 to Aes4 was scored as similar (0; Figs 181, 185-186), or much larger (1; Fig. 192). State (1) was autapomorphic for *Labidostomis*.

(L28). The relative size of Aes2 to Aes1 was scored as much larger (0; Fig. 181), or similar sized (1; Figs 193, 208). The following taxa showed state (1) : *Syneta*, *Semelvillea*, *Aprionota*, *Lexiphanes*, *C. venustus* and all but five Australian Cryptocephalina.

(L30). The relative size of Aes3 to Aes1 or Aes4 (whichever was most similar) was scored as similar (0; Fig. 197), much smaller (1; Fig. 200), or much larger (2; Fig. 189). State (1) was present in *Leasia* sp. 2 and five species of Ditropidina, and (2) in *Edusella* and *Smaragdina*.

(L33). The position of Aes1 relative to the frontal suture and Aes2 was either distant, not forming part of the row of setae Aes2-4 (0; Fig. 189), or Aes1 was part of that row or even closer to the suture (1; Fig. 193). State (0) was restricted to *Edusella*, *Syneta*, *Oomorphus*, Chlamisini, Clytrini, both *Ditropidella* species, *Aprionota* and *Lexiphanes*.

(L34). The ratio of the distance between setáe Aes1-2 and Aes2-3, was much less than 0.75 (0; Fig. 185), 0.75-1.5 (1; Fig. 189), or much greater than 1.5 (2; Fig. 192). These character states appear to be continuous but in most taxa were well defined. The states are clearly ordered. State (0) was limited to *Edusella*, *Syneta*, *Oomorphus*, *Stylosomus* and 18 Australian Cryptocephalina, and (2) was limited to *Labidostomis* and *Leasia* sp.2.

(L35). The ratio of the distance from Aes4 to the frontal suture and Aes3 to the suture was either more than 2 (0; Figs 184, 192), or approximately 1 (1; Fig. 193). State (0) was confined to *Edusella*, *Syneta*, *Oomorphus*, Chlamisini, Clytrini and *Aprionota*.

(L36). Sensillum Aesm1 occurred in four different places relative to the epicranial suture and Aes1 : behind Aes1 and closer to the suture (0; Fig. 181); behind Aes1 and further from the suture (1; Fig. 192), in front of Aes1 and closer to the suture (2; Fig. 185), in front of or level with Aes1 and further from the suture (3; Fig. 222). These states were unordered. State (0) was autapomorphic for *Edusella*, state (2) was restricted to *Oomorphus*, and state (3) was found in most Australian Cryptocephalina. *Syneta* and *Stylosomus* were not scored.

(L37). Sensillum Aesm2 lay in four different areas : between Aes2 and 3 (0; Fig. 185); in front of Aes2 (1); between Aes1 and 2 (2; Fig. 193); between Des1 and Aes3 (3). The states were unordered. Most taxa showed (0) but state (1) was present in *Pachybrachis*, Cryptocephaline A and four *Cryptocephalus*, (2) was present in *Leasia* sp.2, *Arnomus*, *S. nothofagi* and *C. coryli*, and (3) in two species of *Aporocera*. *Syneta* was not scored.

(L38). Setae Fs1-6 were either all present (0; Fig. 193), or one pair was absent (1; Fig. 185). Because of the difficulty of accurately determining which seta was absent I did not specify the seta. The derived state was confined to *Syneta* and *Oomorphus*.

(L39). Frontal setae were either all of similar size (1; Figs 192-193), or two lateral pairs (not specified because of doubts of setal determination) were at least 25% longer than the remainder (0; Figs 181, 185, 186), or Fs1-4 were extremely short compared with the remainder (2; Figs 33, 35). This character attempted to reduce the relative size of frontal setae to three states of one character. It was unordered. Most taxa showed state (1) but (0) in *Edusella*, *Oomorphus* and *C. mimosae* and (2) in *Arnomus*, two *Semelvillea* and *A. castus*.

(L46-47). The configuration of the frons setae is an obvious feature for the differentiation of groups of taxa. In the formation of patterns two processes seem to be operating : the vertical displacement of the lower setae, especially Fs3 and Fs6, and the lateral displacement of Fs2 and Fs3. In the first process the downward displacement of setae results in reduction of the number of setae on the frons above Fs4-6. In the second case the lateral displacement of Fs2 or Fs3 results in reduction of the number of horizontal rows of frontal setae or at least changes in shape of the pattern.

(L46). The outgroup pattern of upper frontal setae was 2 + 2 + 2, designated state (1; Figs 27-32, 40, 181, 193) because in an ordered sequence the two other patterns are most logically independently separately derived from this. The two derived patterns were 2 + 4 (0; Figs 25, 26, 186, 189, 192, 208), and 2 + 2 (2; Figs 35-37, 39, 212, 222). In pattern 2+4 the row of four setae was due to Fs2-3, not to be confused with dorsal displacement of Fs6 with a 2+2 pattern. State (0) was found in *C. mimosae*, Clytrini, *Pachybrachis*, Cryptocephaline A and *Aprionota*, and (2) in *Stylosomus*, *Arnomus*, *S. acaciae*, *D. submetallicus* and all but two of the Australian Cryptocephalina. *Syneta* was not scored.

(L47). To assess changes in lateral displacement of Fs2 or Fs3 the distance Fs2-Fs2 was compared with other lateral distances and found to be roughly equal to Fs5-Fs5 (0; Figs 27, 28, 33, 40), intermediate (1; Fig. 30, 34), or equal or less than Fs3-Fs3 (2; Figs 29, 31, 35, 39). State (0) occurred in *Edusella*, *C. mimosae*, Clytrini, *Pachybrachis*, *S. acaciae*, all Ditropidina, *Aprionota* and three *Cryptocephalus*. State (2) occurred in *Neochlamisus*, three Platycolaspina and all Australian Cryptocephalina. *Syneta* was not scored.

(L48). Sensillum Fsm1 varied in position on the frons from approximately level with Fs1 (0; Fig. 181), to between Fs1 and Fs2 (1; Figs 186, 192, 222), or approximately level with Fs2 (2; Figs 200, 208, 212, 215, 218, 220). The position of Fsm1 varied vertically but frequently also asymmetrically and many taxa were scored as intermediate (1). State (0) was restricted to *Edusella* and *S. acaciae*, whereas (2) was widespread, in *Smaragdina*, *Platycolaspis*, *Leasia*, *Atenesus*, *Stylosomus*, *Semelvillea waraganj*, all Ditropidina, *Aprionota* and *A.* nr *inconstans*. *Syneta, Oomorphus* and *C. frenatus* were not scored.

(L55). The stemmata were either visible in a 4 + 2 arrangement (0; Fig. 10), or entirely absent (1; Fig. 9). In most taxa the possession of six stemmata was very clear. In some taxa the stemmata were only weakly expressed and were harder to observe, for example *Oomorphus*, *Aporocera bynoei*. The outgroup lacked stemmata, although pigmented eye spots were visible in uncleared larvae. State (1) was only present in *Edusella* and *Syneta*.

4.4.1.3 Antenna, L56-57

(L56). The number of antennal segments was 3 (0; Figs 12-22, 222), 2 (1; Figs10, 11, 186, 189, 192) or 1 (2; Figs 9, 181). State (1) was confined to Chlamisini and Clytrini and state (2) to *Edusella* and *Syneta.*

(L57). The sensorium at the apex of segment two showed two distinct forms : elongate, either conical or ovate (0; Figs 12-22, 186, 222), or short, globular or flattened (1; Figs 10-11, 189, 192). State (1) was an autapomorphy for the Clytrini.

4.4.1.4 Clypeolabral complex, L24, 49-54, 58

Structures of the clypeolabral complex are minute or comparatively invariable in the first instar. The characters used here are those recorded in literature or are relatively easily seen.

(L24). The labrum was either freely articulating (0; Figs 13, 181) or fused to the clypeus (1; Figs 14, 185). State (0) was confined to *Edusella* and *Syneta.*

(L49). The shape of seta Cs1 varied like other head-capsule setae, from simple, pointed (0; Fig. 186), papillate and narrow (1; Fig. 189), to papillate and broad (2; Fig. 222). State (1) was found in *Smaragdina*, *Pachybrachis*, *L. minuta*, *Arnomus*, all Ditropidina except *Ditropidus*. sp. 522, four *Cryptocephalus* and three Australian Cryptocephalina. State (2) occurred in *D*. sp. 522, Cryptocephaline A, *C. frenatus* and all but three Australian Cryptocephalina.

(L50). Sensillum Csm1 was positioned at the level of or below Cs1 (0; Figs 185, 186, 222), or above Cs1 (1; Figs 212, 215, 218, 220). State (1) was confined to *Pachybrachis*, all but one Ditropidina (not *Ditropidus* sp. 865, Cryptocephaline A and *C. moraei*. *Syneta* was not scored.

(L51). In cleared specimens the epipharynx was simple and evenly thickened (0), or in the derived state showed a thicker, triangular, ventral sclerotisation at the apex of the labrum (1; not illustrated), noted by Kasap and Crowson (1976). State (1) was found in *Chlamisus mimosae* and all Ditropidina. *Syneta* and *Stylosomus* were not scored.

(L52). Sensillum Lbsm1 was found either near the midline of the labral area (0; Fig. 181), or near the side margins (1; Fig. 186). State (0) was confined to *Edusella* and *Syneta*. *Pachybrachis* was not scored.

(L53). Epipharyngeal setae were either ventral (0; Figs 23-24, 181, 185), or dorsal (1; Figs 25-40, 186, 189). The position of the epipharyngeal setae was most easily seen by SEM, as it was difficult to identify the setae in cleared specimens under light microscopy. State (0) was confined to *Edusella*, *Syneta* and *Oomorphus*.

(L54). The apex of the epipharynx or labrum was rounded to shallowly concave (0; Figs 185, 186), deeply concave (1; Figs 200, 202), or concave but tuberculate medially (2; Figs 193, 222). The epipharynx was centrally tuberculate only in taxa with a deep concavity, thus states (0)-(2) formed a sequence. The three states were fairly scattered in distribution although all Ditropidina showed (0) and all *Cryptocephalus* (2).

(L58). In cleared specimens the frontoclypeal suture was evidently internally thickened (0; not illustrated), or of even thickness (1). The thickening was only visible as a dark bar across the base of the frons. State (0) was found in *Edusella*, *Smaragdina*, *Pachybrachis*, all Ditropidina and Cryptocephaline A. *Syneta*, *Oomorphus*, *Neochlamisus*, *Lexiphanes*, *C. venustus* and *C. frenatus* were not scored.

4.4.1.5 Labiomaxillary complex, L60-61

For the reasons given above this region was only treated superficially. The outgroup taxon *Edusella* showed several differences which in this study were autapomorphies. I could find only two characters which seemed to show suitable variation, but in both the states were difficult to distinguish.

(L60). The lateral margin of the stipes was either smooth (0; Fig. 184), with a line of fine microchaetae (1; Figs 191, 195), or spiculate (2; Fig. 186). Microchaetae were fine minute hairs. Spiculae were short fine spines and were considered to be derived from microchaetae. Neither were articulated. Most taxa showed state (1), but (0) was in *Edusella*, *Syneta*, *Atenesus*, *Aprionota* and two *Aporocera*, and state (2) in

Chlamisini, *Lexiphanes*, two *Cryptocephalus* and *A. bynoei*. *Pachybrachis* and *Stylosomus* were not scored.

(L61). The apex of the galea was clothed with what appeared to be short stout setae but were probably basiconic sensilla. These were either similar sized (0; Fig. 195), or 2 or 3 were flattened and curved at the tip, and usually much longer (1; Figs 50, 191). State (1) was scattered, in *Neochlamisus*, Clytrini, three Platycolaspina, all Ditropidina, Cryptocephaline A and four *Aporocera*. *Stylosomus* was not scored.

4.4.2 Foreleg, L62-73

Most leg characters are self-explanatory. The positions of setae and sensilla were determined by viewing the cleared leg from the side. Because the leg was viewed flat on a slide comparative distances between setae were easy to determine. For L70 and L73 spiculae are taken to be derived from microchaetae, as in L60. Characters L65, 66, 68, 69, 71, 72 were not appropriate to *Edusella*, *Syneta* and the Chlamisini, in which there were either less than or more than four ventral setae.

(L62). The length of the tarsungulus was either more than 2.5 times the depth (0; Fig. 249-252), approximately twice the depth (1; Fig. 253-263), or 1.5 or less times the depth (2; Fig. 240). The states were ordered and generally well defined. State (1) was found in *Arnomus*, *Semelvillea*, four Ditropidina, *Aprionota*, *Lexiphanes*, three *Cryptocephalus* and all Australian Cryptocephalina. State (2) was autapomorphic for Chlamisini.

(L63). The ventral outline of the tarsungulus varied in order from: not angulate (0; Figs 249-251) to angulate at the setal insertion (1; Figs 252-255), to broadly basally lobed (2; Fig. 240). Distribution of states was similar but not identical to L62 : state (1) in *Platycolaspis*, *Semelvillea*, seven Ditropidina, Cryptocephaline A, two *Cryptocephalus* and three *Aporocera*; state (2) autapomorphic for Chlamisini.

(L64). The ventral tibial setae were either all simple (0; Figs 249-255), or at least one was spatulate (1; Figs 240, 257-258). The derived state was restricted to Chlamisini and *Ditropidella*.

(L65). The distance Dts1-2 was either less than Dts2-3 (0; Figs 250, 252, 255), or equal to or greater than Dts2-3 (1; Figs 251, 253, 254, 256). State (1) was found in *Smaragdina, Platycolaspis, Stylosomus, Arnomus, Semelvillea, Aprionota, Lexiphanes*, three *Cryptocephalus* and all but six Australian Cryptocephalina. *Cryptocephalus venustus* was not scored.

(L66). Sensillum Ptsm1 was either closest to seta Dts3 (0; Figs 253-255), or Dats1 (1; Fig. 251). State (1) was present in Clytrini, 10 Ditropidina, *Aprionota*, Cryptocephaline A and all Cryptocephalina. *Pachybrachis, Stylosomus, Lexiphanes* and both described *Cryptocephalus* were not scored.

(L67). Accessory setae on the tibial venter, additional to Vts1-4 were either absent (0; Figs 253-255), one additional seta was present (1; Fig. 252), or more than one (2; Fig. 240). State (1) was autapomorphic for Cryptocephaline A, and state (2) was autapomorphic for Chlamisini.

(L68). Seta Dts3 was either level with or apical to a perpendicular line through Vts3 (0; Figs 250, 255), intermediate (1; Figs 251-254), or level with or basal to Vts2 (2; Figs 261-262). The three states were scattered but with (0) characteristic of most Ditropidina and (2) characteristic of most Australian Cryptocephalina which also lacked state (0). *Cryptocephalus venustus* and *Pachybrachis* were not scored.

(L69). Distance Vts3-4 was greater than 0.5 length of either (0; Figs 253-254), or less than or equal to length of either (1; Figs 251-252, 255). As in L68 the states were scattered but most Ditropidina showed (0) and most Australian Cryptocephalina (1).

(L70). The surface sculpture of the tibia, especially ventrally, was smooth (0; Figs 249, 251, 254, 255), with microchaetae (1; Figs 250, 252, 259), or with spiculae (2; Figs 33-34, 253). These states were considered ordered (increasing consolidation of spines). In some taxa only one or two minute projections were present therefore it is possible that taxa were misscored (0). State (1) was found in *Oomorphus, Arnomus*, eight Ditropidina, *Aprionota* and Cryptocephaline A. State (2) was autapomorphic for *Semelvillea*. *Neochlamisus, Pachybrachis, Stylosomus* and *Lexiphanes* were not scored.

(L71). The distance Vts2-3 was either greater than Vts3-4 (0; Figs 250, 251, 255), or less than or equal to Vts3-4 (1; Figs 253, 254). The states were scattered but state (0) predominated in all groups.

(L72). The distance Vts3-4 was either less than or equal to 0.75 length of these setae (0; Fig.), or greater than or equal to the length of these setae (1; Fig.). As in L71 the states were scattered.

(L73). The surface of the femur was either smooth (0; Figs 252, 255), with ventral microchaetae (1; Figs 250, 252), or with ventral spiculae (2; Figs 253, 254). This was the femoral counterpart of L70. The distribution of states was similar but not identical to L70 : state (1) in *Oomorphus* and *Smaragdina*, and state (2) in *Platycolaspis*, *Arnomus*, *Semelvillea* and *Aprionota*. *Neochlamisus*, *Pachybrachis*, *Stylosomus*, *Lexiphanes* and *C. venustus* were not scored.

4.4.3 Thorax and abdomen, L75-78, L89

Spiracular plates (L75, L76, L89) were easily seen and therefore provided useful characters. I also used the eggbursters (L77), pronotal setae (L79) and dorsal setae of segments VI-VII (L78).

(L75). Although *a posteriori* evidence suggested otherwise, the form of the abdominal spiracular plates could be described as a transformation series, from bicameral (outgroup) (0; Figs 55, 56, 264), to small moniliform with less 10 cells (1; Figs 58, 269), to large moniliform with more than 10 cells (2; Figs 59, 60, 270, 272), to compound cribriform (3; Figs 57, 239, 267). In this hypothetical sequence the compound cribriform state is derived by infilling of the 'ring' of the moniliform type with extra cells. However I was not convinced that this was necessarily the most morphologically likely sequence, therefore this character was unordered. The moniliform and compound cribriform types are obviously very closely related, and both may even be found on the same animal (L89). States were distributed as follows :

(0) in *Edusella* and *Oomorphus*, (1) in *Atenesus* and *D. semicrudus*, (2) in two Ditropidina, *Aprionota*, *Lexiphanes* and most Cryptocephalina, and (3) in the remaining taxa. *Syneta* and *C. frenatus* were not scored.

(L89). The states were : homogeneity of spiracle type between prothorax and abdomen (0), or presence of both moniliform and cribriform types (1). State (1) was autapomorphic for all *Semelvillea*, which had moniliform prothoracic spiracles and compound-cribriform abdominal spiracles. *Syneta* and *C. frenatus* were not scored.

(L76). The relative size of the prothoracic and abdominal spiracles was variable, the former having either less than twice the cells of the latter (0), or with at least twice the number of cells (1; Fig. 239). State (1) occurred in *Chlamisus mimosae*, *Arnomus*, all Ditropidina and three Australian Cryptocephalina. *Syneta*, *Neochlamisus*, *Pachybrachis*, *Lexiphanes* and the described *Cryptocephalus* spp. were not scored.

(L77). Eggbursters were distributed on the meso- and metathorax, and abdominal segment I (0; Figs 52, 239), or only on the thoracic segments (1; Fig. 51). Since the abdominal eggburster is usually smaller and on a smaller sclerite, it may possibly be overlooked. Important taxa were checked with SEM. As with the spiracle type (L75) the two states of this character were found in very closely related taxa. State (0) was found in *Edusella*, *C. mimosae*, two *Semelvillea*, Cryptocephaline A and 12 Australian Cryptocephalina. *Syneta*, *Stylosomus* and *C. frenatus* were not scored.

(L78). The dorsal setae were identical between segments VI and VII in all taxa and showed the following variation : the two innermost pairs almost equal longest (0; Fig. 264), only second pair from midline longest (1; Figs 265-272), second and third pairs from midline almost equal longest (2; not figured). The designation of states for L78 is the most logical for an ordered sequence, involving the loss of one long seta and development of another in two steps. However, in all states the second seta from the midline was always longest and the separation of states may therefore have been artificial. All dorsal setae of *Edusella* were of equal length. State (0) was confined to *Oomorphus* and *C. mimosae*, and state (2) was restricted to *Ditropidella* sp. 724.

However,*Syneta*, *Neochlamisus*, *Pachybrachis*, *Stylosomus*, *Lexiphanes* and the two described *Cryptocephalus* were not scored.

(L79). The pronotal setae were generally simple and pointed (0; Figs 241-248) but in a few taxa papillate setae were present (1; not figured), especially one or more of Aps1-3. Papillate setae were only present in 11 Australian Cryptocephalina.

Note that there is a 'character' L74 in the matrix but this was not used in analyses.

4.5 Analyses

After construction of the matrix the following characters were found to have autapomorphic states for single taxa : L1(0) = *Aprionota*; L14(3) = *Platycolaspis*; L26(1) = *Labidostomis*; L36(0) = *Edusella*; L55(1) = *A. bynoei*; L78(2) = *Ditropidella* sp. 724.

The states in the complete character state list were very close or even identical for a few taxa but as the data set was to be used in conjunction with an adult data set I was not concerned by this.

Three analyses had been completed before a few errors of transcription or observation were detected. These analyses are not described here, but they gave some indications of the likely relationships of taxa. Furthermore they indicated which taxa could be omitted in choosing subsets of the 69 species for which I had larval descriptions.

4.5.1 Analysis one (AL(i)).

This analyis with PAUP was based on the combination of 80 characters and 69 taxa. The taxa are listed in Appendix A and the full matrix in Appendix C. The genus *Stylosomus* was incorporated, since the published description (Medvedev and Zaitsev 1978) was sufficient for the retrieval of most of the larval characters. Only a limited sample of the Ditropidina and Australian Cryptocephalina was used because it was evident that many taxa were separated by single states or were identical. The chosen set of taxa represented each different larval type together with some closely related pairs of species (on adult evidence), for example the two *Leasia* species. This data set was comparable with analyses of the same taxa for adults (AA(ix)) and combined adults and larvae (ALA(i-iv)).

The outgroup was *Edusella*. The following parameters applied: matrix size 80 characters by 46 taxa; SWAP = ALT; MULPARS; ROOT = OUTGROUP; WEIGHTS; deleted taxa 1, 6, 18, 25-7, 29, 30, 32, 36, 38, 40-2, 44, 45, 51-8, 61, 62, 66, 70-3, 78, 79; deleted characters L74, 81-8; unordered characters 2, 15, 16, 36, 37, 39, 66, 75.

There were four minimum-length trees (Figs 924-926), of 257.500 steps length and Consistency Index (CI) 0.309. The four trees differed by a minor change in the position of *Aporocera* [*Chloroplisma*] *viridis* and in the placement of *Lexiphanes*, sister to either (*Aprionota* + *Cryptocephalus venustus* + Australian Cryptocephalina) or to only Australian Cryptocephalina. There were zero length branches at the nodes leading to *A.* [*Schizosternus*] *albogularis*, *Ditropidus antennarius*, the clade with *A.* [*Cyphodera*] *chlamydiformis* at its base, *A. chlamydiformis*, and (*A.* [*Loxopleurus*] *gravatus* + *Lachnabothra braccata*). Two trees were of the following structure : *Oomorphus* + (Chlamisini + (Clytrini + (*Stylosomus* + (*Atenesus* + (((*D.* sp 865 + (Ditropidina + Cryptocephalinae sp. A)) + (*Leasia* + (*Platycolaspis* + (*Leasia* + (*Pachybrachis* + ((*Arnomus* + *Semelvillea*) + (*C. moraei* + (*C. coryli* + ((*Aprionota* + *C. venustus*) + (*Lexiphanes* + Australian Cryptocephalina), whereas the other two trees differed in the position of *Lexiphanes* as described above. The arrangements of Ditropidina and Australian Cryptocephalina are shown in Figs 925-926 respectively. *Leasia* and *Cryptocephalus* were resolved as paraphyletic taxa.

4.5.2 Analysis two (AL(ii)).

The program MACCLADE was used for this analysis, because of the limited numbers of taxa and characters and in order to study the effects of applying the DOLLO and IRREVERSIBLE character transformation parameters. A considerably reduced taxon set was taken, for comparison and combination with adult characters of the same taxa. Only characters deemed to have 'usefully' distributed states were used, that is states which were approximately monophyletically defined by their taxa.

The data matrix was a subset of the matrix of characters and taxa used for PAUP. Twenty-three taxa were chosen, including representatives of Lamprosomatinae, Chlamisini, Clytrini, Pachybrachini, Coenobiina, Ditropidina, Platycolaspina and Cryptocephalina, with *Edusella* + *Syneta* as the outgroup. However the number of taxa represented was actually much larger because alternative states for other taxa within well defined groups were included. Thus the data set combines all states for the two Chlamisini, two *Ditropidella*, two *Leasia* and four *Cryptocephalus* species of the original data set prepared for PAUP. Twenty-four larval characters were used as follows (listed in Section 4.4) : L1, 2, 4, 5, 8, 11, 14, 16 (with states 1 and 2 united), 18, 20, 22 (with states 1 and 2 united), 25, 33, 35, 40, 43, 46, 50, 51, 56, 58, 64, 75, 78. In L14 states (2) and (3) were autapomorphic for *Ditropidus* [*Elaphodes*] *cervinus* and *Platycolaspis australis* respectively.

The following parameters were applied : data matrix 23 taxa by 24 characters; ordered characters L1, 5, 11, 18, 46; irreversible character L56; equal character weights.

Thirty-two shortest trees were found, each of 89 steps and CI 0.45. A concensus of these trees is given in Fig. 927. Monophyly for each of the Cryptocephalina and Ditropidina is supported but is rejected for Platycolaspina. Pachybrachini become a basal group, but this position is based on relatively few scored characters from the description of *Pachybrachis* (LeSage 1985). Coenobiina, represented by *Aprionota*, may be the sister group of the Clytrini or of the remaining Cryptocephalini.

This analysis should be compared with AA (x) and ALA (v) which were based on the same taxon set.

4.6 Discussion

It is evident that the larval character sets cannot be used alone to discriminate taxa of low (generic?) rank. Virtually all the significantly variable characters are provided by the head capsule and fore-leg and these provide a limited set of characters which in the case of cephalic setae are likely to be correlated and subject to frequent reversal. The larvae do provide useful evidence for the 'primitiveness' of Lamprosomatinae and the monophyly of the tribes and subtribes of Cryptocephalinae. The contribution of larval character variation to the phylogeny of Camptosomata will be discussed further in Chapters **7** and **8**.

Chapter 5 : Pupae

5.1 Introduction

The study of pupae was not intended to be an integral part of this project because of the great difficulty in obtaining named specimens and because pupae are very poorly described in literature. However a few pupae, which could definitely be associated with adults, were collected or obtained. These have been studied firstly to examine the potential of pupal characters in the systematics of Camptosomata, and then to contribute additional characters, albeit ancillary to the larval and adult data sets.

The pupae of Megascelidini, *Syneta*, and primitive Eumolpinae are unknown. Pupal descriptions or illustrations have been published for three genera of Eumolpinae (Lysaght 1930; Broodryk 1965; Gressitt 1967) and for Lamprosomatinae (Monrós 1949), Chlamisini (LeSage 1982, 1984a), Clytrini (Erber 1969; Medvedev and Zaitsev 1978) and Cryptocephalini (Reineck 1913a; LeSage 1984b). In all known Camptosomata pupation takes place in the larval case, either in leaf litter, under bark, or on foliage. Ground-dwelling species may climb trees or plant stems to pupate (*Cryptocephalus* : Prell 1925; *Ditropidus*, *Lachnabothra* : pers. obs.), although this has been doubted (Erber 1988). In all known Eumolpinae pupation takes place in the soil.

Pupae have been little used in phylogenetic studies of Coleoptera, although Chrysomelidae have fared rather better than most groups. I suspect that this neglect occurs partly because pupae are harder to obtain than other stages, but also because there is a suspicion that their characters correspond to either adult or larval characters. Certainly it is true that there are only a few uniquely pupal characters. Pupae were used to substantiate a larval classification of Chrysomelinae (Kimoto 1962a), and LeSage (1982, 1984a, 1984b) has shown that camptosomatan pupal characters may be useful in systematics.

5.2 Material and methods

Pupal cases may be distinguished from those of larvae by their apertures, completely sealed with secretionary material. Parasitised larval cases also have sealed apertures but the seal is the silk mesh of the parasite cocoon (see Chapter **10**).

Full collection details of the specimens studied here are given in Appendix A. The pupae of six species, representing five genera, were available, mostly from field collecting. Pupae of two species of *Lachnabothra* were found because the larvae of this subgenus climb stems and pupate at 0.5-1.5m above ground. Some pupae in each population were allowed to develop to establish their identity. Pupae of *Ditropidus* [*Prasonotus*] *submetallicus* were found with larvae and adults among the leaf bases of *Xanthorrhoea*. Three pupae of *Aporocera* [*Cadmus*] *aurantiacus* were collected in an area with very high larval density of *A. aurantiacus* at a time when pupae were to be expected. The exposed pupa of *Edusella* was found fortuitously in an earthen cell under a stone in dry sclerophyll woodland. The pupae of *Aporocera* and *Edusella* were drawn, then allowed to partially develop to establish their identity. Pupae of *Chlamisus mimosae* were obtained from a laboratory culture at the Department of Primary Industry, Brisbane.

Pupae were fixed in KAA and stored in ethanol. Those of Camptosomata have short to minute colourless setae which were stained for by dipping the pupae in acid carmine and/or chlorazol black. This treatment only slightly improved setal visibility. The pupae were examined with a dissecting microscope. No SEM work was undertaken because of the paucity of material.

A few camptosomatan pupae have been illustrated or described : Lamprosomatinae : *Lamprosoma* (Monros 1949); Chlamisini : *Exema* (LeSage 1982) and *Neochlamisus* (LeSage 1984a); Cryptocephalini : *Cryptocephalus* (Reineck 1913a) and *Lexiphanes* (LeSage 1984b); Clytrini : *Clytra* (Erber 1969) and *Labidostomis* (Medvedev and Zaitsev 1978). These descriptions have been used in the following character analysis, but it was only possible to score two characters for *Cryptocephalus* and five for *Labidostomis*. Pupae of Pachybrachini are as yet unknown.

5.3 Pupal morphology (see Figs 279-280, 289-291, 298 for labelling of structures)

Curculionid pupae have been described in more detail than any others in the Chrysomeloidea-Curculionoidea. For example May (1978) has described a complete setal index for the pupae of *Pantorhytes*. I have tried to apply her setal nomenclature as far as possible to the pupae of Chrysomelidae but invariably there is only limited correspondence. On the head I recognise epicranial (Eps = epicranial + upper postantennal + orbital), postorbital (Ps), orbital (Os = lower postantennal), upper frontal (Ufs = upper postantennal [?]), lower frontal (Lfs = rostral), and epistomal (Ets). Other curculionid head setae appear to be absent from all chrysomelid pupae seen. There was no clear pattern of pronotal setae therefore no discrete areas have been distinguished. The legs of chrysomelids may show similar femoral setae (Fs) on the knees (junction of femur and tibia), and there are mesonotal (Mss) and metanotal (Mts) setae as described by May (1978). The chrysomelid abdominal chaetotaxy is essentially similar to the curculionid, with prodorsal (Pras), postdorsal (Poas), spiracular (Sas) and lateral (Las) setae, although the boundaries of these areas may be obscure.

LeSage (1982, 1984a, b) has given descriptions of the camptosomatan pupal type and noted the usefulness of certain features for classification.

Camptosomatan pupae are exarate, white or cream, and have short setae. The appendages are termed thecae, enclosing the developing appendages of the adult. The head, thorax and legs are similar to the adult in structure but may be ornamented with short to minute setae (except the legs), which may be raised on small tubercles. The antennae lie under the side of the pronotum and, if long, are coiled around the first two pairs of legs. The apex of each antennal segment has 4-5 papillae, which may be very small. The elytrotheca may have a swelling or elongate projection at its apex. The abdomen may be simple or may have a pair of 'fleshy' projections on tergites VI and/or VII. All lateral posteriorly directed projections on tergites VI-VII were considered to be homologous for this study. A few short setae may be scattered transversely across each abdominal tergite. The urogomphi on tergite IX are always separate and small or absent. The female egg-laying hollow is not generally obvious but females have a pair of small globular hemisternites in the position of sternite IX, whereas the male abdomen is simple. Similar sexual dimorphism has been described for Cerambycidae (Duffy 1952) and is present in Paropsina, Chrysomelinae (Reid and Ohmart 1989). The abdomen may be ornamented with short setae which are frequently raised on small tubercles and these may be more visible and spinose towards the abdominal apex. Only the front five pairs of abdominal spiracles appear to be functional, the sixth being weakly sclerotised and pale.

Pupae of the suggested outgroup, Eumolpinae, are much less well known. I have seen descriptions or illustrations for *Colaspis* Fabricius (Salt 1928), *Eucolaspis* Sharp (Lysaght 1930), *Syagrus* Chapuis (Broodryk 1965) and *Rhyparida* Baly (Gressitt 1967) and have collected the pupa of *Edusella.* Although these pupae represent two different tribes and four 'sections' (Seeno and Wilcox 1982) they are remarkably similar morphologically. Compared with Camptosomata these pupae have much longer setae (typical of soil-inhabiting pupae, *vide* Paterson 1931), setae on the knees (one of which is modified as a spine), and although there may be lateral projections on segments VI and VII these appear to be thickened setae.

5.4 Pupal characters used in analysis

In exarate pupae there is a dearth of characters to choose from because those associated with adult and larval morphology have to be eliminated, and the pupae are soft and unsclerotised so that surface features are indistinct. Adult characters include the shape of the head and thorax and most appendages, but not the elytron and wing thecae. Although the abdomen is 'larviform' in appearance none of the setae, tubercles or urogomphi appear to correlate with features of the larva. The main independent pupal characters available involve setae and small projections on the appendages or abdomen.

The following list provides the characters and their states together with the distribution of the states in the taxa studied. All taxa used for analysis are listed in Appendix A and the matrix is given in Appendix C.

(P1). Facial setae were present on the frons and epicranium (0; Fig. 279), epicranium only (1; Figs 290, 293, 297), or absent (2; Fig. 285). Progressive loss of facial setae may represent a transformation series. State (0) was unique to the outgroup, state (2) found in all Chlamisini, and the remainder showed (1).

(P2). Apices of the antennal-segment thecae were either papillate (0; Fig. 279) or simple (1; Fig. 285). State (1) was shown by *Chlamisus* and *Ditropidus*, but the seven described taxa were not scored.

(P3). Pronotal disc was either evenly curved (0; Fig. 280) or with at least 2 large tubercules (1; Figs 284-285). Discal tubercles were present in *Chlamisus* and *Neochlamisus* and are presumed to be homologous.

(P4). Pronotal setae were distributed as follows : absent (0; Fig. 284), 20-50, fairly evenly scattered (1; Fig. 280), or 60-100, concentrated around periphery (2; Figs 289, 292, 296). State (1) was considered plesiomorphic, as this number and distribution of setae was widespread outside the taxa considered here. The character was obviously ordered but the apparent discreteness of the states is probably artificial due to the small data set. State (0) was present in all Chlamisini, (1) in *Edusella*, *Lamprosoma* and *Lexiphanes*, and (2) in *Clytra*, *Ditropidus*, *Lachnabothra* and *Aporocera*.

(P5). Metanotal setae numbered four (0; Figs 280, 289, 292, 296) or nil (1; Fig. 284). Metanotal setae were absent in all Chlamisini and in *Clytra*.

(P6). Femoral setae were three (0; Fig. 279) or nil (1; Figs 289, 292, 296). State (0) was confined to *Edusella*.

(P7). The median posterior setae on tergites I-V were variously distributed : three pairs evenly spaced across tergites (0; Fig. 280); three pairs separated into two groups, two pairs near midline and one by spiracle (1; Fig. 289, 292, 296); one pair near midline (2; not figured); no median setae (3; Fig. 284). This seems to be a transformation series but as in P1 it only involves reduction in numbers of setae, which may easily be homoplasious. State (0) was restricted to *Edusella*, (2) to *Exema* and *Lexiphanes*, and (3) to *Chlamisus*.

(P8). Prodorsal setae on tergites I-V were present (0; Fig. 283) or absent (1; Fig. 280). State (0) was confined to *Clytra*.

(P9). Lateral abdominal setae on segments I-VII numbered either 0-2 (0; Fig. 280) or 3+ (1; Fig. 281). State (1) was autapomorphic for *Lamprosoma*.

(P10). The lateral posteriorly directed projections on tergite VI were absent (0; Figs 284, 289), spinose (1; Fig. 280), or fleshy lobes with a subapical seta (2; Figs 295, 299). The states were unordered because of doubts about homology. State (1) was confined to *Edusella* and (2) to *Lachnabothra* and *Aporocera*.

(P11). The lateral posteriorly directed projections on tergite VII were absent (0; Fig. 281), spinose (1; Fig. 280), or fleshy lobes, usually with a subapical seta (2; Figs 288, 289, 295, 299). The states were unordered because of doubts about homology. State (1) was confined to *Edusella* and (0) to *Lamprosoma* and *Labidostomis*. *Clytra* was indeterminate.

(P12). The shape of tergites VI-VII varied as follows : evenly contracted to apex (0; Fig. 281); tergite VII not much narrower than VI, apices quadrate (1; Fig. 284). This character may have an artifactual component. The apex of tergite VII was quadrate in Chlamisini and *Lexiphanes*.

(P13). Apical elytrothecal lobe was absent (0; Fig. 279), present but simply convex (1; Figs 289, 296), or present and acutely produced (2; Fig. 292). State (1) was found in *Ditropidus* and *Lachnabothra*, (2) in *Aporocera*. *Lexiphanes* was indeterminate.

(P14). Urogomphi were present (0; Figs 279, 281, 291, 298) or absent (1; Figs 287, 294). Urogomphi were absent in *Chlamisus*, *Exema*, *Clytra*, *Labidostomis* and *Aporocera*.

5.5 Analyses

The characters listed above (section **5.4**) were used for a phylogenetic arrangement of the pupae. The full set of taxa was not used because the two species of

Lachnabothra were identical, *Aporocera*differed from them by autapomorphy, *Chlamisus* differed from *Exema* only by autapomorphies and the descriptions of *Labidostomis* and *Cryptocephalus* were too poor. The data set was therefore reduced to 8 taxa and 14 characters. The determination of some character states depended on presumably faithful drawings, as most authors had been content to draw and not describe. This problem especially concerned determination of setal pattern on the figures of *Clytra* and *Lamprosoma*. It was not possible to score P2 from drawings. The polarity of P6 was supported by many taxa outside the group considered here.

Analysis was by MACCLADE only.

5.5.1 Analysis one (AP(i))

The cladistic relationship of the pupae of *Lamprosoma*, *Neochlamisus*, *Exema*, *Clytra*, *Lexiphanes*, *Ditropidus* and *Lachnabothra,* was studied using *Edusella* as the outgroup and the 14 characters listed above. Character P2 was not scored for the Chlamisini, nor P11 for *Clytra*. Character transformations were specified as follows : P1, P4 and P7 were ordered; P14 designated irreversible. Weights were equal. The three minimum-length trees (not figured) had length of 23 steps with CI of 0.83. The trees were (a) *Lamprosoma* + (*Lexiphanes* + ((*Ditropidus* + *Lachnabothra*) + (*Clytra* + (*Exema* + *Neochlamisus*)))); (b) *Lamprosoma* + ((*Lexiphanes* + (*Ditropidus* + *Lachnabothra*)) + (*Clytra* + (*Exema* + *Neochlamisus*))); (c) *Lamprosoma* + ((*Ditropidus* + *Lachnabothra*) + (*Lexiphanes* + (*Clytra* + (*Neochlamisus* + *Exema*)))). These can be combined to give (d) *Lamprosoma* + ((*Lexiphanes*) + (*Ditropidus* + *Lachnabothra*) + (*Clytra* + (*Exema* + *Neochlamisus*))).

5.5.2 Analysis two (AP(ii))

This study used the specifications listed above but with substitution of known states from other taxa for unknown states (= ? in matrix). In *Chlamisus* P2 has state (1), therefore this was substituted for (?) in *Neochlamisus* and *Exema*. In *Labidostomis* P11 had state (0) and this was substituted for (?) in *Clytra*. The two minimum-length trees (Fig. 928) were 24 steps long, with CI of 0.79. These trees were described by : (e)*Lamprosoma* + (*Clytra* + ((*Ditropidus* + *Lachnabothra*) + (*Lexiphanes* + (*Neochlamisus* + *Exema*)))) (Fig.); (f) (*Lamprosoma* + *Clytra*) + ((*Ditropidus* + *Lachnabothra*) + (*Lexiphanes* + (*Neochlamisus* + *Exema*).

5.6 Discussion

The camptosomatan pupae are of four main types. These are characterised by (i) *Lamprosoma*, with tapering body shape and lack of abdominal processes; (ii) the Chlamisini, with greatly reduced setae and processes on tergite VII; (iii) *Clytra*, parallel sided and lacking abdominal processes; and (iv) the Cryptocephalini, with ovoid, setose body and abdominal processes on tergites VI-VII. The pupa of *Edusella* (Eumolpinae) is very different from these and although it has lateral processes on segments VI and VII these appear to be thickened setae and therefore probably not homologous.

Pupal morphology provides an independent suite of characters for the study of camptosomatan phylogeny. However these characters are mostly weak because they may involve the loss or reduction of some feature (P1, 2, 4-8, 14), and/or because there may be strong correlation between them, as in setal distribution (P1, 4-8). Character P2 may be correlated with small antennal size in the adult. Furthermore the low number of characters severely limits the number of taxa that can be analysed.

Given the above limitations, some phylogenetic conclusions may be drawn. There are no pupal features which seriously challenge the possibility that Camptosoma and Eumolpinae have a mutual ancestor. *Lamprosoma* is consistently placed as the sister group to all remaining Camptosomata. The groups (*Neochlamisus* + *Exema* + *Chlamisus*) (ie. Chlamisini) and (*Lachnabothra* + *Aporocera*+ *Ditropidus*) are monophyletic. The relationships between the four terminal groups (*Clytra*), (Chlamisini), (*Lexiphanes*) and (*Lachnabothra* + *Aporocera*+ *Ditropidus*) are not well resolved. Monophyly of (*Lexiphanes*) + (*Lachnabothra* etc.) is likely but the pupa of *Lexiphanes* is insufficiently described. It is unfortunate that no pupae are described for the critical groups Synetinae, Pachybrachini, Stylosomina, Platycolaspina and Coenobiina.

The pupae described here show useful differences and similarities at both high and low taxon ranks. The contribution of pupal morphology to phylogeny will be discussed further in Chapter **8**.

Chapter 6 : Adults

6.1 Introduction

Adult Camptosomata have been the subject of specialist taxonomic studies since the early nineteenth century (for example, Klug 1824) and are sufficiently widespread and common in the northern hemisphere to have been included in most morphological surveys of Coleoptera by European and North American anatomists. Members of the Camptosomata have been included in studies of : head capsule (Stickney 1923), mouthparts (Monrós 1951a, 1953b; Sakai 1983), prothorax (Monrós 1951a, 1953b), metendosternite (Crowson 1938, 1944), wing venation (Jolivet 1957, 1959), tarsal setae (Mann and Crowson 1981), abdominal sclerites (Kasap and Crowson 1976), aedeagus (Sharp and Muir 1912; Burlini 1955; Iablokoff-Khnzorian 1966, 1985; Karren 1972; Moldenke 1981), male soft parts (Mann and Crowson 1983; Suzuki 1988), ovipositor (Tanner 1927; Erber 1968, 1969, 1988; Kasap and Crowson 1985) and female softparts (Suzuki 1988). The aedeagus has been commonly illustrated and widely used for discrimination of species, subgenera and even genera (Karren 1972), but the taxonomic female equivalent, the spermatheca, has rarely been illustrated (Berti and Rapilly 1973, 1979). There have been individual studies of the morphology of *Leasia australis* Jacoby (Monrós 1951b) and *Cryptocephalus sericeus* (L.) (de Monte 1948). The karyology of three tribes of Camptosomata and the Eumolpinae has been surveyed (Petitpierre, Segarra, Yadav and Virkki 1988). Comparative behaviour, especially sexual, has been discussed by Erber (1969, 1988) and Medvedev and Pavlov (1988).

No subfamily or tribe of Camptosomata has been comprehensively monographed worldwide since the mid nineteenth-century (Cryptocephalini : Suffrian 1852-66), but there have been many important regional faunistic surveys which have at least included aedeagal structure. For Lamprosomatinae, the world genera (Monrós 1956a) and the species of the significant south-east Asian fauna (Kimoto and Gressitt 1981) have been described. The southern South American Chlamisini were revised by Monrós (1951a), the North American fauna by Karren (1966, 1972), the Chinese by Gressitt and Kimoto (1961) and south-east Asian by Kimoto and Gressitt (1981). The New World genera of Clytrini were revised by Moldenke (1981). Faunal studies to species of Clytrini have included southern South America (Monrós 1953b), North America (Moldenke 1970), Central Europe (Mohr 1966), China (Gressitt and Kimoto 1961) and south-east Asia (Kimoto and Gressitt 1981). Moldenke (1981) suggested a phylogeny of Neotropical genera of Clytrini based primarily on aedeagal structure. Pachybrachini have been badly neglected with no major revisions this century. The European species of Pachybrachini have been described (Mohr 1966) and Lopatin (1979, 1982b, 1984a,b) has described several Asian and Arabian species. Cryptocephalini are also relatively badly neglected. The following regions have had some modern revision of at least part of the fauna : North America (Balsbaugh 1966; White 1968), Europe (Burlini 1955; Mohr 1966), Asia Minor (Berti and Rapilly 1973, 1979), Central Asia (Medvedev 1963), China (Gressitt and Kimoto 1961), south-east Asia (Kimoto and Gressitt 1981), New Guinea (Gressitt 1965) and Fiji (Bryant and Gressitt 1957).

The morphology of Eumolpinae is relatively poorly known. Many of the general studies listed above provide some information. There have been detailed (but inconclusive!) studies of the critical genera *Megascelis* (Monrós 1960a) and *Syneta* (Mann and Crowson 1981).

Adult biology of Camptosomata was reviewed by Erber (1988). Adults are generally short-lived. They feed on a wide variety of plants (Jolivet 1978, 1988), particularly on leaves but also flowers. The biology of Australian species is discussed in more detail in Chapter **10**.

This chapter discusses the gross morphology of both outgroup and ingroup, the characters used for phylogenetic analyses and the results of these analyses.

6.2 Material and methods

Excellent collections of Australian species were available, notably at ANIC, and these formed the basis of morphological studies. However I also actively collected live material for rearing, and this activity usefully supplemented the available collections.

Collecting relied almost entirely on hand-picking or beating with a bamboo framed foldable tray purchased from Watkins and Doncaster Ltd, UK. Beating for Camptosomata was an ideal collecting technique since almost all the species did not grip foliage tightly like Curculionidae, but generally relied on drop-off and thanatosis to avoid predation. Only one species, *Ditropidus* [*Elaphodes*] nr *pilula*, which has relatively large legs, preferred to grip twigs of the host plant. The main problem with beating was that in hot weather (28°C +), the beetles often only dropped a few centimetres before flying away. Beating was also less efficient than hand-picking when collecting small species burrowed deep into flowers of spicate acacias. Generally hand-picking was not favoured because the beetles were sensitive to breath and movement, and because I am red-green colour-blind. Live material was usually kept in small containers until mating and oviposition occurred.

Dried material was preferred for dissection because alcohol preserved specimens were both more brittle and more resistant to the action of KOH. Whole specimens, or abdomens of rare species, were soaked in cold 10% KOH for at least one hour, then dissected and cleaned in water. An hour was long enough for very old material. Dissection was required for microscopic examination in glycerol of the mouthparts, antennae, tarsal setae, mesoscutum, internal thoracic 'sclerites', abdominal segments, rectal morphology and male and female genitalia. The female rectum was carefully scraped clear of muscle, then cut above the chitinring and at the anus. A few specimens were dissected while fresh to confirm published descriptions of the male and female soft parts and to examine the alimentary canal. SEM was used to illustrate or confirm structures seen with light microscopy. Specimens were sonicated and air dried before gold-coating. Use of critical point drying would have prevented eye collapse, but eye collapse was not considered significant.

6.3 Morphology of adults

I was able to obtain and dissect adults of Synetinae (*Syneta*), Megascelidini (*Megascelis*), Eumolpinae, Lamprosomatinae, Chlamisini, Clytrini, Pachybrachini and most genera of Cryptocephalini, including all the Australian 'genera' (Appendix A). Adults of a species of *Achenops* (Achenopini) were available but were not used because the species did not match the available descriptions of *Achenops* (Suffrian 1857; Chapuis 1874).

Adults of the taxa studied show great diversity in body form. The Camptosomata consist of small to medium sized beetles (1-15 mm long), usually strongly sclerotised and cylindrical in form (Figs 303-330). However the two supposed 'ancestral' subfamilies (Mann and Crowson 1981), Synetinae (Fig. 300) and 'Megascelinae' (not figured), differ markedly in body form from the Camptosomata. In both, the head and prothorax are narrower than the elytra, and in *Syneta* the body is rather depressed. Adults of Eumolpinae are very diverse (Figs 301-302), with taxa resembling Camptosomata or *Syneta*.

The degree of compaction leading to loss of definition of head and prothorax has been a traditional delimiting factor for the Camptosomata (Gressitt and Kimoto 1961; Arnett 1965; Crowson 1967; Kasap and Crowson 1979). Features considered indicative of this compaction include overlap of the abdomen on the metathorax, almost hypognathous head capsule and connation of apical ventrites. However degree of compaction is graded and it is difficult to isolate characters.

6.3.1 External anatomy

The following descriptions serve as a general account to include all the taxa considered for analysis. More detailed descriptions of features are given in the list of adult characters (section 6.4).

6.3.1.1. Head

The head capsule (Figs 61-74, 331-350) is usually hypognathous and deeply inserted into the thorax (may even be completely retracted in dead specimens), rarely prognathous with a well developed neck. Eyes are generally well-developed and conspicuous, and may occupy most of the face in holoptic males. Usually the eyes are reniform, but development of a deep invagination on the internal margin (canthus) is variable. Short setae are present at the corners of the facets. The anterior surface of head has various weakly expressed characters which are not included in the cladistic analyses. These include : unpunctured swelling above and interior to antennae (more evident in Galerucinae); groove along midline of frons (external reflection of internal keel); visibility and shape of the weak fronto-clypeal suture; development of scrobe below antennae between eye and clypeus (very difficult to define). The gular region is poorly defined as the sutures are weak and abbreviated. The internal tentoria are weakly sclerotised, as in most chrysomelids (Stickney 1923), and were not used. The external manifestations of internal structure include a pair of pits on the gular sutures and median prolongation of the vertex into the cephalic foramen to form an internal keel.

The antennae (Figs 75-96, 300-330, 348-367) are always eleven segmented, usually with differentiated first and second segments (scape and pedicel), and with more densely sensillate apical segments. They are variable in size and shape and may even have a five-segmented club. The scape has a bulbous base which is inserted into the antennal cavity. The antennae are generally proportionately longer in the male. Relative size of the basal segments, as used by Saunders (1842-7) to distinguish genera, is probably determined by the point of flexure of the antenna for folding along the venter.

The mouthparts are typical of 'higher' chrysomelids, that is, no mandibular mola, simple setose and lobate lacinia, and membranous, reduced ligula. The dorsally setose labrum (Figs 99-100, 368-396) is conterminous with the ventrally sensillate and setose epipharynx. The epipharyngeal setae lie either at the extreme apex of the epipharynx (apical epipharyngeal) or internally in two separate inwardly directed patches (internal epipharyngeal). The shape of the labral tormae showed some variation with probable convergent loss of a short basal internally-directed arm. Presence or absence of this arm was difficult to determine and the evolutionary process appeared to involve convergent loss, therefore this feature was not utilised. The mandibles (Figs 397-425) are not exactly symmetrical (left generally overlaps right), but are usually very similar. In shape the basic form resembles a pyramid with the tip bent inwards. The apex is usually armed with two stout teeth. The membranous prostheca which arises from a hollow near the base of the cutting edge, commonly found in other chrysomelid groups (Sakai 1984), is absent from almost all the taxa considered here. The basal segments of the maxilla (Figs 426-447) comprise a small but thickly sclerotised cardo with basal lobes for muscle attachment, and a quadrate stipes. At the apex of the stipes lies the external palp, consisting of basal palpifer and three palp segments, and the internal two segmented galea and essentially membranous lacinia. The gula usually projects beyond the maxillary bases and at its apex carries the labium (Figs 448-457) consisting of basal transverse mentum, prementum and attached palps with basal palpiger and two palp segments. The prementum is of no significance in the taxa considered here. Sclerotisation of the labial apex is often partial and the boundaries of segments may be obscured.

6.3.1.2 Thorax

The shape of the prothorax (Figs 101-126, 458-499) is variable but not easy to delimit. At each corner of the pronotum there is a large trichobothrial seta and the margins may be bordered. The posterior portion of the hypomeron is generally mesally produced to reach the prosternal process, thereby forming externally closed coxal cavities. This part of the hypomeron may be deeply transversely concave to accommodate the fore legs. The prosternum varies greatly in size and shape. For example it may be produced, partially concealing the ventral mouthparts, or deeply slotted for retention of the antennae, or the process may be reduced to a narrow blade, barely separating the coxae. Frequently the prosternum and hypomeron have different surface sculpture, the former usually being more punctate and pubescent. The notosternal suture is distinct. Each coxa articulates with the walls of the coxal cavity and with the trochantin, which is visible as a small sclerite in the external anterior corner of the cavity. Internally the walls of the prosternum are produced as a pair of pro-endosternites (prothoracic furca of Snodgrass 1935; endopleura of Hlavac 1972), which are obovate and usually have a small basal lobe.

The mesothorax is reduced to a dorsal scutellum and foreshortened ventral sclerites. The mesoscutellum (Figs 127-143, 500-519) is usually externally conspicuous at the base of the elytra. Its anterior part, the concealed mesoscutum, may be transversely grooved to form a stridulatory file in combination with the posterior rim of the pronotum. The elytra (Figs 144-146, 300-330, 559-560) are variable in structure. Each has a well defined, and frequently basally lobed and sinuate, epipleuron, a prominent humerus, an abrupt basal edge abutting the pronotum, and a sutural flange and groove interlocking system which is usually complete from base to apex. The basic number of striae (if present) is 10, plus an abbreviated scutellary striole. Internally there are two patches of wing-folding spinules, one around the extreme apex, the other behind the humerus as present in many Polyphaga (Hammond1981). The characteristics of these patches were hard to quantify and differences seemed slight (Figs 145-146) so they were ignored as characters. The mesosternum (Figs 135-136, 520-526) is reduced and partly obscured by the prosternal process and hypomeron. It has a short process between the mesocoxal cavities, which are closed by the mes-epimeron, mes-episternum, and metasternum (laterally open), although contact between mes-episternum and cavity is slight. Internally there is a pair of thin, kinked and usually basally lobed mes-endosternites projecting from the mesosternum.

The metascutellum has various complex folds and grooves but appeared to be almost uniform in structure amongst the taxa studied and was not included in analyses. The postnotum (Figs 527-528) showed some variation in the development of its posterior margin. The metasternum (Figs 149-150, 520-524) was generally very large and convex, with well-developed flanking met-episterna. The met-epimera are partially membranous and fused to the met-episterna. Although rather variable they were not used for analysis because differences were hard to quantify. Internally, the main structure of the met-endosternite (Figs 529-546) arises from the posterior margin of the metasternum at the point of contact with the basal lobe of the abdomen and is supported by a longitudinal keel shown on the external surface by the median metasternal groove. Morphologically the met-endosternite varies from complex to simple, this variation reflecting both phylogeny and reduction in size. In the most complex forms included here there is a basal stalk, formed from the conjunction of three keels, and two lateral arms each with a lateral process (lamina) and one or two apical processes. A pair of anteriorly directed tendons arises at various distances from the midline and the part of the met-endosternite to which they are attached may be produced.

The wings (Figs 550-558) are almost always fully functional (one non-Australian exception is included in this study), and never brightly coloured as in some other Chrysomelidae. The anterior and apical portions show very little variation, in contrast to the anal region. The most complete wing venation included in this study is similar to that of 'primitive' chrysomelids and other Cucujiformia (Jolivet 1957, 1959; Crowson 1967). The wing venation includes : the three adjacent veins of the anterior margin, the costa (C), subcosta (Sc) and radius (R); the apical branch of the radius, the radial sector (Rs) which subtends the radius-media cross-vein (R-M) creating the triangular radial cell (Rc); the media (M) which appears as a short anterior spur of the well developed cubitus anterior (CuA); the four veins of the anal sector which include cross-veins and enclose two anal cells (outer 2AC and inner 1AC); and a jugal vein. The nomenclature for anal wing veins is subject to debate. Forbes (1926), followed by most contemporary authors (Crowson 1967; Wallace and Fox 1980), designated all veins in the anal region as anal veins. Ponomarenko (1973) has shown that the most anterior 'anal' vein is the cubitus posterior and his system is adopted here. In the plesiomorphic condition the cubitus posterior (CuP) is recurved to reach, but not touch, the CuA . This is followed by the four veins $1A_{1+2}$, $1A_3$+2A, 3A and 4A. Usually there is a well defined jugal lobe anterior to 4A. In some taxa a patch of wing-folding spicules, the subcubital fleck, is present behind the apex of CuA.

The legs (Figs 147-148, 300-330, 547-549) are frequently dissimilar in structure, especially due to modification of the fore or hind legs, and sexual dimorphism is common. The fore coxa and fore and hind femur show varying degrees of enlargement. The junction of trochanter and femur is strongly oblique. The internal and external surfaces of the femur and tibia are often keeled, and this keel may be accompanied by a groove. In a few taxa one or two articulated spurs are present at the apex of the tibia, but these may be obscured by an apical fringe of setae. The tarsi are five-segmented, but functionally only four-segmented, as segment four is generally minute and deeply embedded between the two lobes of segment three. Segment one is commonly enlarged in males. The two claws are always symmetrical and vary from simple to deeply bifid. The angle between the claws may be of some phylogenetic value but was not used in the present study as it seemed to vary according to treatment of the specimen. The ventral tarsal setae are modified for climbing and copulation and differing distributions of modified setae have been used to categorize major divisions of the Chrysomeloidea (Stork 1980; Mann and Crowson 1981). All taxa considered here have normal adhesive setae (*sensu* Stork) on segment 3 only (Fig. 147), except Lamprosomatinae which have adhesive setae on segments 1-3 (Mann and Crowson 1981).

6.3.1.3 Abdomen

The abdominal exoskeleton (Figs 149-153, 300-330, 561-576) has seven visible tergites (tergites I-VII) and five visible sternites (sternites III-VII) although there may be connation of tergites I and II and of sternites V-VII. Laterotergites and parasternites are commonly present, and the seven pairs of spiracles may be free, or fused if incorporated into the tergites. The tergites are frequently heavily sclerotised, and a pygidium may be well developed and completely exposed by the elytra. The sides of the sternites may be differentiated by a keel and dense microsculpture and by their almost vertical displacement. These areas are here called laterosternites and are especially well-developed on sternite III where the laterosternite usually extends anteriorly to partially overlap the met-epimeron. Sternite III has a variably developed inter-coxal lobe. Sternite VII may be hollowed in either sex (usually the female) and rarely has a crenulate apical edge which interlocks with the elytra. In the male the sternites may be armed with various processess and tufts of setae and the whole abdomen considerably reduced in size. In contrast the female abdomen is simple but usually has an apical hollow (sternite VII) and often has greatly expanded sternites.

The remaining segments of the abdomen are internal and form part of the copulatory or egg-laying apparatus. Males (Figs 153-160, 577-700) have a simpler system than females as only one function is being served, and show typical 'higher' chrysomelid structure *viz*. small tergite VIII hooded by pygidium, base of aedeagus fused dorsally, internal sac not partially external, Y-shaped ventral tegmen, Y-shaped spiculum gastrale, sternite VIII reduced to membrane or absent. The aedeagus is always symmetrical and includes an internal sac. In the Camptosomata there a special sclerite for passage of the flagellum, the ejaculatory (=copulatory) guide. The ejaculatory guide should be dissected from the aedeagus for examination but is visible in cleared aedeagi and has therefore been partially and incidentally figured in studies of Camptosomata using the aedeagus (Monrós 1953b; White 1968). This feature was first specifically used by Karren (1966, 1972) to discriminate taxa of Chlamisini, especially genera. The thickly sclerotised exserted flagellum of some other chrysomelids is absent. The aedeagus shows great diversity in shape and surface structure.

In the female the genitalic sclerites (Figs 701-740) are more complex as they perform both copulatory and egg-laying rôles. Considerable reduction of segments and appendages occurs within this group of taxa, therefore the most complete system is described here. Tergite VIII is similar to tergite VII but is covered by that segment and lacks spiracles. The anus lies between tergite IX and sternite IX. Tergite IX is represented by a divided proctiger medially, and a pair of lateral paraprocts. In the Camptosomata there is a lateral narrow sclerotised strap around the base of each paraproct, connecting it to the base of each proctiger, which may be a remnant of the baculus of elongate ovipositors. Sternite IX (possibly including sternite X) is modified as a vaginal palp, comprising valvifer (*sensu* Crowson 1981), coxite and stylus from base to apex. In all taxa considered here the valvifer and coxite are fused (coxite *sensu* Lawrence and Britton, in press). Reference to free articulation of these 'segments' in *Spilopyra* by Kasap and Crowson (1985) is certainly erroneous. The vaginal palpi enclose the vulva which nominally lies between sternites VIII and IX. Sternite VIII is quadrate and has an internal narrow sclerotised projection (spiculum). Modifications of this system include fusion of the vaginal palp segments, reduction of sternite VIII, and elongation to form a telescopic ovipositor.

6.3.2 Soft part anatomy

This aspect of morphology has been considered useful in chrysomelid phylogeny (Kasap and Crowson 1976; Mann and Crowson 1981) and has been more widely used (in desperation?) in Curculionidae (Aslam 1961; Morimoto 1962; Kasap and Crowson 1977; Calder 1989), but I chose to make only partial use of it in this study. Initial studies of the proventriculus, midgut and the soft parts of the male and female reproductive systems revealed little variation in the major part of these character systems.

Furthermore there was a lack of fresh material of many taxa. However there were already known to be important differences in the female hindgut of different Camptosomata (Erber 1968) and this part of the anatomy was studied in detail here. In addition, some aspects of the male and female reproductive systems were used for analysis. Other anatomical observations were made on select species.

Briefly, the gut (Figs 852-854) shows the following morphology. The foregut has a simple tube, the oesophagus, which joins the midgut through the proventriculus approximately at the junction of the head and thorax. The proventriculus is internally lined with irregular rows of posteriorly directed weakly sclerotised spines which are occasionally multifid, but the complex structures observed in Curculionidae (Kissinger 1963a) are absent. The midgut is very large and clearly differentiated into a large smooth- and thin-walled anterior sac which passes through the thorax and fills almost half of the abdominal cavity, and a narrower coiled tubular part. The anterior sac may have a ring of caeca at its anterior end, and the posterior coil may have regenerative crypts over much of its posterior half. There are six equal-sized cryptonephridic Malpighian tubules, which are approximately attached at the pyloric valve and therefore mark the beginning of the hindgut. Between this point of origin and the cryptonephridic re-entry of the tubules further down the gut, the hindgut (ileum) is tightly coiled. The Malpighian tubules combine into two tubules before re-entry as illustrated for Cerambycidae (Crowson 1981 : Fig. 81). The beginning of the rectum is indicated by a chitinous ring or chitinring (Erber 1968). The rectum is simple in males but may be very complex in females, developing a complex pattern of 'sclerites' and an internal armature of dentate sensilla. The nomenclature of this system is discussed separately below.

The structure of the nervous system has not been investigated in the taxa included here.

The soft parts of the male genitalia (Figs 855-856) are relatively simple but two nomenclatures are available (Mann and Crowson 1982; Suzuki 1988). Suzuki's treatment is in general agreement with Snodgrass' (1935) review of the Insecta and is followed here. In Cryptocephalinae, each of the two separated globular testes is surrounded at its origin by a single thick coil of assessory gland which therefore conceals the vas deferens. Short lateral ejaculatory duct arms lead to the common ejaculatory duct, the distal part of which is usually differentiated into a thick-walled muscular pump and may include a valve. The apex of the ejaculatory duct enters the internal sac of the aedeagus. In Lamprosomatinae and Eumolpinae the assessory gland is free and often of considerable length, the testes may be paired and the vasa deferentia may be exposed.

The soft parts of the female genitalia (Figs 701, 703, 741-805) are also comparatively simple (Suzuki 1988). A pair of ovaries consisting of many ovarioles is connected by short lateral oviducts to the common oviduct or vagina. The vagina usually has a small distal swelling, the bursa copulatrix, to which the spermatheca is attached. Internal sclerotisation of the bursa copulatrix is systematically important in some Chrysomelidae (Silfverberg 1976) but was present in only one of the species considered here. Large colleterial or vaginal glands, opening dorsal to the vaginal palp, are present in the Eumolpinae. The spermathecal duct and capsule (the latter generally named the spermatheca) are sclerotised and are well known to show features of taxonomic importance in Chrysomelidae at species and genus levels, for example in Alticini (Samuelson 1973). The spermatheca (Figs 741-805) consists of an apical retinaculum, usually sickle- or hook-shaped,and a basal pump mechanism connecting the unsclerotised spermathecal gland. Generally the shape of the spermatheca is very conservative but there are two important exceptions. In several unrelated species the spermatheca is peculiarly modified (in different ways) and therefore an autapomorphic feature. In one group of species, Coenobiina, the spermatheca is reduced to what appears to be a globular pump mechanism only, with a massive but short spermathecal duct (Figs 704-706).

The morphology of the female rectum (Figs 815-851) is diverse. The normal (simple) rectum is an undifferentiated tube which is delimited internally by a chitinring (Erber 1968) and may have circular sensilla scattered on the internal wall, as found in the males of all taxa. In females of Camptosomata there appears to have been progressive development of thickened ridges and plates (rectal sclerites) together with modification of the shape and distribution of the sensilla. The ridges, plates and sensilla combine to produce flattened scales of excrement which are used in construction of the scatoshell. These modifications of the rectum have been studied by de Monte (1957) and Erber (1968) in a few taxa and a sclerite nomenclature is therefore available. Erber's nomenclature is retained here for a few of the specialised structures as the German compound nouns serve their purpose well. Thus the whole unit of specialised rectal morphology is termed the kotpresse. The detailed nomenclature is based on the recognition of a primary division into dorsal and ventral surfaces and subsequent division of these surfaces into anterior and posterior regions depending on the development of transverse sclerotisation. The transverse sclerotisation may be on the internal wall of the rectum (chitinpolster) or on the external wall (transverse sclerites). At its minimum the kotpresse, as understood here, is at least represented by the development of chitinpolsters, but it may also have four pairs of lateral sclerites (dorsal and ventral, anterior and posterior), dorsal and ventral transverse sclerites, with or without apodemes, and sensilla present or absent in each of the four major areas. Furthermore, the transverse sclerites may be secondarily divided either transversely or longitudinally.

6.4 Adult characters used in analysis

This section gives the characters, and determination of polarity, for the whole adult data set with Eumolpinae as outgroup. The overall total of traditional chrysomelid characters, characters used in classification of Camptosomatan groups, 'obvious' morphological attributes and characters from detailed studies of certain anatomical features, produced a list of 228 characters.

Originally a set of 206 characters was used but this was unsatisfactory in two major ways. First, this initial matrix did not allow a monophyletic ingroup because characters or states unique to the outgroup were not included. This especially affected the position of the most basal Camptosomata, the Lamprosomatinae. Second, careful examination of some supposedly complex multistate characters showed that they were in reality multi-character features. These were accordingly disentangled to become more easily defendable characters.

Several taxa were sexually dimorphic for various characters, for example development of canthus, antennal length, surface tuberculation. These taxa are noted in the proceeding character descriptions. In all cases the female was morphologically more conservative and the female state was chosen for the matrix. Choice of the female was also appropriate because for most taxa represented by a single sex the sex was female and because the female sex provided more characters. This analysis is therefore female biased.

In the following discussion of characters and state polarities the term 'primitive outgroup taxa' refers to the combination of *Macrolema* and *Spilopyra*, which from many aspects forms a basal monophyletic unit within the Eumolpinae. In cases of mixed outgroup states, states shared by these two genera were assumed to be plesiomorphic, a procedure recommended by Maddison *et al.* (1984). Consideration of polarity (plesiomorphy or apomorphy) is for the whole of the ingroup based upon occurrence in the outgroup unless the outgroup is inappropriate (for example, characters of the female rectum). Obviously, what is apomorphic for a clade may be plesiomorphic within that clade.

The term 'Holarctic Cryptocephalina' refers to the following taxa : *Diachus*, *Lexiphanes*, *Stegnocephala*, *Cryptocephalus* (including *Bassareus*) and *Melixanthus*. 'Australian Cryptocephalina' refers to *Melatia*, *Cadmus* s. lat. and *Aporocera* s. lat.

6.4.1 Head capsule, A1-13, 220, 225-6

(A1) : shape of internal margin of eyes. The degree of development of a canthus has been widely used as a generic or tribal feature in the Chrysomelidae, including

Camptosomata. In general the excision was clearly either less than 90° (1; Figs 71-72) or not (0; Fig. 73-74), but it was indeterminate in *Megascelis* (Fig. 332), *Megalostomis*, *Ditropidus* [*Elaphodes*] *pilula* and *Ditropidella* sp. 5, and sexually dimorphic in *Labidostomis* (Fig. 340) and *Ditropidus* sp. 865 (female = plesiomorphic state). With the exception of *Megascelis* noted above the outgroup had consistently shallowly excavate eyes, and this was scored as the plesiomorphic state. State (1) was found in all Chlamisini, Coenobiina and Australian Cryptocephalina, and state (0) in *Syneta*, all Pachybrachini, *Stylosomus* and Platycolaspina. Otherwise distribution of the states was scattered.

(A2) : slope of posterior margin of eyes from above. In the plesiomorphic state, shown by all outgroup members, the eye bulges from the vertex as a simple dome (0; Figs 66-70, 334). In these species the head is exserted and even slightly prognathous. Species with the head inserted into the hood of the pronotum show either an abrupt truncation of the posterior curvature of the eye (1; not figured), or complete flattening of this part of the eye (2; Fig. 74). The latter state is characterised in museum specimens by complete retraction of the head into the prothorax (Fig. 64). State (0) was present only in *Syneta*, some Clytrini, *Ambrotodes*, *Stylosomus* and Platycolaspina; state (1) in all Australian Cryptocephalina; state (2) in all Holarctic Cryptocephalina and Coenobiina. In other groups states (1) and (2) were mixed.

(A220) : convexity of the eye in anterior view. Eye convexity is a traditional loosely defined generic character in Chrysomelidae. Considerable variation was present in the degree of convexity present both in terms of curvature and asymmetry. All outgroup members had eyes which protruded at a distinct angle from the vertex (0; Fig. 331); flat eyes were considered apomorphic (1; Fig. 335). State (1) was characteristic of Lamprosomatinae, Chlamisini, Coenobiina and most Ditropidina and Holarctic Cryptocephalina; it was also found in some Clytrini and Pachybrachini.

(A3) : ratio of length of eyes to distance between them. The maximum straight eye dimension possible was taken to be eye length. Small eye size has not been considered important in the classification of Cryptocephalinae, in contrast to other chrysomelid groups, and was difficult to categorize. Proximity of the eyes has been considered important. I concentrated on isolating those taxa with close or proximal eyes (as used for example by Suffrian (1857) to define *Coenobius*). The selected ratios were relatively easily determined. All outgroup members had eye length < 1.75 distance between eyes (0; Fig. 331); two further states being length 2-2.5 distance (1; Fig. 344), and >3 (2; Figs 335, 339). In *Acolastus* and *Ditropidella* this ratio was sexually dimorphic (eyes more distant in female). Distribution of states : (1) in *Lexiphanes*, *Ditropidella* and some Australian Cryptocephalina; (2) all Coenobiina and *Stegnocephala*.

(A4) : position of antennal base relative to lower margin of eye. In anterior view the antennae were usually either inserted at the lower margin of the eye (0; Fig. 333), or at least a third of eye length from the lower margin (1; Fig. 335). Scoring of this character was difficult for several taxa (unresolved in 9) and the outgroup held both states, therefore no polarity was attached to the character states. State (0) was present only in *Syneta*, Lamprosomatinae, Clytrini, Pachybrachini, *Leasia australis* and two Ditropidina. These taxa all have relatively small eyes.

(A5) : surface sculpture of upper frons. Either unreticulate (0; Figs 69-70) or densely microreticulate (1; Figs 61, 67). Outgroup polarity was equivocal but the primitive taxa had an unreticulate frons and this was considered plesiomorphic. Three taxa showed intermediate sculpture : *Oomorphus*, *Ditropidus* [*Euditropidus*] *variabilis*, and *Aporocera* [*Schizosternus*] *albogularis*. This character is usually only used for separation of species. As expected there was no clear distribution pattern, except that all Pachybrachini scored (0).

(A225) : structure of frons. In profile the frons is judged to be either roughly straight (0, all outgroup except *Spilopyra*; Figs 332, 336, 343, 346), or bulging outwards between and below antennae (1; Fig.). State (1) was confined to *Spilopyra* and *Ditropidella*.

(A226) : structure of frons. The frons in all the outgroup and most of the ingroup is structurally very simple with none of the prominent swellings and grooves of other chrysomelid subfamilies (0; Fig. 331), but in a few taxa there was a groove between the antennal sockets (1; Figs 64, 335). State (1) was found in all Coenobiina and one *Ditropidella.*

(A6) : punctation of vertex immediately behind eyes. Punctation was simple in all outgroup taxa (0; Fig. 61) and the apomorphic state was the development of irregularly rugose puncture-striae curving behind the eyes (1; Fig. 72). Two taxa were indeterminate for this feature : *D.* [*Elaphodes*] *aeneolus* and *A.* [*Mitocera*] *viridipennis.* State (1) had a scattered distribution, being prevalent only in Australian Cryptocephalina.

(A7) : development of an occipital carina. The occipital carina has been used in some beetle families to discriminate genera or subgenera. The various development of a carina was treated as a progression from complete and circular (0; Figs 61-62, 73) to complete but angled forwards in the middle (1; Fig. 343), to partial, behind eyes (2; Fig. 346), to absent (3; Figs 63, 71). States (0) and (3) were both present in the outgroup but the primitive taxa were without a carina so the plesiomorphic state was considered to be (3). Presence of carinae was widely scattered amongst the taxa, although all Coenobiina had a carina and all Australian Cryptocephalina were without.

(A8) : projection of mentum into buccal cavity. Identification of the three states proposed for this character (absent, short, prominent and recurved (Fig. 334)) required a degree of accuracy not present with the lightmicroscope and they were barely separable. Many states were plausibly misidentified and others left unknown so this character was abandoned and omitted in all analyses.

(A9) : development of posterior flange on vertex. Seen from above the flange was usually trapezoid to equilaterally triangular and continuing as a keel into the head capsule, and this state (1; Fig. 334) was considered plesiomorphic. The two other extreme states lay on either side of this middle range, that is with a narrow extended and acutely pointed flange which may be raised (0), or with this short and very transverse with no trace of an internal keel (2). 14 taxa were not scored because of difficulty in assigning a state. All three states were scattered throughout the set of taxa, suggesting little phylogenetic usefulness.

(A10) : shape of the tentorial cicatrices adjacent to the occipital foramen. In the outgroup these were somewhat triangular in shape and often small (0; not figured), whereas all other taxa, except *Syneta*, had oval cicatrices (1; Fig. 334). The shape of the cicatrices in *Megascelis* was intermediate.

(A11) : length of tentorial connection to gula. The two states, half length of gula (0; Fig. 334) or almost whole length (1; Fig.), represent extremes. In most taxa the states were easily identified but at least 11 were indeterminate and because of variable visibility of this feature some others were probably wrongly scored. In view of this I decided to ignore this character in analyses.

(A12) : shape of apex of fronto-clypeus. In all outgroup taxa this was simple (0). In *Scaphodius striaticollis* the margin was toothed (1; not figured). This character state was therefore autapomorphic and not useful for analysis.

(A13) : shape of tentorium-gula juncture. As the two character states, parallel (0; Fig.) or convergent (1; Fig. 334), proved to grade into each other, and as this character was difficult to see it was abandoned and ignored in all analyses.

6.4.2 Antenna, A14-22

Many of the antennal characters seem trivial. Nevertheless, these are based on various traditional formulations for the discrimination of genera in Camptosomata. The antennae have been very important in this respect.

(A14) : width of antennomere 2 relative to 1 and 3. All but one (*Macrolema*) of the outgroup had antennomeres 2 and 3 approximately equally wide, narrower than 1 and this was taken to be the plesiomorphic state (1; Fig. 363). The two other states were assumed to be extremes on either side of this : 1=2=3 (0; Fig. 360) and 1=2, or at least 2 much wider than 3 (2; Fig. 364). However all three states seem inter-derivable and therefore should be unordered. Better still this character should have been treated as two : antennomere 2 versus 1, and antennomere 2 versus 3. Some difficulty was experienced separating states (1) and (2) of the character as it stood. Seven taxa had indeterminate states. The states were scattered but state (2) predominated.

(A15) : length of antennomere 2 relative to 3. In almost all taxa the states were well defined : 2 clearly shorter than 3 (0; Fig. 351), or 2=3 (1; Fig. 352), or 2 clearly longer than 3 (2; Fig. 354). The outgroup (except *Pachnephorus*) showed state (0). One taxon *(Aprionota* [*Loxopleurus*] *ruficollis*) was not scored. States were scattered in the taxa set.

(A16) : length of antennomere 4 relative to 3 and 5. For some reason best known to himself Saunders (1842-5) made great use of this character for the discrimination of genera. For scoring purposes it proved impossible to separate a state with 3=4=5 from 3=4<5, 3<4=5, or 3<4<5. These were amalgamated as state (0; Figs 354-356) with two further states for the easily distinguished extremes of relative length of antennomere 4, less than each of 3 and 5 (1; not figured) or greater than 3 and 5 (2; not figured). Most outgroup taxa scored state (0), except *Edusella* and *Megascelis*. One taxon (*Leasia* [*Agetinella*] sp.2) was not scored. Distribution of states : (1) many Australian Cryptocephalina; (2) three Pachybrachini.

(A17 and 18) : development of antennal sexual dimorphism. A17 scored absence (0) or presence (1) of antennal sexual dimorphism and A18 the nature of this dimorphism: greatly increased length (0; Fig. 362), difference in number of expanded segments (1; Figs 357, 864), or both states together (2). The outgroup antennae were simple. Simply scoring any sexual dimorphism as the same apomorphic state (Character A17) would seem to be fallacious, but if not used in analysis it at least serves as a useful marker for those taxa. Distribution of states of A18 : (0) nine species of Australian Cryptocephalina; (1) *Chlamisus aterrimus*, *Acolastus* and *Aporocera* [*Cryptocephalus*] *bihamatus*; (2) was autapomorphic for each of *Ditropidus* nr *antennarius* and *Lachnabothra braccata*.

(A19) : asymmetric expansion of antennomeres. Three states in apparent progression from apically asymmetric (0; Fig. 319), to medially asymmetric (1; Fig. 321), to parallel antennomeres (2; Fig. 324), but there is only a subtle division between the extremes, and this character was unordered in analyses. This was sexually dimorphic in *L. braccata* and *A. bihamatus* (female asymmetric). The outgroup taxa had asymmetric antennomeres (0), except *Edusella* and *Megascelis* (2). State (1), expansion of middle segments only, was confined to *Aporocera* [*Chariderma*] *pulchella* and the female of *A. bihamatus*. State (2) was shown by *Lamprosoma* and nine Australian Cryptocephalina.

(A20) : modification of apices of antennomeres to hold peg-like sensilla. Here treated as a progression from unmodified and without clustered sensilla (0; Fig. 94), to development of an apical sensillar patch (1; Fig. 96), to sensillar patch in a circular depression with a well developed rim (2; Fig. 86). In practice there was some difficulty in distinguishing the first two states. The outgroup included states (1) and (2) but the primitive members had state (1) so this was considered plesiomorphic. Presence of the sensillary patch was used to distinguish the sensory segments of Character A21. I was unable to determine the state in *Aporocera* [*Loxopleurus*] *pauperculus*. State (2) was present in all Chlamisini, five out of seven Clytrini, five out of six Pachybrachini, *Stylosomus*, Ditropidina and Holarctic Cryptocephalina except *Diachus*. The remaining taxa showed either (0), including all Coenobiina, or (1), most species.

(A21) : distribution of sensory antennomeres. These were defined as those with states 1 or 2 of character 20, or if this was not appropriate, those with clearly greater density of peg-like sensilla and setae. The sensory antennomeres are usually easily distinguished because they are more expanded. The sensory segments are always apical (although the last segment in *Stylosomus* and some Holarctic Cryptocephalina lacks a sensory area) and may be 5 to 8 in number, thus the following states defined by sensory segment number : 4-11 (0; Figs 79, 355-356); 5-11 (1; Fig. 303); 6-10 or 11 (2; Figs 85, 365-367); 7-11 (3; Figs 87, 364). This has traditionally been a very important generic character in Camptosomata, for example in Chlamisinae and Cryptocephalinae.

However it showed sexual dimorphism in *Acolastus*, *Ditropidus* nr *antennarius*, and *Aporocera* [*Cyphodera*] *chlamydiformis* (in each case male with one more sensory segment). Sensory development started from antennomeres 6 or 7 in the outgroup but no state was considered plesiomorphic for the Camposomata. Distribution of states : (0) *Chlamisus mimosae* and four Clytrini; (1) three Clytrini, and *Stegnocephala*; (2) all Pachybrachini, four Platycolaspina, all Coenobiina, *Lexiphanes*, four Ditropidina, all remaining Cryptocephalina except *Diachus*; (3) *Syneta*, Lamprosomatinae, *C. aterrimus*, four Platycolaspina, *Diachus*, all remaining Ditropidina.

(A22) : length of antennae. this was recognised as a graded set of three states to allow scoring of the extremes 'very long', more than 3 times head width or 2/3 body length (0; Fig. 316) and 'very short', less than or equal to 1.5 times head width (2; Fig. 304), as against 'average' (1; Fig. 300). These states are tradionally important but show sexual dimorphism in this sample and thus are very closely linked to characters A17 and 18. In such cases (*Acolastus*, *D.* nr *antennarius* and *L. braccata*) the female antennae were shorter (plesiomorphic) and this sex was used for scoring. Most taxa were easily categorised and most of the outgroup (except *Pachnephorus* and *Edusella*) showed the intermediate state which was taken to be plesiomorphic. All taxa were scored. Distribution of states : (0) *Cryptocephalus* [*Bassareus*] and 14 Australian Cryptocephalina; (2) Lamprosomatinae, Chlamisini, Clytrini, two Pachybrachini, *Stylosomus*, *Leasia*, four Coenobiina, *Lexiphanes*, *Stegnocephala*, all Ditripidina, *Melixanthus*, four Australian Cryptocephalina; (1) all others.

6.4.3 Mouthparts, A23-48, 56, 207-210

(A23) : shape of labrum. The distinction between quadrate (or elongate) (0; Fig. 370) and transverse (1; Fig. 371) was rather fine and polarity was not resolved by comparison with the outgroup. In a few taxa with produced mandibles labral shape was sexually dimorphic (elongate in male). Eight taxa were not scored. State (1) was scattered throughout the taxon set.

(A24) : number of pairs of labral setae was arbitrarily divided as 2-3 (0; Fig. 371); 4-5 (1; Fig. 373); 6+ (2; Fig. 372). This was a difficult character to score because of frequent asymmetry, missing setae and confusion with apical epipharyngeal setae. The selected size classes were intended to reveal overall trends towards more or less setae. The outgroup held all three states, and as distinctions between the states were small this character was left unordered. Although the states were scattered there was also some pattern; for example all Clytrini showed (2).

(A25) : number of apical epipharyngeal setae. Most taxa seemed to have obviously more (0; Fig. 374) or less than 10 (1; Fig. 373) so this was made the threshold value. The outgroup members had more than 10 setae. This character must be correlated with size to some extent. *Scaphodius* and *Ditropidus* [*Polyachus*] *geminus* were not scored. State (1) was present in Lamprosomatinae, Chlamisini, *Stylosomus*, five Platycolaspina, Coenobiina, most Ditropidina, most Holarctic Cryptocephalina, *Aporocera* [*Loxopleurus*] sp. 1049. In small species there was probably confusion with dorsal setae and internal epipharyngeal setae.

(A26) : number of internal epipharyngeal setae. In this case most taxa had either more (0; Fig. 375) or less (1; Fig. 374) than 20 internal setae, and in a few these were absent (2; Fig. 383). The outgroup showed all three states so none was chosen to be plesiomorphic. *Griburius*, *D. geminus* and *D. variabilis* were not scored. Distribution of states was similar to A25 but more scattered and state (2) was confined to *Leasia minuta* and *Ditropidus comans*.

(A27) : length of labral tormae compared with labrum, equal to or less than length of labrum (0; Fig. 370), or longer (1; Fig. 371). This was a simple character but the states were not always easy to determine because the base of the labrum was often membranous. The outgroup showed short tormae. *Stegnocephala* and *D. comans* were not scored. State (1) was widely distributed in the data set but absent from all Australian Cryptocephalina.

(A28) : shape of labral apex. Both primitive members of the outgroup had round or straight labral apices and this was taken to be plesiomorphic (0; Fig. 370). The apomorphic state included varying degrees of concavity (1; Figs 374-375, 381), which I was unable to discriminate, leading to the deeply dissected labrum of *Atenesus* (Fig. 381). *Ditropidus* [*Elaphodes*] *cervinus* was not scored. There was no obvious pattern to distribution of the states except that all Platycolaspina and Cryptocephalina scored (1).

(A29) : setosity of external face of mandible. Several setae were present in most taxa (0; Fig. 397), including the outgroup, but in a few cases only 1 or 2 conspicuous setae were present (1; Figs 401, 407, 418) or setae were apparently absent (2; Figs 413-416). This was treated as a simple character state sequence but is probably partially correlated with size. *A. pauperculus* was not scored. Distribution of states : (1) *C. aterrimus*, *Diachus*, four Ditropidina; (2) all Coenobiina, *Scaphodius* and *Aporocera* [*Idiocephala*] *consors*.

(A30) : degree of development of apical mandibular teeth. In almost all taxa each mandible was crowned by two strong triangular teeth (0; Fig. 397) but in four completely unrelated taxa, *Megascelis*, *Lychnophaes*, *Acolastus* and *Ditropidella* sp. 729, the apical margin was almost straight and the whole mandible shaped like a shovel (1; Figs 398, 405).

(A31) : development of a tooth on internal surface of mandible. An angular spur or tooth was either present (1; Figs 402, 403, 425) or absent (0; Fig. 392) halfway between the apex and base of the inner surface of both mandibles. In all outgroup members the tooth was absent from both mandibles but in *Aporocera analis* the right mandible had an internal tooth (Fig. 425). State (1) was an autapomorphy for Clytrini.

(A32) : presence of prostheca. Sakai (1983) has shown the presence of a prostheca to be widespread in Chrysomelidae. In view of its similarity in all groups I regard it to be a plesiomorphic feature which has been convergently lost. Within the outgroup a prostheca was present (0; Fig. 397) in only *Macrolema* and in the ingroup only *Syneta* showed a small remnant (Fig. 399).

(A33) : shape of outer margin of mandible. When viewed anteriorly (from above) the mandibles of most species were distinctly angulate in outline (0, all outgroup; Fig. 397) but the mandibles of a few taxa were evenly curved (1; Fig. 414) to almost straight (2; Fig. 405). As there was no clear relationship between the states the character was unordered. In practice I often found this character difficult to assess, especially as the shape varied with the angle of viewing. This character was sexually dimorphic in *Leasia australis* (Figs 408-409) and *Scaphodius* in which the female showed the plesiomorphic state. Four taxa were not scored. State (2) was autapomorphic for *Acolastus* and (1) was confined to *Megascelis*, *Syneta*, *Lychnophaes*, *Aetheomorpha*, *Atenesus*, *Aprionota* [*Pycnophthalma*] *tutuilana*, *D*. sp. 865 and *Ditropidella*.

(A34) : comparison of male and female mandibles. The plesiomorphic state (all outgroup) was for the two sexes to have similar mandibles (0), in contrast to taxa with greatly enlarged or otherwise modified ♂ mandibles (1; Figs 340, 341, 349, 408-409). Modification of the male mandibles was known to be widespread in the Camptosomata and is one of the secondary sexual characters used to characterise genera in Clytrini and Chlamisini, so this character was included to assess its systematic significance, if any. Modified male mandibles were found in two Clytrini, *Leasia australis* and *Scaphodius*.

(A35) : symmetry of male mandibles. This character was difficult to assess as the mandibles were always slightly asymmetric. Ultimately only those taxa with very differently structured mandibles (Fig. 342) were scored as apomorphic (only two, *Megalostomis* and *Stegnocephala*).

(A36) : shape of basal margin of mentum. Either the mentum was rectangular (0, all of outgroup; Fig. 448) or crescentic with loss of the basal angles (1; Fig. 453). State (1) was autapomorphic for Coenobiina.

(A207) : structure of mentum. Either divided (1; Fig. 451) or whole (0; Fig. 449), but this was not always easy to score because the mentum was occasionally damaged in dissection, or the mentum was complete but very narrow in the middle, or divided but the two halves separated by only a narrow strip of integument. All outgroup taxa had complete menta, except *Chrysochus* which was indeterminate. In *Scaphodius* this feature was sexually dimorphic (female divided, male complete). State (1) was scattered, being present in *Syneta*, *Lamprosoma*, *Lychnophaes*, five Pachybrachini, *Arnomus*, 13 Ditropidina and all Australasian Cryptocephalina except *Melatia glochidionis* and *A. pauperculus*.

(A37) : relative lengths of segments 1 and 2 of labial palpi. This character is the variation in relative size of segment 2, from longer than 1 (2; Fig. 452) to shorter (0; Fig. 457). Approximately equal segments (1; Fig. 449) were taken to be the plesiomorphic state (almost all outgroup), with the other proportions of segment 1 on either side of this. *Lexiphanes* and *D. variabilis* were not scored. States (0) and (1) were scattered throughout the data set but (2) was confined to *Megalostomis*, *Aporocera* [*Cadmus*] *aurantiacus* and *Cadmus* (*Brachycaulus*) *mammillatus*.

(A38) : shape of palpiger of labial palpi. Determining the size of this segment was difficult because one side was frequently partially membranous. Length and width equal (0; Fig. 448) was considered plesiomorphic (most of outgroup, not *Spilopyra*), in contrast to transverse (1; Fig. 450). *Chrysochus* and *Lychnophaes* were not scored. State (0) occurred in only a few unrelated taxa.

(A39) : relative width of segments 1 and 2 of labial palpi. This character is similar to character A37 and, as in that character, the median state was considered plesiomorphic (all outgroup except *Edusella*). The state could not be determined for 9 taxa. State (0; not figured) was confined to *Edusella* and (2; Fig. 454) was found in a few taxa throughout the matrix.

(A40) : relative widths of maxillary palp segments 1-3. Characters A40-42 are sexually dimorphic in at least some Eumolpinae, but not in any of the outgroup or ingroup taxa used here. Although several relative widths were possible I thought it was useful only to distinguish those taxa with a relatively expanded segment 3 (0; Fig. 433). The outgroup showed both states although state (1; Fig. 430) (segments equal or 1 widest) was almost universal in the matrix and this was the probable plesiomorphic state. State (0) was present in *Lamprosoma* and was also autapomorphic for *Semelvillea*.

(**A41**) : relative lengths of maxillary palp segments 2 and 3. The two states were 3 greater than 2 (0; Fig. 428), or less than or equal to 2 (1; Fig. 430). This character had no clear outgroup state and also was difficult to score for several taxa. The state was not determined for six taxa. State (1) was scattered, predominating in Australian Cryptocephalina.

(**A42**) : shape of maxillary palp segment 3. This segment was almost always cylindrical or conical (0; Figs 427, 428), but clavate (1; Figs 426, 433, 435) in *Semelvillea, Platycolaspis* and one member of the outgroup (*Macrolema*). A42 (1) is evidently a subset of A40 (0).

(**A43**) : number and distribution of digitiform sensilla on maxillary palp segment 3. In general the sensilla were either arranged as 5+ in a single even row near the base (0, usually six or more, rarely only five; Figs 26, 427, 429, 438, 441) or 2-5 either in an irregular row or scattered towards the apex (1, from five to two; Figs 96, 428, 431, 432, 436, 437, 439, 442, 447). All outgroup taxa had the former arrangement. Different sensilla arrangements of state (1) were not discretely determinable and showed considerable variation between closely related taxa. State (0) was confined to *Syneta*, *C. mimosae*, *Stegnocephala*, *Adiscus* and *Scaphodius*.

(**A44** and **A208**) : distribution of setae on inner and outer margins of galea. The presence (0; Fig. 433) or absence (gaps between setae at least 1/4 length of galea) (1; Fig. 428) of a row of setae seen in profile on inner (A44) and outer (A208) margins was frequently difficult to determine and the outgroup held all states. Character A208 was not scored for *Ditropidus* sp. 469. Because of the difficulty in determining states both characters were discarded for analysis.

(**A45**) : structure of setae at apex of inner edge of galea. In the outgroup the setae were simple (0; Fig. 428), but many ingroup taxa had a subapical patch of short, blunt, inwardly curved setae (1; Fig. 432). State (1) occurred in three Pachybrachini, three

Coenobiina, four Ditropidina and all Australasian Cryptocephalina except *Aporocera* [*Diandichus*] *analis* and *A*. sp. 1049. Five species were not scored.

(A46, A209 and **A210)** : shape of lacinia. The apomorphies for these characters were mutually exclusive but seemed to be derived from the plesiomorphic broad, rounded lacinia (0) (all outgroup taxa; Figs 426-428) in three different ways so were treated separately as three characters. In Character A46 the states represented increasing angularity and reduction. State (1) (Figs 442, 444), trapezoid with short outer margin, was defined by obvious asymmetry and state (2) (Fig. 446), minute and triangular, by reduction so that less than 10 setae were present on the margin. In Character A209 state (1) (not figured) was for a concave apex (bilobed) whereas in state (2) (*vide* Monrós 1953, Fig. 49) the lacinia was cleft to its base (bifid). In the apomorphic state (1; not figured) of Character A210 the lacinia was crescentic, tapering to a point. A46 : 11 species were not scored including all those with a sclerotised lacinia (A47 (1)); state (1) was found scattered in Coenobiina, Ditropidina and almost all Cryptocephalina; state (2) was autapomorphic for *A*. [*D*.] *analis*. A209 : state (1) was confined to *C. mimosae* and two Clytrini; (2) was autapomorphic for *Megalostomis*. A210 : state (1) was limited to three Clytrini.

(A47) : degree of sclerotisation of lacinia. In most taxa, including outgroup, the lacinia was largely membranous with a weakly sclerotised strip near the outer margin (0; Fig. 427). In a few taxa the lacinia was thickened, brown, and well sclerotised (1; Fig. 430). The state for *Lychnophaes* was intermediate. State (1) was found in six Clytrini, *Leasia australis* and *Ditropidus* sp. WA.

(A48) : structure of setae on internal margin of lacinia. The apomorphic state (1; Fig. 432) was presence of comparatively thin and weak long setae, at least 1.3 x length of other setae. Internal setae of the outgroup were all simple (0; Fig. 427). *A*. [*D*.] *analis* was not scored. State (1) was scattered but absent from Lamprosomatinae, Chlamisini, Platycolaspina (except *Atenesus*), and *Cryptocephalus*, and predominant in Australasian Cryptocephalina.

(A56) : structure of setae on external margin of lacinia. Differentiation of states was as for Character A48. All outgroup taxa except one (*Chrysochus*) had long thin setae (Fig. 427) but this was considered to be an apomorphic state for the outgroup as it was completely absent from the ingroup, including *Syneta.*

6.4.4 Prothorax, A49-55, 57-81, 204-206, 211-213, 221-222, 228

(A49) : structure of hind margin of pronotum. This was probably one of the most critical characters but was not always easily scored. The following character state sequence was considered likely : (i) presence of simple thickened border (0; Figs 169, 301), (ii) loss of border without further modification (1; Fig. 466), (iii) development of teeth evenly along margin (2; Fig. 127), (iv) partial or complete loss of teeth (state (3), scored when teeth reduced to presence of only central or laterocentral; Fig. 123), (v) possible redevelopment of border. The plesiomorphic state was obviously presence of a border without teeth (all outgroup taxa except *Megascelis*), but for two species, *Atenesus* and *Aprionota* sp. Tonga, the apparently simple border as seen with low power was faintly crenulate under higher power microscopy (Fig. 122). Viewed *a priori* there was no means of separating the possible convergence of stages (i) and (v), nor of (ii) and (iv). Distribution of states : (1) *Syneta*, Chlamisini, *Mylassa*, *Aprionota*; (3) *Diachus*, *Ditropidus* sp. 469 and *M. glochidionis*; (2) all remaining Cryptocephalini except Platycolaspina.

(A50) : length of middle teeth of posterior margin of pronotum, shorter than basal breadth (0; Figs 119-120) or longer than broad (1; Figs 118, 127). In all taxa with pronotal teeth the middle teeth were generally longest. This character was absent from the outgroup but long teeth were believed to be the apomorphic state because of their limited occurrence and the postulated mode of origin of pronotal teeth (see below). State (1) was confined to *Stylosomus*, two Coenobiina and three Australian Cryptocephalina.

(A51) : relative size of central tooth on pronotal border. The middle teeth were either similar sized (0; Fig. 118) or the central absent (unscored; Fig. 119) or enlarged (1; Figs

115, 498-499). The character was absent from the outgroup but it was polarised on the assumption (possibly erroneous) that all teeth arose uniformly, then differentiated. The state present in *Tappesia* was unclear, and those taxa with a strongly projecting triangular posterior pronotal margin were scored (0) because although the central tooth was prominent at the apex of the angulation, it did not show any particular enlargement. State (1) was present in all Holarctic Cryptocephalina except *Cryptocephalus coryli* and most Australian Cryptocephalina.

(A211) : relative size of laterocentral teeth. These teeth, usually at the outer corners of the basal pronotal process if present (A53 (1)), were scored as in the central teeth of character A51, that is, simple (0; Fig. 498) or enlarged (1; Fig. 499). This character was absent from the outgroup. In two taxa (*Diachus*, *M. glochidionis*) the teeth were very obtuse angulate prominences and the surrounding teeth absent. The states for *A. ruficollis*, *A. tutuilana*, *Coenobius* and *Isnus* were not determined. State (1) occurred in all Holarctic Cryptocephalina except *Cryptocephalus coryli* and most Australian Cryptocephalina.

(A52) : development of central tooth on pronotal border, present (0; Figs 495-499) or absent (1; Figs 119, 486-487). This has been a generic character in the Monachini, although discarded by Lea (1921). As Lea noted, the central tooth in this group is often grooved ventrally and in some taxa this groove continues to the dorsal surface giving a bifid process with no central tooth. There were no scoring problems with the species under consideration. The character was absent from the outgroup but loss of the central tooth by the process described above was considered apomorphic (1). State (1) occurred in *Coenobius*, *Diachus*, 12 Ditropidina and *C. mammillatus*.

(A53) : shape of posterior margin of pronotum. This has been a generic character in the Camptosomata, especially Clytrini, although poorly defined. Three shapes were distinguished : margin straight or evenly curved (0; Fig. 461); with a broad, short and approximately truncate lobe (1; Figs 458, 468, 492); with a narrow, long and roughly triangular lobe (2; Figs 103, 106-108, 481). To some extent the three states intergrade and are probably inter-derivable. State (0) also included taxa with the whole border rather strongly curved (for example *Lamprosoma*). All but one (*Spilopyra*) of the outgroup were included here. State (1) included species with at least slight sinuation towards the sides, from the bluntly produced or truncate middle third or quarter of the base. In *Mylassa* the truncate lobe is strongly projecting. State (2) included species with the middle quarter or less produced in roughly triangular fashion with an evenly and often acutely pointed apex. *Lychnophaes* was not scored (indeterminate, between (0) and (2)). Distribution of states : (1) all Clytrini, all Pachybrachini, *Semelvillea acaciae*, *Atenesus*, all Cryptocephalina except *A.* [*D.*] *analis* and *A. pauperculus*; (2) Chlamisini, all *Leasia*, five Coenobiina, all Ditropidina.

(A54) : structure of the posterior margin of the pronotum. The junction of the posterior foramen and pronotum was either coincident with (0; Figs 105, 113) or overlapped by the posterior margin of the pronotum (1; Figs 103-104). The outgroup scores were equivocal (overlapping in *Spilopyra* and *Pachnephorus*) but most taxa showed overlap. State (1) was predominant except in Pachybrachini and Platycolaspina.

(A55) : form of posterior angles of pronotum in dorsal view. The three states were thought to represent a sequence from rounded (0; Figs 303, 468), to angular but not produced (1; Fig. 458), to posteriorly produced hind-angles (2; Figs 479, 492-493). Most taxa fitted surprisingly well into the three states but nine were unplaced because of lack of a clear distinction between angular and posteriorly produced (compared with basal margin) hind-angles. The median state was also the plesiomorphic (all outgroup). Distribution of states : (0) was restricted to four Clytrini, *Acolastus* and *Semelvillea acaciae*; (2) to two Coenobiina, five Ditropidina and all Holarctic Cryptocephalina.

(A57) : comparative width of pronotum across base and apex. Two states were identified, the prothorax being either roughly parallel-sided (0; Figs 300-303), or strongly contracted towards the anterior angles (1; Fig. 309). It was not possible to discriminate between the two states for all taxa, 14 of which were scored unknown. Some Australian taxa not included in analysis were known to be sexually dimorphic for this character. All outgroup members had the two widths of comparable size (0). State (1) was present in Lamprosomatinae, Chlamisini, *Ischiopachys*, two Pachybrachini, *Leasia* sp.2 and all Cryptocephalina except nine Australian species.

(A58) : length of narrowest part of prosternum between coxal cavity and anterior margin. This area of the anterior part of the prosternum varied greatly in size in the ingroup, but was flat and punctured and pubescent as on other parts of the prosternum (0; Figs 106-108, 458) in all but one of the outgroup (*Pachnephorus*; Fig. 101). The most extreme shortening of the prosternum reduced the prosternum to an impunctate ridge between coxa and head (1; Figs 104-105, 468). This was another character for which scoring was difficult but taxa with antennal slots (A72 state (1)) were scored (1). The states for 17 taxa were indeterminate. State (1) was predominant in all higher taxa except Ditropidina.

(A59) : structure of lateral border of pronotal disc. The presence of fine and irregularly crenulate lateral borders (1; not figured) was sparsely scattered throughout the taxa. A few species had regular strongly and wholly crenulate margins similar to the basal teeth of the pronotum (2; Figs 314-315). It is likely that for at least some taxa these states are unrelated as the crenulations are so different but because of the possibility of a relationship I kept them as states of one character. All but one (*Edusella*) of the outgroup had simple margins. State (1) was confined to *Acolastus* and five Australasian Cryptocephalina including *M. glochidionis*; state (2) to four Australian Cryptocephalina.

(A60) : structure of lateral border of pronotal disc. The anterior of the lateral margin was either simple (0; all outgroup, Fig. 498), or deeply incurved just behind the anterior angles (1; Fig. 499). State (1) was restricted to *A. albogularis* and *A. bihamatus*.

(A61) : loss of carinate lateral border to pronotal disc. This is frequently a generic character in the Chrysomelidae. All but two (*Macrolema*, *Megascelis*) of the outgroup had a carinate border so this was considered the plesiomorphic state (0; Figs 463, 466) with loss of at least the anterior half being apomorphic (1; Figs 460, 470). However within the ingroup this state was autapomorphic for *Acolastus*, therefore this character was deleted from analyses.

(A62) : structure of anterior pronotal angles and insertion of seta, viewed from above. This character was considered to have three sequential states from absence of a setal projection (0; Figs 106, 114), to seta on a 90° tooth (1; Figs 109-110) to the tooth being very acute (2; not figured). Although the states for almost all the taxa were determined the differences were very slight and I suspect that some were wrongly scored. The outgroup had states (0) and (1) and the plesiomorphic state was left undetermined. Distribution of states : (1) *Syneta*, two Pachybrachini, *Stylosomus*, Platycolaspina, *Aprionota insularis*, *C. moraei* and four Australian Cryptocephalina; (2) two Pachybrachini.

(A63) : position of seta at anterior pronotal angles. The anterior pronotal seta shows some variation in position in Chrysomelidae, and may be found on the ventral part of the prothorax (1; Fig. 496), as used for example in defining *Deretrichia* (Selman 1963). This character proved to be autapomorphic for *M. glochidionis* and was therefore not used in the analyses.

(A64) : position of seta at posterior pronotal angles, viewed dorsally. The comments on difficulty of scoring of A62 apply equally well to this character, but only the first two states, without prominence (0; Fig. 104) or with 90° angulation (1; Fig. 110), were present. The outgroup scores were mixed. State (1) was sparsely scattered through the taxon set except that it occurred in all Platycolaspina.

(A65, A212 and **A213)** : shape of posterior apex of prosternal process. Historically the shape of the apex of the prosternal process has been one of the most important generic propagators in the Cryptocephalinae. A65 involves the delimitation of variation of the shape of the apical margin into three logically sequential categories, from convex (0; Figs 109-110) to truncate (1; Figs 114-115) to concave (2; Figs 116-118). A212 and 213 involve two different modifications of the simple concave apex (0). In A212 the apical angles are produced beyond the line of the arc of curvature between them (1; Fig.

118) and in A213 the midpoint of the apical concavity is produced (1; Fig. 490). Three characters were recognised, although the distinction between state (2) of A65 and state (1) of A212 was certainly subtle. Distinction of these two states depended on whether the apical angles or processes were merely continuous with the internal apical curvature (state (2) of A65), or projected at an angle to that. A65 included five historic character states used to differentiate taxa (prosternal process triangularly or arcuately excavate, truncate, rounded or triangularly produced; Chapuis 1874) from which only three states were recognised in this study. The prosternal processes of the outgroup taxa showed all three states of A65 but were otherwise simple. Distribution of states : A65 states were rather scattered but (0) was absent from Lamprosomatinae, Coenobiina, Ditropidina (except *D. saundersi*) and Holarctic Cryptocephalina; (2) was absent from Chlamisini, Pachybrachini and Platycolaspina; A212 (1) was confined to *D.* [*Bucharis*] *suffriani* and *C. moraei*; A213 (1) was confined to *Stegnocephala* and *Adiscus*.

(A66) : structure of sides of prosternal process. In the apomorphic state (1, absent from outgroup; Figs 116-118) the edge of the prosternal process is thickened at the base beside the coxal cavities and forms two subparallel ridges running perpendicular to the hind margin, cutting off the almost vertical lateral corners of the process. The state in *Melixanthus* was indeterminate. State (1) was present in all Coenobiina, Ditropidina, *Lexiphanes*, *Stegnocephala* and *Diachus*.

(A67) : structure of middle of prosternum. In the apomorphic state (1; not figured) there are two parallel ridges near the midline from the anterior margin to the apical half of the prosternal process. These ridges appear to be unrelated to the ridges of A66, hence their treatment as a separate character. State (1) was restricted to *Cadmus* (*Brachycaulus*) *ferrugineus* and *C. mammillatus*.

(A68) : development of deep antennal slots on sides of prosternal process (1; Figs 101-103). These slots effectively divide the apico-lateral corners of the process from the main trunk. In the outgroup they were present only in *Pachnephorus*. In the ingroup they occurred in Lamprosomatinae, Chlamisini and *Adiscus*.

(A69, A221 and **A222)** : shape of the prosternal process. The shape of the prosternal process was measured in three different ways : ratio of length to breadth (A69); ratio of apical width to basal width (A221); shape in profile (A222). For A69 the length of the process was measured from the anterior margin of the procoxal cavities to the furthest point of the process and the width across the narrowest point between the coxae, and the three states were considered sequential from transverse (0; Figs 477, 479), to quadrate (1; Figs 108, 115), to very elongate (2; Figs 461, 464, 468). Only two states were admitted for A221 : approximately parallel sided (0; Figs 106, 468, 479) or expanded at apex (1; Figs 109, 458, 472). The three states of A222 were sequential from strongly convex (0; Figs 466, 470), to flat (1; Fig. 488), to concave and sunk between coxae (2; not figured). Discrimination of states of A69 and 221 was difficult in some taxa, and 8 taxa were not scored for A221. The outgroup taxa had state (2) of A69, state (1) of A221 and state (1) of A222 (except *Pachnephorus*) and these were considered plesiomorphic. Distribution of states : A69 either (0) or (1) was characteristic of Lamprosomatinae, Chlamisini, *Mylassa*, *Stylosomus*, Coenobiina, Ditropidina and Cryptocephalina; A221 (0) was present in *Syneta*, Lamprosomatinae, four Pachybrachini, all Coenobiina, all Ditropidina, *Lexiphanes*, *Stegnocephala* and *Melixanthus*; A222 (0) characterised *Syneta*, two Clytrini and *Acolastus* and A222(2) was autapomorphic for *Aetheomorpha*.

(A70) : structure of anterior edge of prosternum. The states were originally conceived in sequence from flat (0; Figs 106-108), to gradually raised anteriorly (1; Fig. 103), to abruptly elevated, forming a distinct ledge (2; Figs 117, 499). These were considered states of the same character because they appeared to be mutually exclusive. Although most taxa were scored, distinction of states was subtle and confusing because of lack of a relative measurement, even though extremes of state (2) were very distinct. All outgroup taxa (except *Chrysochus*) lacked a raised edge. States (1) or (2) were found in three Pachybrachini, three Coenobiina and most Ditropidina and Cryptocephalina.

(A71) : structure of anterior edge of prosternum at lateral angles. Scores were for either absence (0; all outgroup except *Chrysochus*; Fig. 468), or presence of 'antennal' slots (1; Figs 472, 499). The presumed function of deep slots on the anterior margin is for retention of the antennae, especially in those taxa with a strongly elevated margin (state (2) of A70). In some taxa the slots were reduced to very narrow slits by the inflated raised anterior edge of the prosternum (Fig. 499). *Melatia glochidionis* and *M. solomonensis* were not scored. State (1) was confined to Lamprosomatinae, *Ischiopachys*, *Bassareus* and 11 Australian Cryptocephalina.

(A72) : structure of anterior edge of prosternum near midline. Scores were for either absence (0; Fig. 498) or presence of another pair of 'antennal' slots (1; Figs 101-103, 499), also present in one of the outgroup (*Pachnephorus*). State (1) was limited to Lamprosomatinae, Chlamisini, *Adiscus* and five Australian Cryptocephalina.

(A73) : closure of procoxal cavity. This character has assumed fundamental importance in the discrimination of suprageneric categories in almost every subfamily of the Chrysomelidae. The three states were assumed to be sequential, from closed, with hypomeral process touching prosternal process (0; Figs 101-110), to slightly open, but gap much less than length of hypomeral process (1; Figs 113, 468), to wide open, with short hypomeral process (2; Figs 111-112, 464). These states were quite discrete. In the outgroup the coxal cavity was closed (but see A74). Distribution of states : (1) *Clytra* and *Platycolaspis*; (2) *Syneta*, three Clytrini, all *Leasia* and *Atenesus*.

(A74) : method of closure of procoxal cavity. The procoxal closure was found to be due to either the hypomeron being slotted into the prosternal process (0; Figs 459, 467), or the prosternal process into the hypomeron (2; Figs 471, 474, 480). It was assumed that states (0) and (2) could logically only have evolved through an intermediate stage with open or at most weakly closed cavities (1; Figs 111-113, 476, 478). The outgroup showed state (0) except *Edusella* (1). Distribution of states : (0) all Lamprosomatinae; (1) all Clytrini, *Acolastus*, all Platycolaspina except *Semelvillea acaciae*.

(A75) : development of oblique lateral depressions on pronotal disc. In the apomorphic state a pair of depressions are directed from the middle of the base towards the anterior angles (1; Figs 319, 323), as distinguished from an evenly convex disc (0; Figs 320, 322). In its extreme form this feature was easily scored but in species with either a depressed or tuberculate disc this character was obliterated. The pronotal disc of all outgroup members was simple. 6 taxa were not scored. State (1) was scattered in the data set.

(A76) : development of tubercles (large swellings) on pronotal disc. State (2; Fig. 314) was scored if a deep groove was present along the midline of the swollen disc, and was considered a modification of state (1; Fig. 326) in which only a single central swelling was present. In *L. braccata* this character was sexually dimorphic, the female with the plesiomorphic state (0). All outgroup taxa were simple. State (1) was separately autapomorphic for *C. mimosae* and *A. chlamydiformis* and (2) only occurred in *C. aterrimus* and three Australian Cryptocephalina.

(A77) : development of a keel separating posterior and lateral faces of pronotum. This character was often difficult to assess since there was little difference between angular flexure (0; Fig. 468) and development of a ridge (1; Figs 479-482) at this point on the pronotum. The two states graded into each other as the corner became less obtuse and more angular and nine taxa were unscored. Some taxa may have been mis-scored. Most of the outgroup showed an evenly curved junction of the faces (not *Edusella, Chrysochus*). State (1) was common throughout the data set.

(A78) : presence of a row of basal pronotal tubercles (1; Fig. 123). This was found to be autapomorphic for *Diachus*, and was not considered further.

(A79) : development of a collar at the anterior margin of pronotum. A collar was considered present (1; Fig. 479) if it included preapical constriction of the lateral margin and at least presence of a groove at the sides of the anterior margin (the collar was sometimes effaced dorsally). In 10 unscored taxa these features were very faint or obliterated. The outgroup showed a simple pronotum (0; Fig. 482). The collar was present in three Pachybrachini, Coenobiina, three Ditropidina and most Cryptocephalina.

(A80) : structure of pro-endosternite. In the plesiomorphic state the furca is large and broad-based with a subsidiary small internally directed lobe near the base (0; Fig. 459). This structure shows progressive reduction by loss of the basal lobe (1; Fig. 483) and considerable reduction in width (2; Fig. 474) and may become an elongate spatulate process (3; Fig. 478). The states showed some gradation and in some taxa the very small basal lobe of state (0) may have been overlooked. All outgroup taxa showed state (0). *Syneta* and *C. coryli* were not scored. Distribution of states : (0) *Semelvillea nothofagi* only; (1) all Ditropidina and Cryptocephalina, otherwise scattered; (2) scattered; (3) four Clytrini, three Platycolaspina. In reality the states were not discrete.

(A81) : structure of prosternal process. Either presence (1; Fig. 461) or absence (0; Fig. 458) of an angulation of the middle of the sides of the process, locking into the procoxae. The process was present in three members of the outgroup (*Edusella*, *Megascelis* and *Chrysochus*) but absent from the 'primitive' species. Absence was therefore considered plesiomorphic. The apomorphic state of this character was confined to the outgroup.

(A204) : clothing of upper surface of pronotum (and elytra). Only two states were recognised, involving the presence (0) or absence of visible pubescence or scales (1). This character is widely used in the Chrysomelidae at generic and lesser ranks. The clothing is in the form of setae arising from dermal punctures, and although the distinction of visible and non-visible works fairly well, in reality all taxa have at least a small stub of seta in each pore when examined microscopically (compare Figs 164 and 167). Scales were treated as modified setae. The outgroup were mostly glabrous (not *Edusella*, *Megascelis* and *Pachnephorus*). Individuals of *A.* [*D.*] *analis* showed either state. State (1) was present in all Lamprosomatinae, Chlamisini, *Semelvillea*, Coenobiina and Holarctic Cryptocephalina, but was otherwise scattered.

(A205) : crenulation of front margin of pronotum, at least at sides. The crenulation was either present (1; Fig. 314) or absent (0, all outgroup). This character is almost certainly strongly correlated with A59 (2). State (1) was confined to five Australian Cryptocephalina.

(A206) : development of front angles of pronotum compared with anterior margin of prosternum. When observed ventrally the front angles of the pronotum were either roughly a continuation of the anterior margin of the prosternum (0; Fig. 464), or abruptly jutting forwards (1; Fig. 458). All the outgroup except *Spilopyra* showed the simple state. State (1) was found in *C. mimosae*, two Clytrini and eight Australian Cryptocephalina.

(A228) : width of base of pronotum compared with width of elytra across shoulders. The ratio of base of pronotum to shoulders of elytra was either narrower (ratio < 0.8), or broader (ratio > 0.8). A simple character which was proposed to help separate the outgroup from the ingroup. In practice this did not give a clear cut separation of taxa although there are certainly trends within both groups towards opposite body shapes. This character was discarded from the analyses.

6.4.5 Mesothorax, A82-99, 214

(A82) : shape of mesosternal process. The process was either elongate (0; Figs 126, 523), square (1; Fig. 520), or transverse (2; Figs 125, 522), when measured from the anterior of the mesocoxal cavity. All three states were present in the outgroup so the median state (1) was made plesiomorphic, since states (0) and (2) are logically derived from it. The states were scattered although (0) was absent from Coenobiina, Ditropidina and Cryptocephalina and (2) was absent from Lamprosomatinae, Chlamisini, Clytrini, Pachybrachini and Platycolaspina.

(A83) : shape of apex of mesosternal process. Although scored as a morphological sequence from simple (0; Fig. 520) to bilobed (1; not figured) to biconcave (2; Fig. 525) each state could have been considered separately, as done for the prosternal process (A65 and 213) or the states left unordered. Most of the outgroup showed the simple state (not *Spilopyra*). *D. aeneolus* and *Aporocera* [*Cryptocephalus*] *jacksoni* were not scored. Distribution of states : (1) three Clytrini, *Ambrotodes*, *A.* sp.Tonga, two Ditropidina, five Australian Cryptocephalina; (2) *Stegnocephala*, two *Cryptocephalus*.

(A84) : development of mesosternal keel. A longitudinal mesosternal keel was either present (1; Fig. 521) or absent (0, all outgroup; Fig. 529). State (1) was confined to *Lychnophaes* and Chlamisini.

(A85) : surface sculpture of mes-epimeron. The mes-epimeron was scored as punctate (0; Fig. 126) even if the punctures were confined to only a portion of the surface - it seemed impossible to isolate this as a separate state because of gradation. State (1; Fig. 125) was the retention of coarse and dense transverse microreticulation in the absence of punctures. For state (2) both punctures and microsculpture were apparently absent. The outgroup showed state (0), except *Pachnephorus*. Distribution of states : (1) Lamprosomatinae, *Babia*, *Mylassa*, five Platycolaspina, all Coenobiina, all Ditropidina, all Holarctic Cryptocephalina except two *Cryptocephalus*, all but five Australian Cryptocephalina; (2) two *Cryptocephalus*.

(A86) : mode of elevation of scutellum from anterior field of mesonotum (mesoscutum). Three discrete states were recognized which were presumed to follow a linear development sequence, from gradual elevation of scutellum (0; Figs 131-135, 139), to elevation perpendicular to mesoscutum (1; Figs 141, 143, 512-513), to perpendicular elevation with a 'step' (2; Figs 137-138, 506). State (2) was considered to be derived from (1) through pronotal overlap superimposed on an already abrupt juncture. Most of the outgroup showed state (0), but not *Chrysochus* and *Pachnephorus* (1). *Stylosomus* and *Adiscus* were not scored because of their reduced scutella, and *Ditropidus* nr *antennarius* was indeterminate. Distribution of states : (1) *Lychnophaes*, *Oomorphus*, Chlamisini, *Mylassa*, *D.* sp. 865, all Cryptocephalina; (2) *Lamprosoma*, all Coenobiina and all remaining Ditropidina.

(A87) : development of lateral ridges on anterior field of mesonotum. The sides of the mesonotal anterior were either simple (0; Figs 131-133, 139) or with raised more or less straight ridges (1; Figs 135-138, 141-143). The outgroup showed only the plesiomorphic state. State (1) was present in Chlamisini, Pachybrachini, Platycolaspina except *Semelvillea* and *Atenesus*, and all Coenobiina, Ditropidina and Cryptocephalina.
(A88) : development of central longitudinal 'suture' on anterior part of mesonotum (1), marking the junction of the ventral mesophragma. Much difficulty was experienced in identifying this feature and then scoring it so this character was abandoned and ignored in all analyses.
(A89) : structure of base of scutellum. In some taxa the base of the scutellum was notched (1; Figs 141, 511, 514-516, 518), this notch corresponding with the median tooth of the pronotal posterior margin. All outgroup taxa were simple. State (1) was found in *C. aterrimus*, *Stegnocephala*, two Ditropidina and most Cryptocephalina.
(A90) : development of microchaetal patches on lateral lobes of mesonotum. Distinct patches of dense microchaetae were either present, often in a slight hollow (1; Figs 138, 141), or absent (0; all outgroup except *Macrolema*; Fig. 500). State (1) was confined to all Ditropidina (except *D*. sp. WA), *C. moraei*, *Melixanthus* and most Australian Cryptocephalina. The few minute spicules on the lateral lobe of *Mylassa socia* (Fig. 503) may have been homologous but were ignored for analyses.
(A214) : shape of lateral lobe microchaetal patches (requires A90, state (1)). The patches were of two discrete shapes : circular to oval, usually confined to the anterior half (0; Figs 141, 518-519), or in a narrow strip adjacent to the scutellar base (1; Fig. 138, 508-510, 514). The only relevent outgroup member had a circular patch, but this is certainly independently derived. The narrow strip of microchaetae was present in all the Ditropidina (except *D*. sp. WA) and *Melixanthus* and the round or oval patch was confined to *Cryptocephalus moraei* and all Australian Cryptocephalina except *M. glochidionis*, *Aporocera* [*Loxopleurus*] *gravatus* and *C. mammillatus*.

(A91) : scutellum externally visible or not visible between conjunction of elytra and pronotum. Strictly speaking the scutellum was never completely absent because there was always at least a small raised area on the apex of the mesonotum. But if this region was depressed or flattened in any way and was invisible with closed elytra it was scored absent (1; Figs 505, 508). The scutellum was fully-developed (0) in all outgroup taxa. State (1) was confined to *Stylosomus* and *Adiscus*.

(A92) : shape of scutellum. An attempt was made to provide discreet categories allowing for all the variation in the taxa concerned. This was encompassed in the following states : triangular or semicircular, the apex more or less pointed (0; Fig. 500); quadrate, trapezoid or transverse rectangular, the apex truncate (1; Fig. 501); elongate rectangular or wedge-shaped, length more than twice width at base (2; Fig. 507); fusiform to ovoid, broadest at the middle (3; Fig. 138); trapezoid, broadest at apex (4; Fig. 502). The states listed show an approximate progression from scutellum broadest at base to broadest at apex but the five states are not necessarily related to each other and were left unordered in analyses. Some difficulty was experienced separating states (0)-(2). Most of the outgroup (not *Edusella* and *Megascelis*) had triangular scutella (0) and this was deemed the plesiomorphic state. The scutella of *Griburius* and *Metallactus* were indeterminate between states (0) and (1). Distribution of states : (1) two Pachybrachini, all Platycolaspina (except *Leasia* sp.2), *Ditropidus* [*Tappesia*] *saundersi*, most Cryptocephalina; (2) *Leasia* sp.2, three Coenobiina, three Australian Cryptocephalina; (3) two Coenobiina, all Ditropidina except *D. saundersi*; (4) autapomorphic for Chlamisini.

(A93) : development of subscutellar lobe of mesonotum. The sclerotised connection between the basal flange of the mesonotum and the scutellum may be simple (0, outgroup; Fig.) or may be produced as far as or beyond the scutellar apex (1; Figs 138, 509). State (1) was sparsely scattered.

(A94) : shape of the basal flange of the mesonotum below the scutellum. Five states of the posterior margin were recognised : simple, with curved or straight margin (0; Fig.

502); as above, but pointed in the middle (1; Fig. 500); whole margin angulate (2; Fig. 507); median area bilobed (3; Figs 511-512); median area truncately produced (4; Fig. 514). These are not necessarily sequential, and were therefore unordered. In practice there was some difficulty in separating the states, and although all taxa were scored, some may have been erroneously. The outgroup held three states, (0)-(2). States (0) and (1) were absent from Coenobiina, Ditropidina and Cryptocephalina, and states (3-4) were absent from Lamprosomatinae, Chlamisini, Clytrini, Pachybrachini and Platycolaspina.

(A95) : profile of mesonotum. The slope of the scutellum was either less than 30° (0, all outgroup; Figs 506, 512, 513), or at least 30° compared with the anterior field of the mesoscutum (1; Figs 519). I did not compare the tilt of the scutellum with the elytra, because these were often irregularly surfaced, and could be tilted independently of the scutellum. The state in *Clytra* was indeterminate. State (1) occurred in two Clytrini, four Pachybrachini, three *Cryptocephalus* and all Australian Cryptocephalina.

(A96) : junction of scutellum and elytra. Either the scutellum and elytra compactly fitted together (0, outgroup except *Chrysochus*), or the sides of the former overlapped the latter (1; Figs 127-130). In several taxa the degree of overlap was very slight and may have been mis-scored. *D. saundersi* and *D. geminus* were not scored. State (1) was scored for Chlamisini, Platycolaspina and *D. variabilis*. In retrospect this character was generally mis-scored because only extremes in a continuous spectrum of variation were noted.

(A97) : surface of scutellum. The median surface was either with (1; Fig. 518) or without (0, all outgroup; Fig. 519) a median longitudinal keel or angulation, at least in the apical half. State (1) was confined to seven Australian Cryptocephalina.

(A98) : development of sides of mesonotal flange. The flange at the posterior of the mesonotum either tapered laterally to a blunt point (0, all outgroup; Fig. 501) or curved anteriorly to reach the mesonotal side margin, enclosing a weakly sclerotised hollow (1;

Figs 502, 504). All taxa were scored and the outgroup had only state (0). State (1) was present in almost all ingroup taxa, the few exceptions being diverse.

(**A99**) : development of stridulatory mechanism on anterior surface of metanotal anterior field. In most taxa this area was microreticulate, usually with scattered punctures, although relatively smooth. This condition (0; Figs 131-132, 135-140, 143) occurred in all outgroup taxa. In some taxa punctures were absent and the microsculpture was very transverse and regular but still reticulate (1; not figured), whereas in others the surface was covered in dense and extremely fine parallel grooves which gave an iridescent reflection because of light diffraction (2; Figs 134, 142). It was assumed that these three states represented a transformation series. Distribution of states : (1) *Ditropidus* sp. WA and three Australian Cryptocephalina; (2) all Clytrini and four Australian Cryptocephalina.

6.4.6 Metathorax, A100-105

(**A100**) : presence of lateral processes on arms of metendosternite. Crowson (1938, 1944) has shown that the presence of lateral processes (laminae) is plesiomorphic for the Chrysomelidae (= hylecoetoid type). The three states represent progressive loss of this feature, from broad lobes (0; Fig. 529), to narrow straps (1; Figs 530, 534), to complete absence (2; Fig. 531). The processes were well developed in both 'primitive' members of the outgroup, absent from the rest. Distribution of states : (0) no ingroup members; (1) Lamprosomatinae, three Pachybrachini, *Adiscus*; (2) remaining taxa.

(**A101**) : position of median metendosternite tendons. *In extremis* the tendons were either close to each other and at the base of the arms (Fig. 530) or about a third of the way along the arms (most of outgroup, Fig. 529). There were too many intermediate taxa so this character was ignored in all analyses.

(**A102**) : position of median metendosternite tendons. Situated on distinct, separate processes (0; Fig. 529), or these processes more or less obliterated (1; Fig. 530), or these processes combined together medially to form a broad blunt anteriorly directed lamina (2; Fig. 531). Crowson (1967) has suggested that (2) is typical for Camptosomata (his Clytrinae *sensu* 1967). Nevertheless, the separation of these states was difficult. State (1) was considered ancestral to (0) and (2) and was shown by most of the outgroup (not *Macrolema* and *Chrysochus*). *D. suffriani* was not scored. Distribution of states : (0) *Oomorphus*, *Atenesus*, *D.* sp.WA, *C.brunnipes*; (1) other Lamprosomatinae, four Platycolaspina, five Ditropidina; (2) remaining taxa.

(A103) : width of lateral arms of metendosternite. Two states of arm width were proposed but in practice it was not possible to separate two classes, and this character was discarded and ignored in analyses.

(A104) : shape of stem of metendosternite. Variation in shape of the stem was taken to be a morphological sequence from elongate (basal triangle plus narrow stalk) (0; Fig. 531-532), to triangular (1; Fig. 530), to transverse trapezoid (both top of triangle and stalk missing) (2; Fig. 529). The intermediate state was considered ancestral, by virtue of being intermediate, but was shown by only two of the outgroup (*Edusella* and *Chrysochus*). Six taxa were not scored. Distribution of states : (0) *Syneta*, six Clytrini, six Platycolaspina, all Coenobiina, 12 Australian Cryptocephalina; (2) *Lychnophaes*, *Oomorphus*.

(A105) : shape of posterior, internal, margin of metanotum. This is the metendotergite or metathoracic phragma of Snodgrass (1935). The apical margin was either simple with the edge straight (Fig. 527) or curved (reduced phragma), or with a thinly sclerotised posterior expansion with bisinuate apex (Fig. 528). The distinctions were gradual in practice and because of confusion in scoring these grades the character was rejected and ignored in analyses.

6.4.7 Elytron, A106-113

(A106) : number of elytral striae. Distinct striae were either present from one side of the elytra to the other or at least partly absent (scored unknown = 9). If present there were 10 (0, all outgroup; Figs 162-166) or 9 (2) striae, ignoring the short sutural stria, or a morphologically intermediate state where two striae were partially anastomised (1). The outgroup showed states (0) or (9). Distribution of states : (1) two Coenobiina; (2) *Oomorphus*, three Coenobiina.

(A107) : development of abrupt declivity at base of elytra. At the point of contact with the pronotum, the angle between the upper surface and basal surface of the elytra was either smooth and rounded (0) or sharp, angulate and less than 90° (1). The outgroup mostly showed the former state (not *Pachnephorus* and *Chrysochus*). *Platycolaspis* was indeterminate. Most taxa showed state (1), but not *Syneta*, six Clytrini and four Pachybrachini.

(A108) : development of an incision near the base of the elytral epipleura. Originally I intended to separate three states, two of which were for degrees of development of the incision, but separating taxa without a nick from those with a very slight one proved too subjective (in *Prasonotus*, *Ditropidella*, *Adiscus*, two Ditropidina and *Coenobius* it was very small but still visible). Only one taxon (*Scaphodius*) had a deep triangular incision, so, having become autapomorphic, this character was not used in analyses.

(A109) : form of apex of sutural locking grooves. Each elytron has a groove and projecting lip along the internal margin of the suture. The interlocking mechanism was either closed (complete to apex), as shown by all outgroup members (0; Fig. 144), or open, with the grooves splaying out and becoming evanescent before the elytral apex (1; Figs 161, 897). State (1) was confined to *Semelvillea* and *Platycolaspis*.

(A110) : structure of elytral surface. Only two states were allowed to represent the wide and mostly gradual variation in the elytral surface. The surface was recognisably either smooth to canaliculate (0), or with discrete raised areas (tubercles) (1; Figs 314, 318, 326). All outgroup taxa had smooth elytra. State (1) was restricted to Chlamisini and seven Australasian Cryptocephalina.

(A111) : structure of the interlocking mechanism at the base of the elytra. This character has been of some importance in the Chlamisinae. The elytral locking system shows a slight modification in some taxa with development of a few irregular teeth at the extreme base (1; Fig. 499), and in other taxa the upper flange may be crenulate for all or most of its length, especially apically (2; Fig. 857). These states were considered to be logically ordered. Six taxa were indeterminate between states (0) and (1), either because the basal teeth were flattened out, or because of possible independent development of a less distinct system. All outgroup taxa were simple (except *Megascelis*), so this state was considered plesiomorphic. Distribution of states : (1) *Ischiopachys*, Coenobiina, all Ditropidina, all Holarctic Cryptocephalina, five Australian Cryptocephalina; (2) Chlamisini.

(A112) : shape of elytral epipleuron. This character is very important at generic level in Clytrini but unused elsewhere in Camptosomata. The three states allocated to the wide variation present were considered to be sequential. The outgroup had a simple, evenly tapering, epipleuron (0; Fig. 300). Epipleura with broadly expanded base and rapidly attenuate apex were scored 1 (Fig. 303) and those with a similar broad but also angulate base were given state 2 (*vide* Monrós 1956a, fig. 9). In practise the difference between states (0) and (1) was difficult to determine, but only *Spilopyra* and *Metallactus* were not scored. Distribution of states : (1) Clytrini, Pachybrachini, *Stylosomus*, four Platycolaspina, all Coenobiina, most Ditropidina and all Cryptocephalina; (2) Lamprosomatinae.

(A113) : structure of elytral epipleura near base. In most taxa, including all outgroup, the whole epipleuron is visible laterally (0; Figs 300-330), but in a few taxa the upper margin crosses over the lower in side view (1; Figs 559-560). State (1) was confined to *Adiscus* and *Ditropidus* nr *antennarius*.

6.4.8 Wing, A114-123

The wing characters of this group of Chrysomelidae were of limited value because they generally represented loss or reduction of veins. *Oomorphus* was unscored, due to brachyptery.

(A114-116) : presence or absence of veins CuP, $1A_{1+2}$, $1A_{3}+2A$, 3A. The anal part of the wing in Chrysomelidae in its plesiomorphic state has been shown to have five veins (not counting jugal) (Jolivet 1957), but none of the taxa here have more than four (Figs 550-558). These three characters record the loss of anal veins as apomorphies. The outgroup showed a variety of vein combinations but a complete complement of the four veins was present in the two 'primitive' taxa. As it was difficult to determine which of veins CuP or $1A_{1+2}$ had been lost where one was certainly missing these two veins were treated in conjunction (A114) with loss of one vein as state (1) and loss of both veins as state (2). A115 was presence (0) or absence (1) of anal vein 3A and A116 was presence (0) or absence (1) of anal vein $1A_{3}+2A$. The only ingroup taxa to show A114 (0; Fig. 553) were all Lamprosomatinae; state (2) was autapomorphic for *Platycolaspis*. A115 (1) was present in *Stylosomus*, four Platycolaspina, Coenobiina, five Ditropidina, *Diachus* and *M. glochidionis*; A116 (1) was autapomorphic for *Diachus*.

(A117) : development of the most anterior anal vein. The most anterior anal vein (CuP, or CuP+$1A_{1+2}$) was either connected to the anal cell through anal vein $1A_{3}+2A$ (0, all outgroup; Figs 550, 552-553), or free and well removed from this vein (1; Figs 554-558). State (0) was only found in Lamprosomatinae.

(A118) : development of jugal lobe. The jugal lobe was either not strongly differentiated at the wing margin (0; all outgroup except *Edusella* and *Megascelis*; Figs 550, 553), or was separated from the rest of the wing margin by an acute incision or deep cleft (1; Fig. 552). State (0) was confined to Lamprosomatinae.

(A119) : number of anal cells. From 3 to 0 (states 0-3) anal cells were present and this might have been seen as a simple progressive loss. However from all the evidence to hand (Crowson 1946; Jolivet 1957; Linsley 1961; Crowson 1967; Suzuki 1969, 1970; Wallace and Fox 1980) the plesiomorphic chrysomelid wing has 2 cells, which was taken to be the plesiomorphic state in this matrix (1; Figs 552-553, 554-556, 558). The presence of three cells (0; Fig. 550) was found to be an autapomorphy for *Macrolema*.

From 3 to 1 (Fig. 557) cells were present in the outgroup wings. States (2) and (3) were sparsely scattered in the data set, except all Coenobiina.

(A120) : size of anal cell 2AC relative to cell 1AC. The relative size of the two anal cells seemed significant. At one extreme (0; Fig. 552), cell 2AC was at least as large in area as cell1AC (most of outgroup), the intermediate state had cell 2AC approximately half the size of cell 1AC (1; Fig. 550) and finally cell 2AC was reduced to a small fraction of 1AC (2; Figs 554, 558). The 'primitive' members of the outgroup showed state (1), the others (0). Four taxa were indeterminate *Aorocarpon* [*Brachycaulus*] *posticalis*, *A. (L.) pauperculus*, *D. suffriani*, *D. comans*). Distribution of states : (0) Lamprosomatinae, most Ditropidina; (2) Chlamisini, four Pachybrachini, *Adiscus*, *Melixanthus*, *A. flaviventris*.

(A121) : structure of cell Rt. The cell was either closed (all outgroup; Fig. 550), or basally open through loss of part of the cross vein to the radial sector (1; not figured). State (1) was confined to Chlamisini, *Platycolaspis* and *Ditropidus* sp. WA.

(A122) : presence or absence of the CuP back-vein connecting the anal region with CuA. In the outgroup the basal extension of vein CuP curved forwards to proximity with CuA (0; Fig. 550), whereas in almost all of the ingroup this part of CuP was absent (1; Figs 554-558). State (0) was restricted to Lamprosomatinae.

(A123) : development of subcubital fleck. Two stages of development of a subcubital fleck of wing-folding spicules (Hammond 1979) were recognised. Firstly, a simple ill-defined and fairly extensive patch (1; Fig. 550), and secondly two distinct elongate patches in parallel (2; Fig. 551). There is evidence that the subcubital fleck could be considered a synapomorphy for the Eumolpinae, though subsequently lost by some taxa (*vide* Jolivet 1957), and its absence was therefore considered plesiomorphic (0). The subcubital fleck was present in all outgroup taxa except *Megascelis* but was completely absent from the ingroup.

6.4.9 Legs, A124-134

(A124) : structure of ventral surface of claws. Amazingly, this is perhaps the single most important character in traditional chrysomelid taxonomy. Kasap and Crowson (1976) have already cast doubts on its usefulness. The three states, simple, appendiculate, and bifid, have been used throughout the Chrysomelidae to define genera and even tribes (see, for example, in Chrysomelinae : Weise 1915; Selman 1979). Use of the terms appendiculate and bifid has not been consistent in literature. Here the state 'simple' (0; not figured) includes variation in claw shape from smooth ventral surface to basal angular tooth since these forms grade into each other. State 'appendiculate' applies to claws with an often almost right-angled basal lobe which is separated distally from the apical hook by a deep cleft (1; Figs 147-148). State 'bifid' is for claws with an elongate tooth similar in form and size to the rest of the claw, and arising from the base of it (2; not figured). I regard these states as following a logical morphological sequence. The outgroup included all three states but the primitive taxa had simple claws. Distribution of states : (1) *Lamprosoma*, *C. mimosae*, two Clytrini, *Platycolaspis*, *Semelvillea.* all Coenobiina, *Lexiphanes*, *Diachus*, six Ditropidina, *M. glochidionis*; (2) autapomorphic for *Syneta.*

(A125) : structure of claws. The claws were either free and usually separated by at least 120° (0, all outgroup except *Megascelis*), or fused basally and approximately 90° apart (1; Fig. 547). State (1) was autapomorphic for *Lamprosoma.*

(A126) : shape of tarsomere 1. The vast majority of the taxa including all outgroup had elongate first tarsomeres (0; Fig. 147), in a few taxa these were quadrate to transverse (1; Fig. 549). This character was indeterminate in *C. mimosae*, *A. tutuilana*, and *Melixanthus*. State (1) was restricted to Lamprosomatinae, Chlamisini and *C. ferrugineus.*

(A127) : size of profemora relative to other femora. The femora were either all of similar size (0; all outgroup except *Edusella*; Fig. 308), or the profemora were obviously much longer and wider (1; Fig. 306). State (1) was autapomorphic for Pachybrachini except *Mylassa.*

(A128) : development of a ventral keel on the profemora. For the two states the ventral surface of the femur was either smoothly rounded (all outgroup taxa except *Edusella*), or with an angular keel or carina (1). However, in practice the keel included the raised edge of a shallow groove and the keel could be reduced to a ventral angulation. Five taxa were not scored and several may have been mis-scored. The character was discarded.

(A129 and **A130)** : number of flexible spurs at apices of meso- and metatibiae. The spurs were distinguished from the apical spiniform setae of typical chrysomelids by their dark colour, large or small size, acute apices, and position on the ventral edge of the apex. On each tibia there were either two (0), one (1; Fig. 548), or nought (2) apical spurs. The plesiomorphic state for Chrysomelidae is presence of two spurs so the derived states of these characters are the progressive loss of spurs. Only the 'primitive' members of the outgroup had the full complement of spurs on these tibiae. Distribution of states : A129 (0) *Syneta*, ; A129 (1) Pachybrachini except *Mylassa*; A130 (0) *Syneta*; A130 (1) three Pachybrachini.

(A131) : structure of apex of metatibia. Almost all taxa had simple metatibiae, but two (*Edusella* and *C. mimosae*) had single elongate apical teeth (only in the male of *C. mimosae*), although different in structure. Since this state was clearly convergently autapomorphic the character was ignored in analyses.

(A132) : development of an external tibial keel (1). The keel was an angular ridge, the result of flattening of the anterior and posterior surfaces, and was sometimes accompanied by a parallel groove which was often too slight to be worth distinguishing. This character is very similar to A128 since the states are similar and development of a keel is graded. Outgroup tibiae were mostly simple (not *Edusella* or *Chrysochus*), and only *Griburius* was considered indeterminate. State (1) was scattered, but absent from Clytrini and Pachybrachini.

(A133) : development of a large apicodorsal excavation on tibiae (a hollow for the folded basitarsus). To a certain extent all tibiae have at least a shallow or very short excavation for retention of the tarsus in thanatosis. The apomorphic state was for the hollow to be deepened and extended at least a quarter of tibial length. The character was not easily scored in smaller members of the matrix, and is probably correlated with size. Simple tibiae were considered plesiomorphic although modified tibiae were present in *Pachnephorus*. The modified tibia of *Pachnephorus* is fringed with long setae and appears to be pseudo-analogous. *C. aterrimus* and *D. cervinus* were not scored. State (1) was recognised in two Coenobiina and six Ditropidina.

(A134) : distribution of clavate ventral setae on female protarsomeres. These setae were present on tarsomeres 1 to 3 (0), or on 3 only (1, including all outgroup; Figs 147-148). The polarity given is the reverse of the outgroup because I thought that having all segments with spatulate setae was more likely to be plesiomorphic. However state (1) appears to be plesiomorphic for Chrysomelidae (Stork 1980; Mann and Crowson 1981). State (0) was confined to Lamprosomatinae.

6.4.10 Abdomen (external), A135-157, 202, 203, 215, 227

(A135) : degree of cover of pygidium by elytra. An exposed pygidium is supposed to be diagnostic for the Camptosomata minus Lamprosomatinae. The three states, pygidium completely covered at least in male (0; Fig. 300), pygidium only half covered (1; Fig. 306) or completely exposed (2; Fig. 305), are really grades which did not separate easily, although only six taxa were unscored. The main problems were separation of (1) and (2), and sexual dimorphism. The female was thought to show the apomorphic state if sexually dimorphic, because of its expanded abdomen. This character was therefore based on the male. All outgroup taxa showed state (0). States (1) and (2) were scattered through the taxon set, but (0) was confined to *Syneta*, Lamprosomatinae, four Clytrini, all Platycolaspina and two Australian Cryptocephalina.

(A136) : shape of hind margin of sternites III to VI, straight (Figs 563, 565) or concave (Figs 562, 569). This is also a traditional character defining the Camptosomata minus Lamprosomatinae (Crowson 1967). However I found it impossible to make use of with any accuracy because the degree of concavity depended on the convexity of the venter (and hence the sex), on the overlap of the abdominal segments in individuals, and very much on the angle of view. Many taxa had males with straight margins but females concave and as this concavity seemed intimately connected with the egg-hollow the character was abandoned in favour of the latter, and was not used in analyses.

(A137) : development of telescopic abdominal segments. The abdominal segments were either simple (all outgroup), or segments III-VI were telescoped permanently and appeared externally as a series of narrow rings (1; Fig. 564). State (1) was autapomorphic for Chlamisini.

(A138 and **A203)** : state of junction of sternites V, VI and VII. Connation of the apical abdominal ventrites is another suggested characteristic of the Camptosomata. The states of A138 were either free and flexibly overlapping sternites VI and VII (0, all outgroup; Fig. 562), or these sternites fused, not capable of any relative movement (1; Fig. 565). A203 included the same states for sternites V and VI (Fig. 569). A138 (0) was confined to *Syneta* and Lamprosomatinae and A203 (1) was found in *Stylosomus*, *S. nothofagi* and all Ditropidina except *Adiscus*.

(A139) : situation of abdominal spiracles in segments II to V. The spiracles were either outside the tergites in the pleural membrane (0; all outgroup except *Edusella* and *Megascelis*, Figs 567-568), or attached to or within the the tergites (1; Figs 563-565). This character is to some extent a measure of the degree of tergal sclerotisation (A151). State (0) was present in *Syneta*, *Oomorphus*, five Clytrini, four Platycolaspina and *C. ferrugineus*.

(**A140 -142**, and **215**) : development of lateral lobe of abdominal sternite III. The degree of overlap of the sides of the abdomen against the thorax is another character supposedly diagnostic for Camptosomata (Kasap and Crowson 1976). However it was difficult to select discrete states for this 'characteristic', which has never been properly quantified. A140 is an attempt to quantify the size of the abdominal lobe, either absent to barely projecting (0; Fig. 561), or large and prominent (1; Fig. 563). The 'primitive' outgroup taxa showed state (0). *Leasia* sp. 2 was not scored. A141 describes the composition of the lateral lobe of sternite III. In state (0), all outgroup (Fig. 561), the lobe comprises a combination of pleurite and sternite, both parts reaching the apex of the lobe. In state (1) (Fig. 566) the pleurite is reduced and terminates at the base of the lobe. A142 and A215 describe the shape of the lateral lobe. These are two closely related characters, whose states are close but generally not difficult to separate. The three unordered states of A142 were : narrow, with rectangular apex (0; Fig. 573), acute angulate (1; Fig. 575), and broad with rounded apex (2; Fig. 576). A215 describes the sclerotisation of the dorsal angle of the lateral lobe, whether present (0; Fig. 566) or absent (1; Fig. 562). If sclerotisation was incomplete A142 was scored unknown (9). For A142 the outgroup showed state (0) (narrow rectangular), except *Pachnephorus* (1) and *Megascelis* (9), and for A215 all were simple, state (0). Distribution of states : A140 (0) *Syneta*, *Oomorphus*, Chlamisini, *Stylosomus*, four Platycolaspina and two Ditropidina; A141 (0) *Syneta*, Lamprosomatinae; A142 (0) *Oomorphus*, two Coenobiina, two Ditropidina, *Melixanthus* and *Diandichus*; A142 (1) three Pachybrachini, two Ditropidina and two Australasian Cryptocephalina; A215 (1) *Syneta*, Chlamisini, *Stylosomus*, four Platycolaspina.

(A143) : connection between basal border and lateral lobe of abdominal sternite III. In almost all taxa the basal border abutting the coxa extends to the ventral edge of the lateral lobe (0, all outgroup; Fig. 561), but in a few the border clearly turns posteriorly before reaching the lobe (1; Fig. 569). *Syneta* was not scored because the basal border was completely obliterated. State (1) was confined to four Clytrini, *Platycolaspis* and *Semelvillea*.

(A144) : shape of intercoxal lobe of sternite III. Most taxa had lobes which belonged to either of two states : transverse with approximately straight apex (0; Fig. 572), or quadrate with rounded to triangular apex (1; Fig. 569). The outgroup scored equivocally, the 'primitive' taxa having the lobe rounded (1). The state for *Megalostomis* was indeterminate. State (1) was present in *Syneta*, *Lychnophaes*, Chlamisini, Clytrini, *Stylosomus*, Platycolaspina, *Cryptocephalus coryli* and all Australian Cryptocephalina. In retrospect a further character could have been made from the structure of the posterior edge of the metasternum which did not seem to correlate with the states of A144.

(A145) : structure of sides of sternites III-VI. The sides of the sternites were either separated into a vertical lateral face by a well defined angulation or keel (1; Fig. 563), or smoothly rounded (0; Fig. 565). All outgroup taxa except *Macrolema* and *Megascelis* were keeled but neither state was considered plesiomorphic. *A. ruficollis* was not scored. State (1) occurred in Lamprosomatinae and *A. tutuilana*.

(A146) : fusion of sclerotised tergites I and II. These tergites were either distinctly free, separated by integument (0, all outgroup except *Edusella* and *Megascelis*; Fig. 567), or fused, often with tergite I considerably reduced (1; Fig. 563). *Oomorphus* was not scored because all the tergites were unsclerotised. State (0) was confined to *Syneta* and two Clytrini.

(A147-149) : development of various modifications to male sternites. Secondary male structures have been used in the definition of *Cryptocephalus* subgenera, and genera of Clytrini and various other Coleoptera (notably Melyridae). Modification of the mandibles is described above (A34-5). Several abdominal structures have already been widely noticed in the Australian fauna (Lea 1904) and a few examples were therefore included in the analysis. The characters were : A147, sternite V with (1; not figured) or without (0) a pair of tubercles; A148, disc of sternite VII with (1; Fig. 574) or without (0) a deep hollow; A149, sternite 7 with (1; Fig. 574) or without (0) a pair of tubercles. All outgroup males were simple except *Edusella* (A148 state (1)). A147 (1) was found to be autapomorphic for *C. brunnipes* and was therefore dropped from the analysis.

Distribution of states : A148 (1) Chlamisini, *Clytra*, *C. brunnipes*, *C. sericeus* and three Australian Cryptocephalina; A149 (1) *C. brunnipes* and *C. sericeus*.

(A150) : degree of expansion of female abdomen. In some chrysomelids the female abdomen becomes increasingly swollen with gravidity (notably in *Oides* spp. in Galerucinae) but in Camptosomata the segments are strongly sclerotised and not capable of significant expansion; their shape is therefore fixed. This character measured the degree of convexity of the sclerites by determination of whether the abdomen was widest at the elytral juncture (0, all outgroup), or bulged outwards before meeting the elytra (1; Fig. 871). *Pachybrachis* was not scored. State (1) was confined to Chlamisini and two Australian Cryptocephalina.

(A151) : degree of sclerotisation of abdominal tergites. The tergites were either very thin, soft and flexible (0; all outgroup except *Megascelis*, Fig. 576), or thick, rigid and strongly coapted (1; Fig. 563). State (0) was present in *Syneta*, *Oomorphus*, five Clytrini, *Stylosomus*, Platycolaspina, two Coenobiina, five Ditropidina and two Australian Cryptocephalina.

(A152) : development of femoral lines on sternite III. In a few taxa femoral lines were present which are grooves for the infolding and retention of the hind legs (1; Fig. 563). In all outgroup taxa sternite III was simple (0). *Adiscus* was not scored. State (1) was autapomorphic for Lamprosomatinae.

(A153) : development of transverse rows of setae on the anterior half of tergite I. Transverse rows of dense setae were either present (1; Fig. 567) or absent (0). Such setae were absent from the outgroup. State (1) was restricted to three Clytrini.

(A154) : structure of pygidium (tergite VII). The pygidium was either simple (0, all outgroup except *Pachnephorus*), or with a biconvex shallow ridge across the middle isolating the basal wing folding spicule area from the apex (1, best seen when viewed by transmitted light; Figs 570-571). The state of *Isnus* was indeterminate. State (1) was confined to four Coenobiina.

(A227) : development of pygidial slot. The disc of the pygidium may be simple (0, 'primitive' members of outgroup), or with an elongate central groove for retention of the elytra (1; not figured). The apomorphic state was only found in three members of the outgroup.

(A155) : development of pleurites. Pleurites were either present and free or loosely attached to sternites (0, all outgroup except *Megascelis*; Fig. 563), or absent through loss or fusion with other sclerites (1; Figs 564, 567). This character has been used in phylogenetic studies of Curculionoidea (Morimoto 1962, 1976). State (1) occurred in Chlamisini, Clytrini except *Megalostomis*, two Pachybrachini, *Stylosomus* and Platycolaspina except *Atenesus*.

(A156) : structure of apex of sternite VII. The apex was either simple (0, all outgroup except *Pachnephorus*; Fig.), or strongly and coarsely crenulate (1; Fig. 563). The crenulations slot into similar grooves at the ventral apex of the elytra. This feature has been described as a stridulatory organ by Monros (1956a) which seems most unlikely as the teeth are very coarse and the elytra interlock without any evidence of a plectrum. It probably simply serves to hold the elytra in place. State (1) was autapomorphic for Lamprosomatinae.

(A157) : development of keel posterior to lateral lobe of sternite III. Three supposedly discrete states were recognised : keel complete (0; Fig. 563), keel partial (1; Fig. 561), and keel absent (2; Fig. 565). The distinction between absence and partial development of a keel was very slight because the base of the lobe was often angularly continued on the sternite, and several taxa may have been erroneously scored. *D. pilula*, *C. sericeus* and *Cadmus australis* were scored unknown. This character is also correlated with the keeling of sternites IV-VII (A145). All of the outgroup (except *Megascelis*) showed a more or less complete keel. State (0) was present in only Lamprosomatinae, five Platycolaspina and Coenobiina, but states (1) and (2) were scattered.

(A202) : development of egg-hollow in sternite VII of female. The size of this hollow was variable and difficult to categorise. The character was presumed to show a progression from flat and simple sternite VII (0, all outgroup; Fig. 563), to shallowly or deeply depressed (1; Figs 151, 153, 563), to broadly and usually deeply impressed and at least indenting the posterior margin of sternite 6 (2; Figs 152, 573). The outgroup had simple sternites. Distribution of states : (0) *Lamprosoma*, *Oomorphus*, ; (2) *Griburius*, Coenobiina, most Ditropidina, most Australian Cryptocephalina.

6.4.11 Male genitalia, A158-169

Males were not available for *Lamprosoma*, *Oomorphus*, *Babia*, *Ischiopachys*, *Smaragdina*, *Griburius*, *Ambrotodes*, *Isnus*, *Diachus*, *Ditropidus suffriani*, *D. saundersi* and *C. coryli*. In at least two species, *Oomorphus concolor* and *Diachus auratus* (Reid 1988), there is indirect evidence to suggest that populations may be parthenogenic.

(A158) : length of ejaculatory duct. In general the ejaculatory duct was either very long (1) or very short and the discrimination point was arbitrarily determined to be five coils. The outgroup taxa had short ducts (0; Figs 855-856), except *Chrysochus*. *Atenesus*, *M. glochidionis*, *A. gravatus* and *Cadmus pacificus* were indeterminate. State (1) was sparsely scattered throughout the taxon set.

(A159) : structure of ejaculatory duct. The duct was either normal, thin and translucent (0, all outgroup; Fig. 662), or greatly thickened, sclerotised and opaque (1; Figs 642-644). State (1) was autapomorphic for Coenobiina.

(A160) : development of sperm pump in ejaculatory duct. The normal ejaculatory duct consists of two sections which may be separated by a slight sclerotised swelling (not figured) which may have some function in a pump mechanism. The identification of this feature was difficult because of preparation and size problems and it was therefore discarded from the analyses.

(A161) : structure of base of tegmen. The tegmen of the outgroup was flat and simple at the base and this was presumed to be the plesiomorphic state (0; Fig. 577). The base of the tegmen was keeled (1; Fig. 585), or keeled and bilobed (2; Fig. 586), in the derived states. Distribution of states : (1) Lamprosomatinae, Chlamisini, *Stegnocephala*, *D.*

variabilis, *C. ferrugineus*; (2) Clytrini, Pachybrachini, four Platycolaspina, 11 Ditropidina and all Cryptocephalina except *Stegnocephala*, *M. glochidionis* and *C. ferrugineus*.

(A162) : shape of tegmen. Four states were recognised in some kind of progression from broadly expanded with narrow arms (0; Figs 579, 582), to broadly expanded with expanded arms (1; Fig. 620), to V-shaped (2; Fig. 588), to Y-shaped (3; Fig. 585). 'Broadly expanded' refers to a basic V-shape with the sides convexly bulging. Three states, including both extremes, were present in the outgroup therefore no plesiomorphic state was designated. The states were generally mixed among the taxa, but states (2) and (3) predominated.

(A163) : development of ejaculatory guide. Because of difficulties in determining limits of folds and other aspects of shape only two stages of its development were recognised, either 'normally' convoluted (1; Figs 586, 603, 604, 607, 608, 613, 617, 624, 630, 645, 647, 659, 668, 674, 683, 690, 692), or distally reduced to a long narrow stiletto (2; Figs 599, 638, 655, 656). This structure was absent from the outgroup (0). Distribution of states : (0) *Syneta*, Lamprosomatinae; (2) two Clytrini, *Stylosomus*, five Platycolaspina, *Stegnocephala*, six Ditropidina, *Melixanthus*, two Australian Cryptocephalina; (1) remaining taxa. It is quite clear from the illustrations that the state 'normally convoluted' includes a great diversity of forms.

(A164) : remnant of tergite IX in male. A pair of sclerotised lateral struts were either present (0, 'primitive' members of outgroup; not figured) or absent (1). State (0) was confined to *Syneta* and Chlamisini.

(A165) : shape of apex of penis. The shape of the apex has been used in the diagnosis of chlamisine genera (Karren 1972). The shape of the aedeagus is diverse in Cryptocephalini, but all variability was reduced to a choice of either centrally pointed (0; all outgroup except *Edusella*), or truncate (1; Figs 879, 883), as used by Karren. State (1) was confined to Lamprosomatinae, Chlamisini and *Ditropidella* sp. 5.

(A166 -169) : development and position of setae on aedeagus. A166 was presence (1; Figs 154-160, 584) or absence (0; Fig. 578) of setae. Apical aedeagal setae are thought to be characteristic of the Camptosomata and were absent from all outgroup taxa. Of those taxa with setae the plesiomorphic state was assumed to be setae on both dorsal and ventral faces (Figs 154-158) and the apomorphies the loss of setae from each of these faces. Therefore in A167 (dorsum) and A168 (venter) the absence of setae was scored as state (1). An attempt to delimit sizes of dorsal setae (A169) was abandoned because the states were not discrete, and this character was not used in analyses. Distribution of states : A166 (0) was limited to *Syneta*; *C. mammillatus* and *A. pauperculus*; A167 (1; Figs 159-160, 590) was scattered except absent in Platycolaspina and in Ditropidina except *Adiscus*, present in all Cryptocephalina except *Stegnocephala*; A168 (1; Figs 674, 678) was confined to the taxa completely lacking setae, *C. mammillatus* and *A. pauperculus*.

6.4.12 Female genitalia, A170-177, 179-184, 216, 217, 223, 224

(A170) : development of female sternite VIII. Sternite VIII showed a reduction sequence from fully developed with a spiculum gastrale (0, all outgroup; Figs 702, 707), to minus spiculum but still sclerotised and setose (1; Figs 709, 715, 717), to extreme reduction, becoming membranous and non-setose or absent (2; Figs 732, 734). Distribution of states : (0) absent from ingroup; (1) *Syneta*, Lamprosomatinae, *Megalostomis*.

(A171) : structure of ovipositor. The ovipositor was either of open construction, the sclerites having little relative longitudinal movement (0, including 'primitive' members of outgroup; Figs 701-705, 715-718), or cylindrical, the sclerites capable of being telescoped (1; Figs 706-714). The apomorphic state was absent from the ingroup, including *Syneta*.

(A172) : development of vaginal palp. Three states were recognised, which chart the progressive fusion of the stylus to the coxite + valvifer : stylus freely articulated (0; Figs

701, 706, 710); stylus discernible but basally fused (1; Fig. 717); stylus not visible (2; Figs 715, 718). All outgroup members showed state (0). State (0) was absent from the ingroup and (1) was confined to Lamprosomatinae.

(A173) : internal sclerotisation of bursa copulatrix. The bursa copulatrix was either with (1; Fig. 749), or without (0), a pair of sclerites at the base of the spermathecal duct. The variable sclerotisation of the bursa copulatrix has been used in discrimination of galerucine genera (Silfverberg 1976). Only one taxon, *Pachybrachis*, was found to have internal sclerites and this, therefore autapomorphic, feature was not used in analyses.

(A174) : structure of spermatheca. The spermatheca was either of the normal receptaculum and gland composition (0, all outgroup; Figs 741-763), or reduced to a large bulbous pump-like structure (1; Figs 764-766). State (1) was autapomorphic for the Coenobiina.

(A175, A176, A216 and **A217)** : shape of spermathecal reservoir (receptaculum). The characters used to circumscribe spermathecal receptacle variability are as follows : A175, receptacle bent, blunt and of uniform width (0; Fig. 741), or bent, falciform (1; Fig. 749); A176 (unordered) appendix at apex of receptacle minute or absent (0; Fig. 753), or extended, hooked (1; Fig. 749), or extended and flattened (2; Figs 783-784); A216, basal pump mechanism simple (0; Fig. 891), or coiled (1; Fig. 892); A217, retinaculum U-shaped as A175 (0; Fig. 782), or irregular in shape, in two parts (1; Figs 781, 786). Spermathecal shape has given some support to the classification of Pacific Alticinae (Samuelson 1973). The four characters recognised represent different modifications of the basic bent, blunt, and curved cylindrical shape present in all the outgroup except *Megascelis* (A175 (1)). Distribution of states : A175 (0) was sparsely scattered throughout the taxon set; A176 (1) *C. aterrimus*, *Ischiopachys*, two Ditropidina; A176 (2) *C. brunnipes*, *Cryptocephalus incertus*; A216 (1) *Oomorphus*, *C. mimosae*; A217 (1) *Diachus*, *M. glochidionis*. The derived states of these characters are mostly single species autapomorphies.

(**A177** and **A179**) : modifications of the spermathecal duct. The spermathecal duct was simple or the base or apex was thickened or sclerotised in different ways. For unordered A177 the apex was simple (0; Figs 741-744), swollen at contact with the spermatheca (1; not figured), or with a bulbous appendage (2; Figs 745, 792). For unordered A179 the base was simple (0; Fig. 749), or swollen, but unthickened (1; Figs 746, 767), or was dark and thickened with sclerotisation (2; Fig. 785). The apex was simple in all outgroup taxa except *Edusella*, but all three states of A179 were present in the outgroup and no clear plesiomorphic state could be discerned. Distribution of states : A177 (1) absent from ingroup; A177 (2) *Lychnophaes*, *B. ferrugineus*; A179 states (1) and (2) were sparsely scattered amongst the taxon set.

(**A178**) : length of spermathecal duct. The duct was almost always either very short (all outgroup except *Pachnephorus*) or very long, expressed as either <5 times length of spermatheca (0; Fig. 749), or much longer and convoluted or coiled (1; Fig. 746). State (1) was thinly scattered throughout the data set.

(**A180**) : presence of setae on internal apex of female tergite 8. In the outgroup taxa the apex was simple but in the apomorphic state (1; not figured) the apex was setose internally with few to many, dense, setae. Eight taxa were not scored because it was not clear whether the setae were apical or internal. State (1) was rather scattered but absent from all Holarctic Cryptocephalina and present in all Australasian Cryptocephalina except *Melatia*.

(**A224**) : shape of basal hemisternite (= vaginal palp). The various shapes of the hemisternite when viewed ventrally are here reduced to a choice of either broad, quadrate to transverse (0; Figs 715-739), or elongate (1; all outgroup, Figs 701, 706, 710). This character was introduced to characterise the outgroup taxa, which have long ovipositors, and the apomorphic state was absent from all ingroup taxa. It would be more sensible from outgroup theory to have reversed the polarities, although the score of a binary character is immaterial to the PAUP analysis.

(A181) : shape of outline of outer face of basal hemisternite (taxa without distinct vaginal styli). Four sequential states of shape were recognised, from evenly convex (0; Fig. 731), to straight or slightly concave (1; Fig. 724), to strongly concave (2; Fig. 740), to lobate (3; Fig. 739). Lobate refers to deep convexity plus narrowing of the internal apex, but in practice states (2) and (3) were not discrete. As the feature was absent from the outgroup it was not possible to assign an a priori plesiomorphic state. Distribution of states : (1) *Semelvillea acaciae*, *A.* sp. Tonga, three Ditropidina; (2) *Lexiphanes*; (3) *Syneta*, *Stegnocephala*; plus all four states were shown by Australian Cryptocephalina.

(A182) : shape of base of inner face of basal hemisternite. Three possibly sequential states were recognised from curved (0; Fig. 724), to quadrangular (1; Fig. 729), to presence of a basal projection (2; Fig. 739). The transformation was not clear-cut so this state was kept unordered. This character was not scored in the outgroup. Distribution of states : (1) *Syneta*, Coenobiina, *Adiscus*, *Lexiphanes*, *A. bihamatus*, *Stegnocephala*; (2) most Australasian Cryptocephalina.

(A183) : sclerotisation of outer face of basal hemisternite. The hemisternite either had complete sclerotisation along its outer margin (0; Fig. 731), or was transparent to the edge (1; Fig. 730). The character was absent from the outgroup. State (1) occurred in most taxa including all Cryptocephalina.

(A184) : shape of apex of female tergite 8. Three states are distinguished here in series, from simply convex (0), to shallowly indented (1), to deeply excised (2; Fig. 153). The outgroup showed state (0), except *Chrysochus*. States (1) and (2) were scattered throughout the taxon set.

(A223) : presence of a pair of large accessory vaginal glands. Either present (all outgroup), or absent. All members of the outgroup have a pair of bifurcate glands which open into the sides of the vulva and extend internally beyond the base of the ovipositor (1; Figs 701, 706, 710). Absence of these glands was scored (0). It would be more sensible from outgroup theory to have reversed the polarities, although the score of a binary character is immaterial to the PAUP analysis. State (1) was confined to *Syneta.*

6.4.13 Female rectum, A185-190, 192-201, 218, 219

The 18 characters described below for the female rectum are all part of the complex organ, termed kotpresse (Erber 1968), which manufactures the scatoshell of the egg. In determining the limits of the characters and their polarities it has been assumed that the overall trend is towards complexity, each part being evolved (and lost) independently rather than the whole complex appearing dramatically *in toto*.

(A185) : presence of a kotpresse. If some part of that organ was present, at least the chitinpolster, then the kotpresse was scored as present. Only *Spilopyra* had any sign of the kotpresse (chitinpolster only; Figs 701-705) in the outgroup, but because of its universal occurrence in the ingroup, including *Syneta,* possession of the kotpresse was considered the plesiomorphic state (0). Absence of the kotpresse was therefore state (1) (not figured). State (1) was absent from the ingroup.

(A186 and **A218)** : development of dorsal longitudinal fold on rectum. A186 was the presence (1; Figs 808, 819) or absence (0, all outgroup; Fig. 812) of a dorsal longitudinal fold along the rectum. A218 recognised two states for the dorsal fold : either full length of rectum (1; Fig. 819), or terminating halfway in a pouch (0; Fig. 808). This character is clearly closely connected to the development of the dorsal transverse sclerite (A197). Distribution of states : A186 (0) *Syneta,* Clytrini and two Pachybrachini (*Acolastus* and *Mylassa*); A218 (0) Lamprosomatinae and remaining Pachybrachini.

(A187) : development of chitinpolster. Either a complete ring was present (0, *Spilopyra* of outgroup only; Fig. 806), or the dorsal and ventral surfaces were separated by lateral unspiculate strips (1, all other relevent taxa; Figs 807-851). For morphological reasons state (0) was considered plesiomorphic although present only in *Spilopyra.*

(A188 and A189) : distribution of sensilla on venter of rectum. Sensilla were either present (0; Figs 808) or absent in the anterior half (1; Figs 810-811, 818) (A188), and scattered (0; Fig. 808) or confined to an apical band (1; Figs 810-811, 818) in the posterior half (A189). The apomorphic states were determined as theoretical specialisations, although the only outgroup taxon showed state (1) for Character A189. Distribution of states : A188 (0) Lamprosomatinae; A189 (0) *Syneta*, Lamprosomatinae, *S. acaciae*.

(A190) : shape of anterior sensilla on internal dorsal surface of rectum. Each sensillum is a complex of pore plus surrounding sclerotised rim. This rim is usually unidirectionally elongated towards the anus, either as a simple rounded or bluntly pointed extension (0; Figs 806, 808), or as an elongate tooth which has straight or concave sides (1; Figs 809-810). The sensilla were rounded in *Spilopyra*, the only relevent outgroup member. State (1) was scattered but absent from all Australian Cryptocephalina.

(A192) : development of ventral transverse rectal sclerite. Four states were recognised which appeared to follow a logical sequence : absent (0; Figs 807-808); present and whole (1; Fig. 819); present but middle section absent (2; Fig. 811); and present with what appeared to be secondary thickening of the middle of the previous state (3; Fig. 816). The outgroup taxon *Spilopyra* had state (0). Distribution of states : (1) *C. aterrimus*, Platycolaspina, Coenobiina, Ditropidina except *Adiscus*, Holarctic Cryptocephalina except two; (2) *C. mimosae*, Clytrini, *Stylosomus*, *Adiscus*, 10 Australian Cryptocephalina; (3) autapomorphy for three Pachybrachini.

(A193) : width of ventral transverse rectal sclerite relative to rectum. A sequence of three states was proposed, from narrower than rectum (0; Fig. 834), to equal in width (1; Fig. 835), to extending beyond (2; Fig. 829). The character was absent from outgroup taxon *Spilopyra*. Distribution of states : (0) *A. tutuilana*, *Adiscus*, all Australian Cryptocephalina; (2) all Clytrini, Pachybrachini, *Stylosomus*, five Platycolaspina, eight Ditropidina.

(A194) : shape of lateral arms of ventral plate (if A193 state (2)). The two states, square (0; Fig. 830) or expanded (1; Fig. 812), were not very distinct although the expanded arms of state (1) typically had a ribbed appearance, like a clam. The character was absent from *Spilopyra*. Six taxa were not scored because of indeterminate shape. State (0) was found in *Platycolaspis* and four Ditropidina and (1) in those remaining taxa showing A193 (2).

(A195) : development of dorsal transverse rectal sclerite. This sclerite was either present, if only partially (1; Figs 810, 812, 819, 821), or absent (0; *Spilopyra*; Figs 806-809). State (0) was restricted to *Syneta*, Lamprosomatinae, *C. mimosae* and two Australian Cryptocephalina.

(A196) : presence of lateral arms on dorsal rectal sclerite. Lateral arms, extending beyond the sides of the rectum, were present (1; Fig. 812) or absent (0; Fig. 818). This character was absent from *Spilopyra*. State (1) was scattered in the taxon set, but absent from Pachybrachini and all Cryptocephalina except *Diachus*.

(A197) : structure of dorsal rectal sclerite. Three states are defined as a possible logical sequence: sclerite separated into three sections with unsclerotised gaps between (0; Fig. 812); sclerite whole (1; Fig. 817); sclerite separated into two pieces with unsclerotised gap between (2; Fig. 818). The extreme states can only be linked by the intermediate condition of a complete dorsal sclerite, if it is assumed that the separate central plate is a fragment of the whole dorsal sclerite and not independently derived from state (2) with a wider gap. A197 was absent from outgroup. Distribution of states : (0) Clytrini, *Acolastus*; (1) *Mylassa*; (2) all remaining taxa with dorsal sclerites.

(A198) : development of lateral sclerites. This character is the presence (1; Figs 818-819), or absence (0; Figs 806-811), of lateral sclerites in any position. These may have been little more than a slight thickening of the lateral margins but were always visible as a brown or black strip at the edge of the gap between the dorsal and ventral chitinpolster. Lateral sclerites were absent from the outgroup. State (0) was found in *Syneta*, Lamprosomatinae, Chlamisini, Clytrini (except *Ischiopachys*) and *A. tutuilana*.

(**A199**) : position of lateral sclerites. The states are considered to represent a sequence from anterior of rectum only (0; Fig. 818), to both anterior and posterior (1; Fig. 819), to posterior only (2; Fig. 833). The character was absent from outgroup. States (1) and (2) were scattered.

(**A200** and **A219**) : sculpture of internal surface of posterior half of rectal venter. For both characters the plesiomorphic state is with simple walls (0; Figs 810-811) and the apomorphic state is finely and closely ridged (A200; Figs 806, 816, 818, 840, 846, 847) or shallowly pitted (A219; Fig. 808). *Spilopyra* had a finely grooved rectum. Distribution of states : A200 (1) three Pachybrachini, *D. suffriani*, three Holarctic Cryptocephalina; A219 (1) *Lamprosoma*, *Lychnophaes*, *Ischiopachys*.

(**A201**) : structure of dorsal transverse rectal sclerite. If present, the dorsal sclerite is usually simply transverse (0; Fig. 820), but in a few taxa there is an oblique posteriorly-directed sclerotised extension (1; Figs 821-821, 831, 843, 844). This extension is irregular in shape and may not be homologous in all taxa. The character is absent from the outgroup. State (1) was confined to *Arnomus*, *Semelvillea*, *Coenobius*, four Holarctic Cryptocephalina and *A.* sp. 1049.

In the above list it should be noted that A191 was ignored because of scoring errors. However there is a 191st character, albeit meaningless, in the data matrix.

6.4.14 Summary of characters not contributing to the structure of the ingroup

The following 16 character states were found to be autapomorphic for single species in the data set ingroup : A12(1) = *Scaphodius*; A39(0) = *Edusella*; A46(2) = *A.* [*Dandichus*] *analis*; A61(1) = *Acolastus*; A63 (1) = *M. glochidionis*; A78(1) = *Diachus*; A80 (0) = *S. nothofagi*; A108(1) = *Scaphodius*; A115(2) = *Platycolaspis*; A116(1) = *Diachus*; A124(2) = *Syneta*; A125(1) = *Lamprosoma*; A131(1) = *C. mimosae*; A147(1) = *C. brunnipes*; A173(1) = *Pachybrachis*; A209(2) = *Megalostomis*. These characters were not deleted from the PAUP analyses because their presence or absence would have no effect on phylogenies, although their presence improves the consistency indices.

Several characters were discounted because of scoring problems : A8, 11, 13, 44, 101, 103, 105, 128, 136, 160, 169, 191, 208, 228. These characters were deleted from all analyses.

Finally, a few characters were autapomorphic in the outgroup only : A56, 81, 123, 171, 185, 224, 227. These characters had been deliberately included to ensure monophyly of the morphologically diverse outgroup.

6.5 Analyses

Originally I worked from a matrix of 206 adult characters by 92 taxa. This data set was analysed by PAUP which forced midpoint rooting on the phylogenetic trees, suggesting that the ingroup was not monophyletic. Non-monophyly of the ingroup was contrary to all external evidence, therefore the data set was examined for problem characters and taxa. It was found that the combination of shared extreme specializations and numerous plesiomorphies in all Lamprosomatinae and *Pachnephorus* (Eumolpinae) was causing the ingroup division. For example the Lamprosomatinae and *Pachnephorus* shared ventral prosternal antennal grooves (A68) and pygidial crenulations (A156). The data set lacked synapomorphic characters for the Eumolpinae which would show quite clearly that the specializations were convergent. Some of the 206 characters were split, new ones added and four new species introduced, resulting in a data set with 228 characters (as listed above) for 96 taxa (Appendix 2).

This data set of 228 characters against 96 taxa was the basis for all subsequent analyses with either PAUP or MACCLADE. However, the first version of the character matrix was changed as a result of discovered typing errors, changes in interpretation and re-examination of the animals. Over 300 changes of state designation were made. The majority of these were reductions in number of character states, but other changes significantly affected the analyses, rendering previous work obsolete. Only analyses based on this improved data set are described here.

6.5.1 Analysis one (AA(i))

The whole adult data set was analysed. The deleted characters included those with scoring problems, the constant A191 and those autapomorphic for single species. The following parameters applied : matrix size 196 characters by 95 taxa; SWAP=ALT; MULPARS; ROOT=OUTGROUP; WEIGHTS; deleted taxa = 1; deleted characters = A8, 11, 12, 13, 35, 38, 41, 44, 62, 63, 64, 77, 78, 88, 96, 101, 103, 105, 108, 128, 131, 133, 136, 147, 157, 160, 164, 169, 173, 191, 208, 228; unordered characters = A9, 14, 18, 19, 24, 70, 83, 92, 94, 142, 162, 176, 177, 179, 182. Outgroup was all Eumolpinae plus *Syneta*. Deletion of the autapomorphic character A168 was overlooked, there were therefore functionally 195 characters.

Five minimum-length trees were found, each 1126.083 long with CI of 0.174. There were no zero length branches but the node leading to *Aporocera aurantiacus* was only 0.5 steps long. The five trees differed by minor changes within the Australian Cryptocephalina clade. The trees are summarised in Fig. 929.

The hypothetical phylogeny proposed by this analysis is a curious mixture of fact and phantasy. Many groups of lower rank which would be intuitively considered monophyletic were resolved as such : Lamprosomatinae, with monophyly of New World species; Clytrini, with separation of Old World and New World species (Fig. 931); *Atenesus* and *Leasia* with the questionable association of *Stylosomus*; *Arnomus* and *Semelvillea* (Fig. 931); all Australian Cryptocephalina except *Diandichus* (Figs 934-935); Pachybrachini (Fig. 930); Australasian Ditropidina except *Adiscus* (Fig. 933); Coenobiina, with separation of African and Australasian species (Fig. 932). Conversely the association of these groups into higher rank categories makes little sense, and *Cryptocephalus* is made serially paraphyletic (Fig. 929).

6.5.2 Analysis two (AA(ii))

This analysis by PAUP was of a reduced set of 47 taxa for which larval data were available (except that *Griburius* and *Stegnocephala* were included). The corresponding larval analysis (of 46 taxa) is AL(i) and analysis of the larval and adult combination is described under ALA(i-iii). The basic data matrix was as in AA(viii).

The following parameters applied : matrix size 196 characters by 47 species; SWAP=ALT; MULPARS; ROOT=OUTGROUP; WEIGHTS; deleted taxa 1-5, 7, 9, 10, 13, 15-9, 22, 23, 25-7, 36, 38-44, 47-9, 52, 55, 56, 58-63, 65, 66, 69, 73, 76, 78, 81, 83, 86, 92, 94; deleted characters as in AA(i); unordered characters as AA(i). Outgroup was (*Edusella* + *Syneta*). The autapomorphic A168 was overlooked so that there were functionally 195 characters.

Three minimum-length trees were found, each 630.417 steps long with CI of 0.297. There were no zero length branches. The trees differed in minor changes in the arrangement of Australian Cryptocephalina and Ditropidina. A condensed tree is given in Fig. 936 and the clades for Ditropidina and Australian Cryptocephalina are shown in Figs 937-938.

This tree was one of the least believable of all trees produced by PAUP in these analyses because Platycolaspina and Cryptocephalina were rendered polyphyletic and Pachybrachini, Chlamisini and Lamprosomatinae were reduced to small subgroups within the Cryptocephalini (Fig. 936). Nevertheless, the Australian Cryptocephalina except *Diandichus* and Ditropidina were both resolved monophyletically (Figs 937-938).

6.5.3 Analysis three (AA(iii))

Studies AA(iii-iv) were made on considerably reduced data sets, using the program MACCLADE. The adult and larval data matrices used in PAUP were carefully examined for those characters which defined the robust clades formed in PAUP analyses. In general these clades were also historically well defined. In some characters the number of states was reduced to simplify analysis or remove autapomorphies for single species.

A study was made of higher taxon relationships, based on 16 species and 47 characters, including members of the Eumolpinae, Megascelini, Synetinae, Lamprosomatinae, Chlamisini, Clytrini and Pachybrachini. All three species of Lamprosomatinae were included as one taxon. The characters used were : A7 (reduced to 3 states); 10, 20, 22 (reduced to 2 states), 43, 53, 56, 58, 71, 74, 80 (reduced to 3 states), 81, 85, 98, 100, 101, 102 (reduced to 2 states), 112, 118, 123, 129, 130, 134, 138, 141, 145, 146, 152, 156, 161, 163, 164, 166, 170, 171, 172, 185, 186, 188, 189, 192, 202, 222, 223, 224, 227, 228. Some of these were poorly defined for the overall adult data set but well defined for this selection. The following autapomorphic characters for Lamprosomatinae were retained in the matrix : A112, 134 and 152.

The following parameters applied : data matrix 14 taxa by 47 characters; ordered characters A7, 20, 74, 80, 161; irreversible characters A100, 129, 130, 138, 141, 146, 164, 170, 172; Dollo characters 123, 163, 166, 223; equal weights.

The minimum-length tree found (Fig. 939) was 119 steps long , with CI of 0.51. A tree 120 steps long with the same CI gave a more sensible arrangement of the outgroup by making all Eumolpinae a single clade. In either case the Megascelini were placed unequivocally in the outgroup Eumolpinae and the Synetinae were either sister group to all Eumolpinae or to all Camptosomata. These trees of 119 and 120 steps gave traditional arrangements of the Camptosomatan higher taxa, viz : Lamprosomatinae + (Chlamisini + (Clytrini + remainder[=Pachybrachini])). Placement of Chlamisini as sister group to Pachybrachini (ie. switching the positions of Clytrini and Chlamisini) gave a tree of 121 steps.

6.5.4 Analysis four (AA(iv))

A broader range of taxa than AA(iii) was included, to study possible tribal arrangements within Camptosomata. Furthermore the character set was refined to exclude those of dubious validity (e.g. A228). The characters were selected with the same approach as in AA(iii). The following adult characters were used : A1, 7, 20 (reduced to 2 states, with or without pits), 22, 31, 49, 53, 58, 66, 68, 71, 73, 74, 85, 86, 92 (reduced to three states, 0-2 lumped), 95, 98, 99, 100, 109, 117, 121, 122, 129, 130, 138, 139, 141, 145, 146, 161, 163, 167, 168, 172, 183, 186, 189, 192, 195, 197, 198, 203, 208, 214, 218, 226. This analysis is directly comparable with AL(ii) and ALA(iv) because it used the same taxon set.

The following parameters applied : matrix size 48 characters by 23 taxa; ordered characters A7, 22, 49, 74, 86, 163, 192, 197; irreversible characters A100, 109, 117, 121, 122, 129, 130, 138, 141, 146, 172, 203; Dollo character A195; weights equal.

Eight minimum-length trees were found, each 188 steps long, with CI of 0.33. These trees differ only in the relative positions of the members of the Ditropidina (all combinations of the three terminal taxa are equal) and in relative position of *Leasia.* A strict consensus tree is given in Fig. 940. The selection of characters and taxa makes Lamprosomatinae and *Edusella* sister groups, with *Syneta* in the ingroup. If this pattern is altered to the preferred arrangement of (*Edusella* + *Syneta*) as the outgroup, with Lamprosomatinae sister to the Cryptocephalinae (eight trees with 192 steps, CI of 0.32), the Cryptocephalinae clades are identical to those in the 188 step trees.

These eight modified trees can be summarised as : Lamprosomatinae + (Pachybrachini + (Clytrini + (Chlamisini + (Stylosomina + (((Ditropidina + (Coenobiina + *Lexiphanes*)) + (Platycolaspina + (*A.* [*Diandichus*] + (*Cryptocephalus* + Australian Cryptocephalina)))))))). The eight equal length trees were due to the four Ditropidina taxa swapping positions with each other and *Leasia* being either sister to *Atenesus* or *Platycolaspis*. One combination is illustrated in Fig. 941. In this phylogeny the Australian Cryptocephalina were paraphyletic. Creation of monophyletic Australian Cryptocephalina by moving *Diandichus* led to a tree with 189 (193 if *Syneta* rearranged) steps. Making *Lexiphanes* sister to Ditropidina and Coenobiina also gave a tree of 189 steps. However there were several other tree topologies with 189 steps including : at least one which differs from the shortest by *Stylosomus* being sister to only (Platycolaspina + (*Cryptocephalus* + Australian Cryptocephalina)); at least one in which the arrangement of Cryptocephalini is : *Lexiphanes* + (other Cryptocephalina + (*Aprionota* + (Ditropidina + (Platycolaspina including *Stylosomus*)))); at least one similar to the last but with *Lexiphanes* and 'other Cryptocephalina' swapped over. Evidently there are many trees only one or two steps longer than the shortest and the arrangement of Cryptocephalini taxa is fairly plastic.

6.5.5 Summary of the phylogenetic analyses for adults

6.5.5.1 PAUP analyses AA(i)-(ii)

The following discussion is based on these two analyses only because they were based on the corrected data set. Overall the two phylogenies are strikingly different but they include a few common elements. In both, Ditropidina, Coenobiina + South American Cryptocephalina and *Arnomus* + *Semelvillea* are monophyletic units and Platycolaspina and Australian Cryptocephalina are not monophyletic.

Other interesting associations in AA(i) include: the basal phylogeny Lamprosomatinae + (Chlamisini + (others)); *Mylassa* as sister taxon to the remaining Pachybrachini; Platycolaspina as a paraphyletic outgroup to Clytrini in which the Old and New World taxa are sister groups; African and west Pacific Coenobiina as sister taxa; isolation of *Melatia glochidionis* and *M. solomonensis* as a monophyletic unit; paraphyly of both *Cryptocephalus* and Australian Cryptocephalina.

6.5.5.2 MACCLADE analyses AA(iii)-(iv)

Only partial comparison is possible because of the limited number of taxa in AA(iii). The two phylogenies differ in two ways : (i) *Syneta* is either sister to all Camptosomata (AA(iii)) or to Cryptocephalinae only; (ii) Chlamisini are either sister to all remaining Cryptocephalinae (AA(iii)) or to Cryptocephalini only (AA(iv)).

6.6 Discussion

The adult characters discriminate lower taxa than the larval characters (there are more species in the adult analyses but fewer equally parsimonious minimum-length trees per analysis), but there are many more adult characters. In adults, character-complexes providing synapomorphies are found throughout the body, in contrast to larvae in which synapomorphies were provided by few areas of the body. Higher resolution of taxa by adult characters is helped by less correlation between characters. Nevertheless, the large set of adult characters used in PAUP (AA(i)) did not resolve the adult taxa into the traditional classification. This was probably due to the high level of homoplasy in many adult characters which were known to be weak, such as dorsal vestiture, and the use of many characters with graded states (more obviously so in the large PAUP data set) which may have been discriminating taxa according to artificial cut-off points.

The characters generally function in the classification in one of three ways : they define major clades (subfamilies, tribes), or minor terminal branches (species-groups), or their states are scattered and relatively uninformative for phylogeny (homoplasies). Synapomorphies for groups of subtribes or groups of genera were relatively uncommon.

Numerical analysis of the adult characters provided a classification of the taxa that I consider unsatisfactory, and an alternative classification is proposed in Chapter 8. The contribution of adult characters to the phylogeny of Camptosomata is discussed further in chapters 7 and 8.

Chapter 7 Numerical analyses of combined life-stage data.

This chapter makes use of the egg, larval, pupal and adult data, described in Chapters **3-6**, in various combinations to give possible phylogenies based on more than one life-stage. The taxa studied represent a subset of each of those studied as larvae and adults because the two sets of taxa did not exactly correspond (for some taxa there were larvae but adult data were not used although available, and for many taxa there were adults but no available larvae). Most of the following analyses only used larval and adult data because I wanted direct comparisons of larval and adult character information and because scatoshells were generally uninformative and pupae were not available.

It was assumed that all morphological attributes of all life-stages were inherited and that the attributes of one stage were not correlated with those of the next. Therefore, a phylogeny based on the most parsimonious resolution of all these morphologically independent data sets would be more plausible than a phylogeny based on one life-stage. The analyses described in this chapter were undertaken to find the most parsimonious resolution of large combined life-stage data sets and then to study in more detail the implications of these resolutions for different ranks of taxa.

This chapter describes these analyses and their results are compared with the equivalent analyses of adult or larval data. The results are either rejected or incorporated in the phylogenies proposed in Chapter **8**.

7.1 Methods.

Combined life-stage data (ALA) was analysed in three ways. Firstly, all adult and all larval characters were simply added together to give large matrices with the individual larval (AL) and adult (AA) analyses as subsets. These combined analyses used PAUP which gave single minimum-length trees. It was hoped that the PAUP analyses would suggest, by parsimony, clades of taxa which would be further studied in the next two processes. PAUP analyses ALA(i-ii) were based on the data sets used in AL(i) and AA(ii).

Secondly, characters selected to minimise homoplasy were combined with a reduced taxon set in which terminal taxa represented suprageneric groups recognised by PAUP. The characters for these analyses were selected because they appeared to support the monophyly of clades suggested by PAUP or by general observation. Larval and adult analyses using this taxon set with MACCLADE have been described in Chapters 4 and 6. Analysis ALA(iii) was based on a combination of AL(ii), AA(iv) and egg and pupal characters, using MACCLADE.

Thirdly, character and taxon sets were selected from all life-stage data to elucidate probable relationships of taxa in the three dominant subtribes of Cryptocephalini in Australia : Platycolaspina, Ditropidina and Cryptocephalina. MACCLADE analyses ALA(iv-vi) were used to resolve intergeneric relationships in the monophyletic groups Platycolaspina, Ditropidina and Australian Cryptocephalina respectively.

7.2 Analyses of data : parameters and results

7.2.1 Analysis one (ALA(i))

Study ALA(i) was a combination of the data sets used in AL(i) and AA(ii).

The following parameters applied : matrix size 276 characters by 46 species; SWAP=ALT; MULPARS; ROOT=OUTGROUP; WEIGHTS; deleted taxa 7, 26; deleted characters 8, 11, 12, 13, 35, 38, 41, 44, 62, 63, 64, 77, 78, 88, 96, 101, 103, 105, 108, 128, 131, 133, 136, 147, 157, 160, 164, 169, 173, 191, 208, 228, 302, 309-316; unordered characters 9, 14, 18, 19, 24, 70, 83, 92, 94, 142, 162, 176, 177, 179, 182, 230, 244, 264, 265, 267, 303. Outgroup was (*Edusella* + *Syneta*). As in AA(ii) character A168 was autapomorphic therefore there were functionally only 275 characters.

One minimum-length tree was found (Fig. 942) : 903.5 steps long with CI of 0.296. This tree had the form : Lamprosomatinae + (Chlamisini + ((*Stylosomus* + (Clytrini + Platycolaspina [paraphyletic])) + (Ditropidina + ((*Lexiphanes* + *Aprionota*) + (*Cryptocephalus* + (*Pachybrachis* + (Australian Cryptocephalina))))))). In this case *Cryptocephalus* was monophyletic and *Ditropidus* [*Prasonotus*] *submetallicus* and

Aporocera (*Diandichus*) were the two most basal groups of Ditropidina and Australian Cryptocephalina respectively.

7.2.2 Analysis two (ALA(ii))

This study used the same data set as ALA(i) but the scores for character A49 were changed for *Aprionota* (from 1 to 2) and *Atenesus* (from 0 to 2). Hitherto the pronotal border had been scored as untoothed because this was what was visible with stereo-microscopy. It was known from SEM that faint crenulations were present (Figs 121-122) so these character scores were changed accordingly. Scores for the remaining characters describing hind margin teeth (A50-52, 211) were kept as unknown because of the extremely slight nature of the crenulations.

One minimum-length tree was found (Fig. 943) : 906.0 steps long with CI of 0.295. There were no zero length branches. This tree had the following form : Lamprosomatinae + (Chlamisini + (((Ditropidina + (*Cryptocephalus* + (*Lexiphanes* + *Aprionota*))) + ((Clytrini + Platycolaspina [including *Stylosomus*])) + (Pachybrachini + Australian Cryptocephalina)))). The clades for Ditropidina and Australian Cryptocephalina are illustrated in Figs 944 and 945 respectively. The minimum-length tree was 2.5 steps shorter than the directly comparable minimum-length tree of ALA(i). The sister taxa to *Atenesus* and *Aprionota* remained unchanged from ALA(i), but the change in the one adult character of these two genera made considerable changes to the positions of the groups of genera. Platycolaspina and *Leasia* species were paraphyletic and *Aporocera* (*Diandichus*) and *D. submetallicus* were basal groups. *Cryptocephalus* and Australian Cryptocephalina were resolved as monophyletic groups.

7.2.3 Analysis three (ALA(iii))

In this study the larval and adult data sets used for MACCLADE analyses AL(ii) and AA(iv) were combined and analysed with the same program. The discussions under analyses AL(ii) and AA(iv) give the rationale behind choice of taxa and characters and list the 24 larval and 48 adult characters chosen. Four further characters were chosen from the egg and pupal character lists : E1, E2, P11, P13. The data matrix was therefore 76 characters by 23 taxa.

Two minimum-length trees were found, each of 299 steps and CI of 0.36. These trees included Lamprosomatinae with Eumolpinae, as in the adult analysis AA(xi). When 'corrected' to give a monophyletic Camptosomata (Fig. 946) they were 302 steps long with the same CI. The two trees differed in the position of *A.(Diandichus)* relative to *Cryptocephalus* and Australian Cryptocephalina. These trees can be summarised as : Lamprosomatinae + (Pachybrachini + (Clytrini + (Chlamisini + (Coenobiina + (*Lexiphanes* + (Ditropidina + (*Stylosomus* + (Platycolaspina + (*Cryptocephalus* and Australian Cryptocephalina). In the Ditropidina the most basal taxon is *Ditropidus* sp. 865 and in the Platycolaspina *Platycolaspis* is sister to (*Leasia* + *Atenesus*). In one of the trees (not figured) *A.(Diandichus)* becomes sister to (*Cryptocephalus* + remaining Australian Cryptocephalina).

Two topologies were created, with *Edusella* + *Syneta* as outgroup, which were considered to give possible phylogenies based on assumptions of monophyly of Pachybrachini + Clytrini, Stylosomina + Platycolaspina, Coenobiina + Ditropidina and Cryptocephalina, all four of which assumptions were broken by the minimum-length tree described above (Fig. 946). One topology had Cryptocephalina and Stylosomina + Platycolaspina as sister-groups (Fig. 947) and the other showed Cryptocephalina and Ditropidina + Coenobiina as sister-groups (Fig. 948). These trees were respectively 7 and 10 steps longer than the minumum-length tree for this data set with the same outgroup (Fig. 946). Therefore assumption of monophyly of the four groups was not parsimonious for the data set. My reasons for conserving these monophyletic groups are given Chapter 8.

The internal structure of the clades for Platycolaspina, Ditropidina and Australian Cryptocephalina was examined in the three following analyses.

7.2.4 Analysis four (ALA(iv))

For this analysis it was assumed that the subtribe Platycolaspina was monophyletic. The most parsimonious relationship between the five genera of Platycolaspina was studied with MACCLADE, using a selection of appropriate adult and larval characters with *Stylosomus* as the outgroup. The following characters (with reductions noted) were used : adult : A15, 20 (2 states), 21, 22 (2 states), 42, 49, 53 (2 states), 73, 77, 85, 112, 115, 124, 135, 139, 143, 155, 163, 190, 193, 196, 201, 215; larva : L1, 2, 11 (2 states), 16 (2 states), 18, 25 (2 states), 65, 70 (2 states), 73. The number of states was reduced to simplify analysis or remove autapomorphies for single species. Autapomorphic states for *Stylosomus* in A20, 49 and 135, and for *Atenesus* in A155 were retained. The pronotal hind margin of *Atenesus* was scored as toothed.

The following parameters applied : data matrix 6 taxa by 32 characters; ordered character A73; equal weights.

With *Stylosomus* as outgroup, one minimum-length tree was found (Fig. 949), which was 45 steps long, with CI of 0.73. This separated the five genera of Platycolaspina into two groups : *Platycolaspis* + (*Atenesus* + *Leasia*) and *Semelvillea* + *Arnomus*. If *Platycolaspis* was made the sister taxon of *Semelvillea* + *Arnomus* the tree was three steps longer and if *Platycolaspis* was placed as sister taxon to all remaining Platycolaspina the resultant tree was 51 steps long. Deletion of all the larval characters resulted in the same shortest tree.

7.2.5 Analysis five (ALA(v))

The possible relationships of 14 terminal taxa of Ditropidina were examined with MACCLADE, using a selection of adult and larval characters and taxa, with Coenobiina as the outgroup. In all previous analyses *Adiscus* was the outgroup for all remaining Ditropidina but because scutellar and larval data were lacking for *Adiscus* I used Coenobiina as a supplementary outgroup. Characters were chosen subjectively by avoiding those which varied within most subtribes and those which varied within species groups (for example the *Ditropidella* species pair). The terminal taxa recognised for this study included species groups combined into single taxa as follows : all Coenobiina; two *Ditropidella*; and three species originally placed in *Elaphodes* (*D. aeneolus*, *cervinus* and *pilula*). The following charactes were used : adult : A1; 2 (reduced to 2 states); 3 (2 states); 7, 21 (2 states); 207, 43, 52, 204, 83, 89, 113, 124, 203, 151, 202, 161, 163, 183, 196; larva : L2, 16, 25 (2 states); 30, 31 (2 states), 33, 50, 70. There were no autapomorphic states for single terminal taxa. Larval characters were not available for eight taxa.

The following parameters applied : data matrix 15 taxa by 28 characters; equal weights.

Two minimum-length trees were found (combined in Fig. 950), each of 71 steps and CI of 0.42. The consensus tree showed all the Australian taxa as one monophyletic group with *Ditropidus suffriani* its sister-group, placed all the species of the former genera *Ditropidus* and *Elaphodes* in one clade and placed *D.*[*Elaphodes*] and the pubescent species of *Ditropidus* as one clade. However, there were numerous trees one step longer than this with radically different topologies.

7.2.6 Analysis six (ALA(vi))

Various internal arrangements of taxa of Australian Cryptocephalina were examined with MACCLADE, using a selection of adult and larval characters and taxa and with the combination of *Melixanthus* and *Cryptocephalus* as the outgroup. It was quite obvious that few larval characters varied non-randomly at this level of discrimination, therefore only three were used for this analysis. Adult characters were selected because they appeared to define natural groups but many characters were variably expressed amongst the chosen taxa.

The following terminal taxa were recognised for this analysis, together with their constituent species chosen from the material used in previous analyses (see Appendix A for details) : *Cryptocephalus* (= all Old and New World species), *Melixanthus intermedius*, *Melatia glochidionis*, *M. solomonensis*, *Cadmus* (*Brachycaulus*) (= *C. aterrimus* and *mammillatus*), *Cadmus rugicollis*, *Cadmus* s.str.(= *C. australis*, *C.*

litigiosus, *C. luctuosus*), *Cadmus* (*Cadmoides*) *pacificus*, *Cadmus* (*Lachnabothra*) (= 21 species), *Cadmus* (*Aorocarpon*) [*Brachycaulus*] *posticalis*, *Cadmus* (*A.*)[*Ochrosopsis*] *apicalis* and *Cadmus* (*A.*) *perlatus* as one taxon, *Aporocera* (*Diandichus*) (= *D. analis* and *D.* sp. 435), *Aporocera pauperculus*, *Aporocera* sp. 1049, *Aporocera gravatus*, *Aporocera* [*Cyphodera*] *chlamydiformis*, *Aporocera* [*Cryptocephalus*] *bihamatus*, *Aporocera* species-group [= *Chloroplisma viridis*, *Mitocera viridipennis*, *Cryptocephalus haematodes*, *Cadmus aurantiacus*, *Aporocera analis*, *Chariderma pulchella*, *Ochrosopsis australis*, *O. subfasciatus*, *Rhombosternus jocosus*], *Aporocera* [*Schizosternus*] species-group [=*Schizosternus albogularis*, *Loxopleurus libertinus*, *Idiocephala consors*], and *Aporocera* [*Euphyma*] *flaviventris* and *Aporocera* [*Cryptocephalus*] *jacksoni* combined as one taxon. Each terminal taxon could be justified as a monophyletic unit. The following characters were used : adult : A1, 2, 6, 18 (2 states), 20 (2 states), 45, 46 (2 states), 50, 55, 58, 59 (2 states), 60, 69 (2 states), 71, 72, 76, 85 (2 states), 90, 92, 97, 99 (2 states), 110, 111, 112, 132, 142 (2 states), 148, 180, 182 (2 states), 192 (2 states), 204, 205, 206, 207; larva : L19, 21 (2 states), 34.

The following parameters applied : data matrix 20 taxa by 37 characters; equal weights.

There were five minimum-length trees (one is illustrated in Fig. 951), each of 124 steps and with CI of 0.31. Variation in tree topology was due to the composite taxon *Aporocera* species-group which could be placed in five different positions without altering tree length. A strict consensus of these trees is shown in Fig. 952. This shows that the Australian taxa were resolved as a monophyletic unit with the combination of *Melatia glochidionis* + *M. solomonensis* as the sister-group. *Cadmus* s. str. and its supposed subgenus *Prionopleura* were resolved as one clade, as were all *C.* (*Brachycaulus*) plus *Lachnabothra,* and these two clades were combined as one monophyletic unit.

A topology was created with MACCLADE which had groups of taxa which I felt could possibly be defined as monophyletic using external characters (Fig. 953). This pattern gave a longer tree, of 135 steps (CI = 0.28). A further rearrangement to make both the coarsely ("*Cadmus s. l.*") and non-coarsely ("*Aporocera s. l.*") sculptured Australian species monophyletic resulted in a minimum-length tree of 138 steps (not illustrated). In this latter construct the terminal taxon *Cadmus* s. str. could be placed at the apex of either clade without altering the tree length. Various other combinations of taxa were made which also gave relatively long trees. None of my subjectively derived hypothetical phylogenies were supported by the data set.

7.3 Comparison of proposed phylogenies in ALA(i)-(ii)

Comparison of the phylogenies in ALA(i) and (ii) shows that relatively minor changes to the data set, in this case involving one character of the prothorax and two species, may cause significant changes to the hypothetical phylogenies.

Some constant arrangements suggested by the two analyses ALA(i)-(ii) were : the basal pattern of Lamprosomatinae + (Chlamisini + (others)), non-association of Clytrini and Pachybrachini, monophyly of *Pachybrachis* + Australian Cryptocephalina, monophyly of *Lexiphanes* + *Aprionota*, paraphyly of Platycolaspina but with monophyly of both *Platycolaspis* + (*Arnomus* + *Semelvillea*) and *Atenesus* + paraphyletic *Leasia*, monophyly of Australian Cryptocephalina with *A.*(*Diandichus*) basal, and monophyly of Ditropidina with *D. submetallicus* basal.

7.4 Comparison of ALA(i) and (ii) with corresponding larval and adult phylogenies

This comparison is based upon studies AL(i), AA(ii) and ALA(i) and (ii). Some features were constant to all the analyses : non-association of Clytrini and Pachybrachini; monophyly of each of Ditropidina, *Arnomus* + *Semelvillea*, Australian Cryptocephalina except *Diandichus*; and non-monophyly of Platycolaspina. Platycolaspina were paraphyletic in the combined analyses but polyphyletic in both adult and larval studies. In larval and combined studies, but not adult, the following were constant : the basal pattern of Lamprosomatinae + (Chlamisini + (others)) and monophyly of Australian

Cryptocephalina. In adult and combined studies, but not larval, the following were constant : monophyly of *Cryptocephalus*, and monophyly of *Aprionota* + *Lexiphanes* or *Stegnocephala*. Relationships between monophyletic groups differed considerably in each of the four studies.

7.5 Comparison of ALA(iii) with corresponding larval and adult phylogenies

In the following discussion tree length and CI are given for trees which were arranged to have *Syneta* + *Edusella* as the outgroup. Use of either this outgroup or *Edusella* + Lamprosomatinae did not affect the length of the ingroup trees. The latter outgroup always gave longer larval trees. As in ALA (ii) the corrected scores for character A49 were included for *Aprionota* and *Atenesus*.

There were 32, eight and two minimum-length larval (AL(ii)), adult (AA(iv)) and combined data (ALA(iii)) trees respectively. The topology of each of these adult and larval minimum-length trees was saved, then imposed on the combined data set and the resultant tree lengths noted. When the 32 larval trees were applied to the combined data set the shortest tree was 305 steps long with CI of 0.35 and the shortest of the eight adult trees when applied to the combined data was 304 steps long with CI of 0.36 (Table 2). Therefore the most parsimonious combinations of the taxa using only larval data or only adult data were respectively three or two steps longer than the most parsimonious combination of the taxa using both larval and adult data, which gave two minimum-length trees (ALA(iii)) of 302 steps and CI of 0.36.

Table 2. The relative parsimony, measured in steps, of five topologies (all with outgroup *Edusella* + *Syneta*) matched with larval, adult or combined data sets. The topologies are minimum-length trees for larvae (from AL(ii)), adults (from AA(iv)) and combined stages (ALA(iii)) plus two arrangements of taxa (labelled A and B, see ALA(iii) and Figs 947 and 948 respectively) giving monophyly of the subtribes recognised in Chapter **8**.

Tree	Character set		
	Larva	Adult	Combined
Larva	89	202	305
Adult	99	192	304
Combined	94	195	302
A	98	198	309
B	101	198	312

For the comparison of performance of different topologies with different character sets for one set of taxa, I included minimum-length trees for the larval, adult and combined life-stage data and two extra topologies. The latter represented two possible phylogenies of the taxa as described in Section **7.2.3**. Tree B had the cladistic arrangement of subtribes discussed in Chapter **8** (Fig. 948). Only one of the combined stage minimum-length trees was included, that which had monophyletic Australian Cryptocephalina (Fig. 946). When applied to the adult and larval data sets, the shortest combined data set tree is three steps longer than the shortest adult tree and five steps longer than the shortest larval tree. The adult and larval minimum length trees do not interchange well.

It is evident from Table 2 that, even in a relatively small data set, the use of only larval or adult characters may not provide the most parsimonious approximation to taxon phylogeny. It is also evident that I am 'sticking my neck out' in adopting the 'preferred' tree as a phylogeny for classification purposes. The classification presented in Chapter **9** would certainly not even be remotely countenanced if only minimum-length trees from parsimony analysis were to be considered. Therefore the classification I have adopted below rejects rigorous parsimony.

The four combined data trees (one best fitting larvae, one best fitting adults and two best fitting the combined data) shared the following structures : basal phylogeny of Lamprosomatinae + (Pachybrachini + (other)) and monophyly of the following groups : Cryptocephalini, Ditropidina with *Ditropidus* sp. 865 most basal, *Atenesus* + *Leasia*, *Arnomus* + *Semelvillea* and *C.* (*Brachycaulus*) + *Aporocera*. The positions of *Stylosomus*, Coenobiina, Chlamisini and *Lexiphanes* were variable and effectively ensured that none of the possible tribal and subtribal phylogenies were similar.

7.6 Comparison of minimum-length trees from PAUP analysis ALA(ii) and MACCLADE analysis ALA(iii)

The two data sets used in these analyses differed considerably in number of taxa and characters but included a similar representation of suprageneric taxa. The data matrix used for MACCLADE analysis ALA(v) was a subset of the data matrix for PAUP analysis ALA(iv). In spite of this, the minimum-length trees for the two data sets differed considerably. Some points of agreement included monophyly of : Ditropidina, Australian Cryptocephalina with *A.*(*Diandichus*) most basal, *Leasia* + *Atenesus* and *Arnomus* + *Semelvillea*; and no relationship between Coenobiina and Ditropidina. Otherwise the two potential phylogenies differ considerably, notably in the positions of Pachybrachini and *Cryptocephalus*, the polyphyly of Cryptocephalini and paraphyly of Platycolaspina.

These differences, especially in the internal structure of the Cryptocephalini, probably reflect the differences in reversibility of characters within the two programs (see discussion under **2.4.1**).

7.7 Comparison of subtribal analyses ALA(iv-vi) with other analyses based on larval, adult or combined data

ALA(iv) was the analysis of the combined data set for Platycolaspina, using Stylosomina as outgroup. The same taxa and outgroup were present in both ALA(iii) and ALA(iv) which gave the same arrangement of Platycolaspina. The monophyly of *Platycolaspis*, *Leasia* and *Atenesus* was confirmed and the apparent similarities between *Semelvillea* and *Platycolaspis* rejected as homoplasies. In contrast, anlaysis ALA(ii) made Platycolaspina paraphyletic around *Stylosomus*, but this study included many weak characters.

ALA(v) was the analysis of the combined data set for the subtribe Ditropidina, with Coenobiina as outgroup. In comparing the postulated phylogenies for Ditropidina it should be noted that the number of species in each combined analysis differed : seven species in ALA(iv), four terminal taxa representing five species in ALA(v), and 14 terminal taxa representing 17 species in ALA(vii). Furthermore the sister-groups were different in each analysis : Cryptocephalina, a broad group including Cryptocephalina, and Coenobiina. It was therefore not surprising that each putative phylogeny was also different. The larval analysis AL(i), with seven species, and the adult analysis AA(i) with 17 species, also gave different arrangements of the taxa in common. Analyses ALA(vii) and AA(i) included the same taxa and concurred in having *Adiscus* as sister to all other species. AA(i) failed to make *'Elaphodes'* or *'Ditropidus'* monophyletic. The only consistent element through all analyses was that the Ditropidina were monophyletic.

ALA(vi) was the analysis of the combined data set for the Cryptocephalina, looking particularly at the Australian taxa. Comparison of the minimum-length trees for Australian Cryptocephalina in the various analyses shows lack of consistency in topology, as in the ditropidine analyses. In the combined analyses the numbers of species were : 18 in ALA(iv), three in ALA(v) and 30 reduced to 16 terminal taxa in ALA(viii). Sister-groups were *Cryptocephalus* or *Pachybrachis* (!). There was little correspondence between the arrangements in ALA(iv) and ALA(viii), except that *C.* (*Brachycaulus*) (including *Cadmus* (*Aorocarpon*)[*Brachycaulus*] *posticalis*) +

Lachnabothra s.str. was monophyletic and both *A.(Diandichus)* and *Aporocera* sp. 1049 were relatively basal groups. The monophyletic groups assumed for terminal taxa in ALA(viii) were not supported by ALA(iv). The larval study AL(i) with 18 species (sister-group *Lexiphanes*) and the adult study AA(i) with 26 species (paraphyletic and sister-group *Pachybrachis*) also showed almost no agreement with analysis ALA(viii). The assumptions of monophyly of the terminal species-groups *'Aporocera'*, *'Schizosternus'* and *'Euphyma'* in ALA(viii) were not supported. Monophyly of the Australian Cryptocephalina was not consistent, but was only broken by *Aporocera (Diandichus)*.

7.8 Comparison of use of PAUP and MACCLADE.

It is pertinent to make some comment here on the value of using PAUP and MACCLADE in this study. This discussion may help to explain why the classification presented in Chapter 9 is relatively unresolved and poorly supported by the numerical analyses described above.

7.8.1 Value and limitations of PAUP.

The uses and limitations of PAUP version 2.4 are discussed in its accompanying manual (Swofford 1985). The following comments are made with reference to my own work.

Generally, a great deal of time was spent preparing the matrix for the PAUP program and then analysing it. Some specific problems encountered with the PAUP analyses were as follows : (i) the few *consistent* results were rather obvious or not informative, for example, Lamprosomatinae most basal group, and all tribes of Cryptocephalinae consistently mixed up; (ii) eventually a high degree of subjectivity was involved in appraisal of characters, through reinterpretation and deletion; (iii) the minimum-length tree may be only a small fraction shorter than many other trees, although strict application of the parsimony principle would force one to accept the shortest tree criterion; (iv) the algorithm assumed constant rates of evolution and did not allow either 'fixation of genome' or Dollo's Law: the alternative is to strongly weight individual characters (which may be criticised on grounds of subjectivity); (v) it was not possible to allow characters to evolve in different ways in different clades : for example, some characters were obviously extremely plastic in one clade but had a fixed state in another clade; this would require some kind of differential analysis. Large data sets with a relatively high character to taxon ratio usually have a larger proportion of homoplasious character states and therefore the CI values are reduced. The CI is only useful as a relative value for data sets with similar numbers of characters and taxa. All of the analyses described above had CIs of less than 0.5.

Nevertheless, use of PAUP was helpful. Construction of the data set for analysis gave emphasis to character evolution. Its legacy was a detailed matrix which could be used for non-algebraic analyses and from which subsets of characters and taxa were derived for analysis with MACCLADE. My work with PAUP led to the recognition and analysis of many new character systems in the Camptosomata and Eumolpinae. Character state changes on the cladograms could be detected with the CHANGELIST option and the usefulness of individual characters quantified (with the proviso noted above) by comparison of their CIs.

PAUP is ideal for use with MACCLADE because it suggests robust taxon groups and high consistency characters which can then be further analysed with MACCLADE.

7.8.2 Value and limitations of MACCLADE.

The uses and limitations of MACCLADE version 2.1 are discussed in its accompanying manual (Maddison and Maddison 1987). MACCLADE has little analytic power and does not necessarily find the shortest tree. It is therefore not reliable as a means of finding most parsimonious trees for large data sets.

MACCLADE was ideal for testing combinations of taxa and character combinations suggested by other methods of analysis. The ability to set irreversibility or Dollo's Law on suitable characters (for example wing venation), and the ability to combine character state variation in a single taxon were among its useful assets. It was possible to directly translate the resultant trees into the Macintosh graphics program SUPERPAINT for cosmetic manipulation and laser printing.

7.9 Conclusion.

The comparison of minimum-length trees for larval, adult and combined life-stage data sets (section **7.5**) showed that analysis of the combined data set gave more parsimonious resolution of the taxon relationships than any single life-stage data set. Almost all phylogenies concerned with Chrysomelidae have been derived from adult characters, but it is obvious that these only provide 'half the story'. This study emphasises the importance to phylogenetic work of incorporating as much information from other stages as possible.

In the comparison of the phylogenies in analyses ALA(i) and (ii) (section **7.6.1**) it was shown that a single character state change in two species in a matrix of 46 species and 246 characters caused significant changes to the minimum-length trees. This is true even for a large data set buffered by a high character to taxon ratio, suggesting that caution should be used in deriving phylogenies directly from parsimony analyses. The most important evidence useful for reconstruction of phylogeny is probably the congruence of certain clades of taxa despite variations in character and taxon combinations used in analysis.

In the next chapter the phylogeny of the Camptosomata is discussed in detail. I use information from the analyses described in this and previous chapters, but also assess the contribution of individual characters.

In the beginning Muluku made two holes in the earth, and from one came a man, from the other a woman. God gave them land to cultivate, a pick, an axe, a pot, a plate and millet. He told them to cultivate the ground, to sow it with millet, to build a dwelling, and to cook their food in it. Instead of carrying out Muluku's advice they ate the millet raw, broke the plates, put dirt in the pot, and then went and hid in the wood. Seeing that he had been disobeyed God called up the monkey and the she-monkey, and gave them the same tools and advice. They worked, cooked and ate the millet. And God was well pleased. So he cut off the tails of the monkey and she-monkey, and fastened them to the man and woman, saying to the monkeys : "Be men!" and to the humans : "Be monkeys!".

Mozambiquean creation myth (Fauconnet 1959).

Chapter 8 : Phylogenetic relationships of the Eumolpinae, Megascelidini, Synetinae, and Camptosomata

This chapter discusses the implications of the phylogenetic analyses, compares these with the various historical opininions and my own selective study of the morphological data, and summarises the arguments for the classification presented in Chapter 9. The distribution and significance of selected characters within this classification is then discussed. Details of nomenclatural and taxonomic problems are to be found in Chapter 9.

8.1 Relationship of the outgroups Eumolpinae, Megascelidini, and Synetinae, to each other and to Camptosomata

I was not trying to determine the phylogeny of the outgroup taxa in detail, but it is possible from the limited information presented in the matrix to make some observations, especially concerning Megascelidini and Synetinae. The proposed phylogeny of the subfamilies Synetinae and Lamprosomatinae and the tribes of Eumolpinae and Cryptocephalinae (excluding Achenopini) is illustrated in Fig. 954.

8.2 Eumolpinae, Megascelidini, and Camptosomata

The genus *Megascelis* was placed in Eumolpinae in the numerical analyses of adult characters (AA(i),(iii)). Camptosomata were consistently monophyletic except in MACCLADE analyses, in which eumolpine synapomorphies were excluded.

The few eumolpine taxa chosen for analysis showed a wide range of morphological variation which easily included the Megascelidini. This sample of Eumolpinae showed roughly two morpho-types : (i) 'primitive' Eumolpinae : large species with short, broad non-telescopic ovipositors (Figs 701-705), simple aedeagi (Fig. 578), sternites III-IV connate, lateral lobes on metendosternite (Fig. 529) and tibial spurs; and (ii) 'higher' Eumolpinae : small to large species mostly with modified telescopic ovipositors (Figs 706-709), transversely ridged aedeagi (Figs 580, 583), free sternites, no lateral lobes on metendosternite and no tibial spurs. The Megascelidini lie somewhere between these two groups, although appearing to be most closely allied to the latter. The following features of *Megascelis* are illustrated here : head capsule (Fig. 332); apex of antennal segment 8 (Fig. 353); mandible (Fig. 398); maxillary palp (Fig. 427); prothorax (Fig. 461-463); mesoscutum (Fig. 501); tarsus (Fig. 547); apex metatibia (Fig. 548); wing (Fig. 552); tegmen and median lobe (Figs 579-580); ovipositor (Figs 710-714); spermatheca (Fig. 742). In this study, 'Megascelidinae' and the 'higher' Eumolpinae (*Chrysochus*, *Pachnephorus* and *Edusella*) were distinguished from the 'primitive' Eumolpinae (*Spilopyra* and *Macrolema*) by sharing the following adult attributes : apical clusters of antennal basiconic sensilla in well defined deep circular pits (Fig. 353); prosternal process with an angular projection into each procoxa (Fig. 461) (except *Pachnephorus*, in which the sides of the prosternal process are slots for reception of the antennae; Fig. 101); metendosternite without lateral processes; mesotibiae without apical spurs; struts absent between aedeagus and rectum of male; female genitalia modified into a cylindrical ovipositor; kotpresse completely absent (also true of *Macrolema*). The most significant synapomorphies between adult *Megascelis* and 'higher' Eumolpinae are probably the lateral projections of the prosternal process and the telescopic ovipositor, which are apparently present throughout the 'higher' Eumolpinae (except subtribe Myochroina with deeply grooved prosterna), but are absent from all primitive Eumolpinae, and Camptosomata. The megascelidine larva remains unknown, which strongly suggests that it is soil-dwelling as in Eumolpinae. Significantly only the adult is known as a pest in Central America (King and Saunders 1984). No remarkable features are shared between the Megascelidinae and Camptosomata. The similar wing venation of Megascelidinae (Fig. 552) and Lamprosomatinae (Fig. 553) is plesiomorphic, and the other features mentioned by Mann and Crowson (1981) are neither universal in the Camptosomata nor absent from the Eumolpinae. Note that metatibial spurs are present, not absent as claimed by them. The present study therefore supports Bechyné and Bechyné (1969) in placing Megascelidinae as a tribe within Eumolpinae. An alternative to this action would be the separation of the basal group(s) of eumolpine genera as a subfamily, or subfamilies, in their own right, but this would be difficult to justify from the few taxa studied here.

It is especially interesting that inclusion of the basal eumolpine genera *Macrolema* and *Spilopyra* in this study led to considerable reduction of the possible autapomorphies defining Eumolpinae and Camptosomata as separate entities. Within the matrix only the following adult states are unique to all Eumolpinae (including Megascelidini) : sternite VII of female without an egg-hollow (also true of *Lamprosoma* and *Oomorphus*); sternite VIII of female well developed, with a spiculum gastrale (Figs 702, 707, 711); vaginal palp elongate. In addition to these the prosternal process is convexly raised between the coxae (Figs 460, 463) in all but *Pachnephorus* (prosternal process modified), but this state is also present in Clytrini (Fig. 470). Development of a subcubital fleck (Figs 550-551) is a probable additional synapomorphy for the Eumolpinae, but reference to Jolivet's survey of chrysomelid wing venation (1957) shows that this attribute has been lost in many taxa and it is absent from Megascelidini.

In several key adult features (wing venation, metendosternite, female genitalia), the Camptosomata (with Lamprosomatinae as the basal group) can be derived from the Eumolpinae. It is also notable that *Spilopyra* shows some development of a kotpresse, though this may be homoplasious because it is very simple. I have also seen a similar structure in the avowedly primitive (Monrós 1958c; Crowson 1967) eumolpine genera *Stenomela* and *Eupales* . The larval features of Eumolpinae, in contrast, are so highly modified that little direct relationship is inferable, although it is unfortunate that the larvae of 'primitive' eumolpines are completely unknown. However, even from the larval characters, the Eumolpinae are as or more likely to share a common ancestor with Camptosomata than with any other chrysomelid subfamily except Synetinae (*q.v.*). I feel that the choice of outgroup is vindicated.

On both adult and larval characters the genera *Agetinella* (synonymised here with *Leasia*) and *Platycolaspis*, both originally described as Eumolpinae, are obviously Cryptocephalinae and are discussed below under that section.

8.3 Synetinae

The Holarctic subfamily Synetinae remains a problematic group. It includes only two, closely related, genera (Crowson 1946; Seeno and Wilcox 1982). In the numerical analyses *Syneta* was either placed in Eumolpinae (AL(i), AA(i),(ii)), or as the outgroup to Camptosomata (AA(iii)).

The systematic position of *Syneta* was reviewed by Mann and Crowson (1981) and the late instar larva described by Kurcheva (1967). The larva is remarkably similar to a eumolpine, although, as Kurcheva noted, the similarity is almost entirely due to reduction and loss, the weakest kinds of synapomorphies. The adult shows a mixture of characteristics of various subfamilies, including Galerucinae, Eumolpinae and Cryptocephalinae. The following features are illustrated here : dorsal and lateral of body (Fig. 300); head capsule (Fig. 333); antenna (Fig. 352); labrum (Fig. 371); right mandible (Fig. 399); prothorax (Figs 464-466); abdomen (Fig. 562); ovipositor (Figs 715-716); spermatheca (Fig. 743); rectum (Fig. 807).

The adult mouthparts are similar to Eumolpinae and Cryptocephalinae and have been figured by Mann and Crowson (1981): the galea and lacinia are clothed with spiny setae rather than the dense hairs of more plesiomorphic subfamilies, the mandible is roughly bidentate (Fig. 408), and the lobes of the ligula are contiguous. However the irregular arrangement of the digitiform sensilla is not parallelled elsewhere, and the clypeus is clearly distinguishable, although fused to the frons (Fig. 333). The male genitalia are similar to Galerucinae : the aedeagus is simply curved with a short basal foramen (see Mann and Crowson 1981) and is without apical setae or an ejaculatory guide, the tegmen is greatly reduced, and the accessory gland is free. Furthermore the testes are entirely enclosed in a common sac according to Mann and Crowson (1981), almost as in Galerucinae, although this evidence is implicitly contradicted by Suzuki (1988) who shows the testes without any surrounding membrane. The apical larval tergite is sclerotised and slightly produced which may be roughly similar (analogous) to leaf-mining galerucine larvae (Mann and Crowson 1981), but is more likely to be a convergent adaptation to burrowing, and is in any case not much different from eumolpine larvae (Kurcheva 1967). There is therefore only slight evidence for a relationship with Galerucinae.

Many more features are shared with Eumolpinae and, to a lesser extent, Camptosomata. In general size and shape the adult of *Syneta* is similar to primitive Eumolpinae, and in this study *Syneta* and all Eumolpinae shared the following adult states : tentorial cicatrices triangular; antennae longer than 1.5 times head width (Fig. 300); apical segment of maxillary palp with 5-10 digitiform sensilla; anterior field of prosternum long, not reduced to a ridge between coxa and head (except in the highly modified *Pachnephorus*) (Fig. 464); base of pronotum much narrower than elytra at shoulders (Fig. 300); epipleuron evenly tapering to apex of elytron (Fig. 300); female clavate protarsal setae on segment 3 only; tergites I and II free (fused in *Megascelis* and *Edusella*); base of tegmen flat, not keeled; penis without apical setae; kotpresse at most represented by chitinpolster, without dorsal longitudinal fold (Fig. 807); pair of large assessory vaginal glands present (although these are claimed to be absent from *Syneta* by Mann and Crowson, 1981). Shared larval states (*vide* Kurcheva 1967) include : position of Des1 behind Des2; reduced antennal segmentation and loss of stemmata (also in Galerucinae); similar labrum, mandible, labium, and maxilla; similar body shape and body setae; and remarkable similarity in the legs, both in the shape and size of the tarsungulus and in the chaetotaxy. Most of these adult and larval character states may be symplesiomorphies (but not the lack of stemmata), but determination of this would require comparison with larvae of other chrysomelid subfamilies.

Adult character states shared with Camptosomata studied here include : simple lacinia setae; absence of subcubital fleck; loss of spiculum gastrale in female (Fig. 715); at least chitinpolster of kotpresse present but not a continuous ring (Fig. 807); apical ventrite of female with a well developed hollow (Fig. 562); basal hemisternite (vaginal palp) quadrate to transverse without distinct stylus (Fig. 715). The most conspicuous and potentially significant similarities are in the reduced state of the female genitalia, and the 'egg-hollow', and these at least would appear to be synapomorphies. The fused ovipositor segments do not however exactly correspond in size and shape with those of any Camptosomata, and the completely fused vaginal palp and deep 'egg-hollow' are not found in Lamprosomatinae which are otherwise clearly the basal group of the Camptosomata. In fact the ovipositor is remarkably similar to that of the eumolpine *Eupales*, which is similar to *Syneta* in other ways (pronotum with lateral tubercles, eyes not emarginate, tibial spurs present, reduced anal wing venation, ventrites without lateral borders, metendosternite without lateral lobes, divided chitinpolster), but has closed procoxal cavities and lacks the 'egg-hollow'. Certainly, if the various unusual features of *Syneta*, such as the open procoxal cavities and the 'egg-hollow', are ignored as autapomorphies there is little to separate the two genera. Since the larvae of *Syneta* are soil dwelling, without scatoshells, it would be interesting to know how the supposed egg-hollow is used in oviposition. The larvae of *Eupales* are unknown. It may be significant that *Syneta* and *Eupales* are the only primitive eumolpine or eumolpine-like genera in the northern Hemisphere. I have also found the divided chitinpolster in the Chilean eumolpine *Stenomela* which is clearly related to *Spilopyra* (with chitinpolster complete) and *Macrolema* (chitinpolster absent).

The main larval similarity between *Syneta* and Camptosomata is in the plesiomorphic leg structure and chaetotaxy, though this similarity is less than with Eumolpinae.

Without further study of world Eumolpinae, Galerucinae, Chrysomelinae and possibly Aulacoscelinae (which Monrós, 1949c, has suggested belong with Eumolpinae) it is not possible to be definite about the systematic position of *Syneta*. Furthermore many aspects of the biology of *Syneta* have yet to be discovered (which is remarkable for an unusual Holarctic genus), notably oviposition. I am reasonably convinced that it does not share enough camptosomatan attributes to belong to this group and suspect that it is most likely to be related to an ancestral eumolpine, coming closest in the modern fauna to *Eupales*. I am reluctant to consider *Syneta* sister to the Camptosomata because the adult is morphologically more divergent from the Lamprosomatinae than, say, *Spilopyra*, and the larva appears to be genuinely eumolpine whereas the larva of *Spilopyra* is unknown.

This doubt concerning its position seems to be a good reason for maintaining its subfamilial rank at present.

8.4 Camptosomata

In early analyses (not discussed above), monophyly of the Camptosomata was obscured because of extreme convergence between *Pachnephorus* in Eumolpinae and the Lamprosomatinae. Both groups have similar antennal slots on the ventral surface (Figs 101-103) and crenulate abdominal apices (Fig. 563), and of course share various symplesiomorphies due to the relatively primitive nature of the Lamprosomatinae. The problem was simply corrected by including further characters synapomorphic for at least some of the Eumolpinae. For example *Pachnephorus* has the female genitalia of a 'higher' eumolpine (identical to *Edusella*, Figs 706-709). Once synapomorphies were provided for the Eumolpinae, the analyses always revealed monophyly in the Camptosomata with *Syneta* an occasional outgroup (*qv. supra*).

Lamprosomatinae were always the basal group of Camptosomata. The phylogeny of the remaining taxa was never clear. Pachybrachini, Chlamisini and Clytrini were always monophyletic but the Cryptocephalini were monophyletic (AL(ii), AA(iv), ALA(v)), paraphyletic (AL(i)), or polyphyletic (AA(i),(ii), ALA(i),(iv)).

From all the evidence available the traditional Camptosomata (traditionally Lamprosomatinae, Chlamisinae, Clytrinae and Cryptocephalinae) are certainly monophyletic, and furthermore the well-defined Lamprosomatinae are easily distinguished as the most primitive or basal group within this assemblage.

It has been suggested that Chlamisini and Lamprosomatinae form a monophyletic group (Kasap and Crowson 1976) and they show the following possible synapomorphies : prosternal process with lateral antennal slots (not *Pseudolychnophaes*) (Figs 102-103); mesoscutellum abruptly raised above scutum (Fig. 511); segment 1 of tarsi usually quadrate to transverse (Figs 558, 863, 877); base of tegmen keeled but not bilobed (Figs 585, 881, 885, 889); penis blunt or truncate (Figs 879, 883). The scattered distribution of these states throughout the Eumolpinae and Camptosomata suggests their homoplasious origin and it is quite evident that the antennal slots are morphologically different. Furthermore there are many more synapomorphies (see below) for Chlamisini plus the other cryptocephalines as defined here.

Since the Lamprosomatinae and the remaining groups form two monophyletic units with obscure internal arrangements I recognise two subfamilies in the informal group Camptosomata. If, as seems increasingly likely, some of the current subfamilial divisions of Chrysomelidae are returned to familial status, then the Camptosomata could be designated Cryptocephalidae (as the oldest available family group name, Watt 1979), with two constituent subfamilies, Lamprosomatinae and Cryptocephalinae. Another approach to breaking up the Chrysomelidae might be to include the Eumolpinae, Synetinae, Lamprosomatinae and Cryptocephalinae in one family.

8.4.1 Lamprosomatinae

Lamprosomatinae were almost always the sister-group to the remaining Camptosomata in my analyses, whether the data base was of larval, pupal or adult characters. The only differing analysis, AA(ii), gave Chlamisini and Lamprosomatinae as sister-groups within the Cryptocephalini.

This subfamily has been subjected to recent studies of the genera and tribes (Monrós 1956a, 1958a), and the larvae (Monrós 1949a; Kasap and Crowson 1976). The above authors have also discussed its systematic position and allow Lamprosomatinae a basal position in the Camptosomata. I completely agree with this arrangement. The non-Darwinian theory that evolution is a directed process of increasing complexity has been adopted by some authors (Jolivet 1959) who place the morphologically specialised subfamily Lamprosomatinae as a terminal taxon. This simplistic and non-scientific idea should be completely rejected, but is still evident in references to chrysomelid phylogeny.

The following features of adult Lamprosomatinae are figured here : antenna (Fig. 354); labrum (Fig. 372); mandible (Fig. 400); maxillary palp (Fig. 428); prothorax (Fig. 467); metendosternite (Fig. 530); hind leg (Fig. 549); wing (Fig. 553); abdomen (Fig.

563); tegmen and median lobe (Figs 584-585); ovipositor (Fig. 717); spermatheca (Figs 744-745); rectum (Figs 808-809).

One flaw in this review of Camptosomata is that I did not examine any material of the tribe Sphaerocharitini (including the weakly differentiated Neochlamisini). The adults of this tribe are rare and the larvae unknown. Historically it has been considered intermediate between Lamprosomatinae and Chlamisinae (Chapuis 1874), or close to the Chlamisinae (Achard 1914), but the position was reviewed by Monrós in a broad revision of the Lamprosomatinae (Monrós 1956a). Monrós wrote "no hay motivo para separar *Sphaerocharis* y géneros vecinos en una subfamilia aparte de Lamprosominae [sic] ..." (p. 27). However, recently the systematic position of these minor subfamilies was discussed by Kasap and Crowson (1976) who reinstated Sphaerocharitini as a separate entity, distinguished from Lamprosomatinae, on the basis of a few plesiomorphic character states. I would dispute their decision, from consideration of the descriptions and illustrations given by the above authors. The following features, illustrated by Monrós (1956), are apparently shared apomorphies of Lamprosomatinae including Sphaerocharitini and Neochlamisini : hemispherical form; metallic colour; hind border of pronotum not clearly margined and basally evenly curved or shallowly sinuate; front angles of pronotum strongly curved inwards, not visible from above; epipleural lobe angulate ventrally; prosternum with deep slot between procoxa and process (not *Pseudolychnophaes*); visible part of mesosternum (not process) reduced to a transverse ridge; abdomen relatively flat (may be plesiomorphic). The Lamprosomatinae *sensu lato* also show the following in unison : very short antenna (not reaching hind margin of pronotum); broad prosternal process; triangular scutellum; clavate tarsal setae on segments 1-3; non-connate ventrites; apical abdominal hollow of female absent or very shallow (Fig. 563); simple kotpresse without sclerites (Figs 808-809). All may be plesiomorphic states. I regard the features used by Kasap and Crowson (1976) to separate their Lamprosomatinae and Sphaerocharinae [sic] as of relatively minor importance ; the wing venation is variably reduced in both Lamprosomatini and Sphaerocharitini, the exposed pygidium of *Sphaerocharis* seems only microscopically so in Monrós' figures, and as shown above the posterior margins of the ventrites may be curved or straight in both Eumolpinae and Camptosomata. The 'stridulatory apparatus' (for which there is no evidence of function; it certainly seems too crude to be used for stridulation) at the apices of abdomen and elytra remains as a good apomorphy for the Lamprosomatini (Fig. 563) (note that this is convergently present in *Pachnephorus*).

Only the larvae of two species of Lamprosomatini are known and these are of quite different structure (Monrós 1949a; Kasap and Crowson 1976). I am reluctant to use Monrós' figures and descriptions of *Lamprosoma* because his figures of larvae generally tend to be sketchy, and because he does not include the first instar. Unfortunately for phylogenetic work, the head capsule of the larva of *Oomorphus* is highly specialised due to the greatly enlarged antennae which are modified as claws (Fig. 185). However from a combination of the evidence from *Lamprosoma* and *Oomorphus* the larvae of Lamprosomatinae look like a potential eumolpine ancestor, but C-shaped to fit the scatoshell. I-was unable to find any synapomorphies for the larvae of these two genera because of the poor description of the *Lamprosoma* larva.

The pupa of *Lamprosoma* (Monrós 1949a) is plesiomorphic; it lacks fleshy projections on tergites VI-VII or on the elytrothecae, and retains the urogomphi (Fig. 281).

8.4.2 Cryptocephalinae

Before discussing the phylogeny of the Cryptocephalinae further it should be noted that material of the monotypic southern African tribe Achenopini was not available. I do not believe that Achenopini will be sustainable as a tribe but suggest in Section **8.3.7** that the genus *Achenops* belongs to either Pachybrachini or Cryptocephalini. The following discussion of the phylogeny of Cryptocephalinae is based on this assumption.

In numerical analyses the Cryptocephalinae were almost always monophyletic (except AA(ii)) and the sister-group of Lamprosomatinae. It was generally possible to distinguish the four tribes treated here as monophyletic taxa, but the Cryptocephalini were often made para- or polyphyletic by intrusion of at least one of the other three tribes.

The following synapomorphies define the Cryptocephalinae. Adults : procoxae open or closed by insertion of prosternal process into hypomeron (Figs 468, 471); anal wing venation reduced, three or less free anal veins (Figs 554-558); lateral lobe at base of abdomen with reduced pleurite (Fig. 565); abdominal sternites VI-VII connate (Fig. 565); ejaculatory guide present (Fig. 586); stylus absent from vaginal palp (Fig. 718); sensilla absent from anterior of kotpresse venter (Figs 810-811); ventral transverse rectal sclerite present. In addition the following states are almost universal but a few taxa show reversal or retention of plesiomorphy : pronotum with medially lobed hind margin (a few reversals); pro-endosternite without well-developed basal lobe; mesonotal flange curved around a circular hollow; metendosternite with median process; female sternite VIII membranous, non-setose; sensilla on posterior half of kotpresse venter confined to apical band. Most of the above involve loss or reduction and are therefore weak. Larvae : mandible with inner tooth either overlapping internal margin or enlarged, prominent; epipharyngeal setae dorsal; spiracles cribriform or moniliform. Pupa : with abdominal processes on tergite VII or processes and urogomphi absent.

Clear recognition of Lamprosomatinae as the sister-group to the remaining Camptosomata should in theory be welcomed as provision of an unequivocal outgroup for analysing the phylogeny of this remainder. However many features of the Lamprosomatinae are either relatively highly derived or uninterestingly plesiomorphic in both larvae and adults and this has caused many problems for phylogenetic analysis. This difficulty is made worse by the relatively highly derived adults of three important ingroups, Chlamisini, Clytrini and Coenobiina, each of which is obviously monophyletic. In fact the major problem with determining the phylogeny of the Cryptocephalinae is not delimiting monophyletic groups of genera, but rather determining the inter-relationships of these groups.

Determination of phylogeny of these groups based on adults is further compounded in two ways : (i) by the general trend towards reduction and fusion of structures in each lineage; (ii) by compaction of body form leading to strong correlations in changes of shape between adjacent structures. These trends reduce the potential number of variable independent characters and therefore increase the degree of homoplasious variation in unrelated taxa. Use of larval structures is restricted by the morphological variation being largely confined to the head capsule and legs.

Here four constituent tribes are recognised : Chlamisini, Clytrini, Pachybrachini and Cryptocephalini. Chlamisini and Clytrini are discrete monophyletic units for which there can only be an argument over rank. The separation of Pachybrachini and Cryptocephalini is more contentious. Pachybrachini have always been placed in the Cryptocephalini, basically on the premise that they lack the distinguishing characters of Clytrini or Chlamisini (Clytrini and Chlamisini were originally considered 'more evolved' than Cryptocephalini and therefore derived from them). However, they also lack the crenulate pronotum of Cryptocephalini and are therefore plesiomorphically defined in traditional classification. In structure of kotpresse and larva they show no relationship to Cryptocephalini, but some similarity to Clytrini. The similarity between the internal teeth of the larval mandibles of Pachybrachini (Fig. 226) and Ditropidina (Figs 228-232) is presumably convergent. Under Sections **8.4.4** and **8.4.5** it is shown that Pachybrachini share many attributes with Clytrini and may be paraphyletic with regard to the latter. Therefore Clytrini and Pachybrachini are placed as sister-groups. Removal of Pachybrachini makes the Cryptocephalini a better defined tribe.

The treatment of Clytrini and Pachybrachini as one monophyletic unit means that there are three possible phylogenies for the tribes of Cryptocephalinae.

Chlamisini have been placed as the sister group of Cryptocephalini (including Pachybrachini) + Clytrini since Baly (1865) removed Chlamisini from Clytrini and suggested that the shared antennal slots with Lamprosomatinae were indicative of relationship. This position of the Chlamisini is only weakly supported by adult anatomy but has some support from egg and larval characters. The problem lies in recognising synapomorphies for Clytrini, Pachybrachini and Cryptocephalini. Only two universal synapomorphies were found for these three tribes : papillate larval setae; scale-like construction of scatoshell. There are many other attributes shared by some taxa of the three tibes but not present in Chlamisini. Furthermore, the larvae of this group enlarge their cases by lateral expansion along a ventral split in the scatoshell (Erber 1988) in contrast to the apical accretion method of Chlamisini. One probable plesiomorphic feature of the Chlamisini is the relatively simple kotpresse.

An alternative arrangement is that the tribes Clytrini plus Pachybrachini are sister to Chlamisini plus Cryptocephalini. This combination of Chlamisini and Cryptocephalini is supported by the following attributes of Chlamisini which are also present in some Cryptocephalini. Adult : eyes with deep internal invagination (canthus); lower margin of eyes well below antennal sockets; epipharynx with less than 10 apical setae; hind margin of pronotum simple, unbordered, and with a narrowly produced central lobe; prosternal process approximately quadrate; mesoscutellum abruptly raised, abutting pronotum; tegmen with base keeled but not bilobed. Pupa with abdominal processes. None of the adult attributes listed above are universal in Cryptocephalini and many are also present in both Clytrini and Pachybrachini but it is notable that adult Chlamisini lack plesiomorphies found in some Pachybrachini, for example lateral processes on metendosternite and tibial spurs. The compact body form of the Chlamisini is constructed quite differently from the similarly compact Cryptocephalini, in that crenulate edges occur in different areas and compacted sclerites are of different shape. The kotpresse is of simple form without the lateral sclerites of Cryptocephalini, although transverse sclerites are present, and the scatoshell is loosely constructed. The common occurrence of antennal grooves on the prosternum in Lamprosomatinae, Chlamisini, *Ischiopachys* (Clytrini) and *Adiscus* (Ditropidina) is convergent. The chlamisine larva has no synapomorphies with Cryptocephalini and discovery of the pachybrachine pupa may show that abdominal processes are synapomorphic for all Cryptocephalinae. There is therefore no good evidence for a sister-group relationship between Chlamisini and Cryptocephalini and this hypothesis is rejected.

A third possible system, that Cryptocephalini are the sister-group of the three other tribes (Chlamisini + others) is partially supported by the larval antennae reduced to two segments in Clytrini and Chlamisini and the adult antennae very short and serrate in both these tribes. But the reduced larval antennae are of different construction. Clytrini, Pachybrachini and Chlamisini only share plesiomorphic character states.

The evidence for these phylogenies is mostly negative but favours the first arrangement of Chlamisini as sister-group to the remaining taxa. I have kept the relatively conservative classification of four tribes to indicate that each may be of similar rank and that the phylogeny of the tribes is uncertain. The phylogeny of the tribes is not indicated by the nomenclature but is potentially useful for polarity detemination of characters through outgroup comparison. However, studies of intra-tribal phylogeny will probably still require knowledge of variation in all other tribes. The immature stage data seem to be of greatest value in providing synapomorphies for tribes. The phylogeny of the tribes is represented graphically as an unresolved trichotomy between Chlamisini, Clytrini + Pachybrachini and Cryptocephalini (Fig. 954).

8.4.3 Chlamisini

The Chlamisini were variously placed by numerical analyses as a sister-group for : the remaining Cryptocephalinae (AL(i), AA(i),(iii), ALA(i),(iv), the Clytrini + Cryptocephalini (AL(ii), only Cryptocephalini (pupae, AA(iv), ALA(v)), or only Lamprosomatinae (AA(ii)). Some relationship with Ditropidina was suggested by the combination of such adult features as the strongly but narrowly lobed pronotal margin and the antennal grooves shared with *Adiscus*, but this was not revealed by any minimum-length tree.

The tribe Chlamisini is clearly monophyletic, with the following synapomorphies. Adult : prosternal process deeply laterally slotted for reception of antennae (Fig. 103); disc of pronotum raised as a single or paired swelling (Figs 858, 866, 872; but simple in a few South American species); mesosternal process with a central longitudinal keel (Fig. 521); mesoscutellum trapezoid, broadest at apex (Figs 502, 857, 865, 871); elytra tuberculate (Figs 857, 865, 871; a few exceptions); cell Rt of wing open (Jolivet 1957); sternites IV-VI telescoped into III (Figs 858, 866, 872). Larva : antenna with two segments (Fig. 186); tarsungulus short, strongly curved, with broad basal lobe (Fig.

240); more than five ventral tibial setae, at least a pair of which are clubbed (Fig. 240). Pupa (Figs 284-288) : entirely without setae; abdominal processes with sharp, sclerotised tips. The adult kotpresse is relatively simple and is probably plesiomorphic for the Cryptocephalinae (Karren 1966; Figs 810-811).

Chlamisini are remarkably morphologically uniform and easily recognised. They appear to mimic caterpillar droppings (Karren 1972). As a consequence of this morphological conservatism in a fairly large species assemblage only 10 to 11 genera are recognised in the tribe (Gressitt and Kimoto 1961; Seeno and Wilcox 1982) and all of these genera are poorly defined. However three species of *Chlamisus* (especially *C. lamprosomoides* Lacordaire) illustrated by Achard (1914b) appear rather different from others I have seen, having narrower scutella (though apparently still broadest at apex), rather broadly lobed posterior pronotal borders, and non-tuberculate upper surfaces.

The generic classification of the Chlamisini is in a state of flux at present (Karren 1972) and elucidation of its phylogeny will ultimately depend on a thorough study of the Neotropical fauna, which has yet to be undertaken. The non-tuberculate Neotropical species noted above may be of interest in this context. The classification of Nearctic genera (Karren 1966, 1972) is purely phenetic and is also based on a subset of the much more diverse Neotropical fauna. Monrós' work (1951a) on the Argentine fauna is also phenetic.

Recently (Karren 1972) some Nearctic elements of the almost cosmopolitan genus *Chlamisus* have been split off as *Neochlamisus* Karren, and the genus *Exema* Lacordaire reinstated from synonymy (synonymy by Gressitt, 1961). *Chlamisus* has subsequently become more rigorously defined for adults (with reservations) (Karren 1972) and larvae (LeSage 1984b). The rediagnosis for North American species of *Chlamisus* is : presence of a tibial spine on at least prolegs of males; lack of tibial spines in females; absence of diagnostic characters of other genera (Karren 1972); larvae with 9 or more pairs of ventral setae on tibiae (LeSage 1984b, following van Emden 1932). Monrós (1951a) gave a key to the world genera and defined the genus for adults of the Argentine species : antennae without an apical club, and antennomeres 3 to 5 as ymmetric;

prosternal process posteriorly elongate, never rectangular; metasternum without anterior projection; claws evidently appendiculate.

Neither of these definitions of adults are suitable for the native Australian species. In the North American key they show a combination of characteristics of *Exema* and *Chlamisus*. According to the key provided by Monrós, one Australian species belongs to *Exema* while the other belongs to *Aulacochlamys* Monrós, although the two species appear to be closely related (Figs 857-870, 879-886). Comparison with other material from south-east Asia (*Chlamisus* and *Hymetes* Lacordaire) and the Americas (*'Exema'* sensu Karren, *Chlamisus*, *Neochlamisus*, *Fulcidax* Lacordaire) and works dealing with these areas (Monros 1951a; Gressitt and Kimoto 1961) shows that adult Chlamisini from the two regions differ from each other (Table 3). However in each of these differences the plesiomorphic condition may be with the south-east Asian fauna, and all of the characters may be correlated. At present it seems best to retain the Australian species in *Chlamisus*.

Table 3. Differences between south-east Asian and American Chlamisini.

Character	South-east Asia	America
Ventral border of junction of pronotum and epipleura	smooth, approximately at right-angles (Fig. 858)	uneven, obtuse (Fig. 872)
Abdominal laterobasal extension	broad, weakly curved (Fig. 858)	narrow, strongly curved (Fig. 872)
Legs	shorter, stouter	longer, thinner

8.4.4 Clytrini and Pachybrachini

These two tribes were not placed as sister-groups in any numerical analysis, although I did put them together in rearrangements of combined data taxa (ALA(v)). This combination of taxa has few universally defining character states but several attributes unknown or rare elsewhere in the Cryptocephalinae are found in all members of one tribe and one or two of the other. The following adult synapomorphies were found for at least one of the Pachybrachini studied (noted in brackets) plus all Clytrini: mandible with internal tooth or ridge (Figs 402-403) (in Pachybrachini absent or at most a ridge); procoxal cavities open or closed without insertion of one sclerite into another (Fig. 468) (*Acolastus*); absence of dorsal longitudinal fold on rectum (Figs 812-815) (*Acolastus*, *Mylassa*); ventral transverse rectal sclerite wider than rectum and apices expanded (Fig. 812) (all); dorsal rectal sclerite whole or in three sections (Fig. 817) (*Acolastus*, *Mylassa*). Both tribes have a posteriorly directed spur near the base of the radial vein (Jolivet 1957) which is probably plesiomorphic although it is absent from Eumolpinae and other Cryptocephalinae. There are no obvious larval synapomorphies and the pachybrachine pupa is unknown. The evidence from this small sample strongly suggests that Pachybrachini are paraphyletic, with *Acolastus* a possible sister-group to Clytrini.

8.4.5 Clytrini

Monophyly of the Clytrini was supported by all the analyses performed, given that only seven species representing four 'tribes' were studied in detail. They generally occupied a basal or near basal position within the Cryptocephalinae. The internal structure of the Clytrini clade either placed the Old World and New World taxa as sister groups or placed the former within the latter, with *Megalostomis* basal.

The following autapomorphies may define the Clytrini : in adults : internally toothed mandible (Fig. 402); sclerotised lacinia (not *Labidostomis*) (Fig. 430); lack of lateral ridges on sides of mesoscutum (Fig. 133); well developed finely striate stridulatory area on mesoscutum (Fig. 134); dorsal sclerite of kotpresse with central plate separated, and without longitudinal fold (also *Acolastus*) (Fig. 812); lateral sclerites of kotpresse absent (Fig. 812); in larvae : vertex between Ls1, Ls2, and epicranial suture rough, with irregular rows of pits (also some Cryptocephalina) (Fig. 189); two antennal segments (also Chlamisini) (Fig. 189); antennal sensory cone globular or flattened (Fig.

189). Lack of apical abdominal projections in the pupa (Fig. 283) may also be an autapomorphy.

8.4.5.1 Subtribal classification of Clytrini.

In this study the Old and New world taxa appeared to belong to separate monophyletic groups. Synapomorphies for the Old World taxa included : pro-endosternites reduced to elongate spatulate processes (Fig. 469); basal border of sternite III posteriorly directed before lateral lobe (Fig. 567); female sternite VIII internally setose. Synapomorphies for the New World taxa included : lacinia bilobed or cleft to base (*vide* Monrós 1953b); mesosternal process bilobed.

Within the Clytrini the subtribal classification has remained substantially unchanged since its inception by Chapuis (1874) who included four subtribes : Clytrina, Megalostomina, Babiina and Ischiopachina (monotypic). To this have been added the monotypic subtribes Eoclytrina (Monrós 1958b) and Arateina (Moldenke 1981). Most clytrine genera are illustrated and briefly described by Jacoby and Clavareau (1906). The subtribal classification is based entirely on adults and it is likely that larval characters will be useful for definition and phylogeny of the subtribes, since they provide good generic characters (Medvedev and Zaitsev 1972). Here four subtribes are recognised for the world species : Clytrina, Eoclytrina, Megalostomina and Babiina.

All Old World Clytrini belong to Clytrina, except for the enigmatic African genus *Eoclytra* discussed below. The remaining Clytrini (the New World taxa) have been divided into two (Monrós 1953b) or four (Moldenke 1981; Seeno and Wilcox 1982) subtribes depending on assessment of the unusual genera *Ischiopachys* and *Aratea*. Monrós, whose revision of the Argentinian taxa remains the most exhaustive treatment of clytrine morphology to date, placed both *Ischiopachys* and *Aratea* in Babiini, and noted their close relationship. Jolivet (1957) noted the similar wing venation of *Babia* and *Ischiopachys*. In contrast Moldenke has given both genera separate subtribal status, on phenetic evidence, and furthermore has claimed that both are more closely related to genera of Clytrina. Megalostomina and Babiina, as constituted by either Monrós or

Moldenke, are weakly defined by a single character (claw shape) although the two type genera are quite distinct. These two subtribes need to be redefined.

From the evidence of the material available to me and the publications cited above I support Monrós' argument for the inclusion of *Ischiopachys* and *Aratea* in Babiina as presently constituted. Only two characters were used by Moldenke to support a relationship between *Ischiopachys*, *Aratea* and Old World taxa, namely elevation of the scutellum and presence of a deep median facial pit. In my view the scutellum is not significantly elevated in *Ischiopachys*, *Aratea* and also several Old World taxa. The facial pit (a reflection of an internal keel) is barely useful at species level in Camptosomata (and most Chrysomelidae) and was not used in the cladistic analyses.

The South African genus *Eoclytra* was not examined in this study but appears from the original illustrations (Monrós 1958b) to be superficially very similar to the Australian genus *Leasia* (Cryptocephalini). That such a similarity between *Leasia* and *Eoclytra* was not discussed by Monrós, who studied both, is probably significant. The following characteristics of *Eoclytra* given by Monrós clearly place it in the Clytrini : serrate antennae (described as weakly serrate but clearly so from the illustrations); internally toothed mandible (described as trifid); procoxae contiguous and prosternum not visible between them. Monrós also suggested that this was the most basal group of the Clytrini because of the non-reniform eyes, 'subserrate' antennae, simple claws, non-seriate elytral punctuation, and pubescence. It is obvious from the data for this study that all of these are weak character states and the correct phylogenetic position of this genus may be within the Clytrina.

In conclusion, the following subtribes are recognised here : Clytrina, Eoclytrina, Megalostomina and Babiina. Redefinition and phylogeny of the subtribes will have to await a more detailed comparison of the numerous genera with respect to Pachybrachini. For this reason, no attempt is made here to discuss the viability of the genera. Larvae of Clytrina are fairly well known and provide useful distinguishing characters at generic level (Medvedev and Zaitsev 1972, 1978).

8.4.5.2 Systematic position of the Australian species of Clytrina.

The two Australian clytrine species are described in the genus *Aetheomorpha,* which has a West African type species. Larvae of this genus are unknown. Here only the Australian species were examined, one of which was included in numerical analysis. In this restricted study the genus *Aetheomorpha* was paired with *Smaragdina* (Clytrina), which it closely resembles, with the following synapomorphies : antennomere 2 much wider than 3 (Fig. 356); scutellum tilted at more than 30° to mesoscutum (Fig. 519); prosteral process flat or sunk between coxae (Fig. 104); spermathecal duct long and tightly coiled (Fig. 746). Furthermore the two genera lack the fused basal tergites of *Clytra* and *Labidostomis*. However *Smaragdina* lacks a densely pilose first tergite (Fig. 567) which would otherwise be a good synapomorphy for the Clytrina.

The generic classification of Clytrina is in disarray (Jacoby 1908b). Most concepts date from the nineteenth century (Lacordaire 1848) and are based on minor character state variations, and recent workers have been content to allow this system to continue with very little criticism. The separation of *Aetheomorpha* from several other genera is unconvincing but a diagnosis of each of these was beyond the scope of this study. Pending such a revision the Australian species are kept in *Aetheomorpha.*

8.4.6 Pachybrachini

Pachybrachini were also generally basally placed in analyses of Cryptocephalinae, although sometimes appearing well within the Cryptocephalini. They were always monophyletic, usually with *Mylassa* most basal.

Pachybrachini have retained a few plesiomorphic features which are absent from almost all other Camptosomata, for example tibial spurs (absent from all other Cryptocephalinae) and lateral lobes of the metendosternite (also present in *Adiscus*). These features, which are unlikely to have been convergently derived, suggest a basal position in the system. Morphology is highly variable in this group of genera, with great diversity of head and prothorax shapes, genitalia and kotpresse. The kotpresse has been described as intermediate between that of *Clytra* and *Cryptocephalus* (Erber1968).

Pachybrachini are weakly defined by the following synapomorphies. Adult : submentum divided (Fig. 451) (not *Mylassa*); anal cell 2A extremely small or absent (*vide* Jolivet 1957) (not *Griburius*); profemora strongly inflated and ventrally keeled (Fig. 306) (not *Mylassa*, Fig. 305); middle of ventral transverse rectal sclerite secondarily thickened (Figs 815, 816, 818) (not *Mylassa*, Fig. 817). Larva (based on my examination of LeSage's original material of *Pachybrachis* and an undetermined Central American specimen which is probably *Griburius*) : mandibular tooth 5 larger than 4 and gap between 3 and 4 shallowly concave (Fig. 226); seta Ms1 papillate (Fig. 226); sensillum Aesm 2 in front of Aes2; sensillum Csm1 above Cs1; frontoclypeal suture thickened (plesiomorphic?). The larval characters look useful but are based on a small sample. A plesiomorphic metendosternite, with lateral processes, is present in *Pachybrachis* and *Griburius* (including *Metallactus*) and a single meso-tibial spur is retained in all genera except *Mylassa*. The larva shows the plesiomorphic 2+4 pattern of frontal setae. The scatoshell of *Pachybrachis*, with its characteristically twisted apex (LeSage 1985), may be apomorphic for Pachybrachini. The pupa is unknown.

It seems clear from the above diagnosis that the South American genus *Mylassa* does not conform with the other Pachybrachini (it lacks characteristic autapomorphies and plesiomorphies) and its removal would allow the Pachybrachini to be much more strictly defined. However, *Mylassa* shares many other attributes with Pachybrachini, although these are frequently homoplasious in the Cryptocephalinae, and shows no obvious relationship to any other Cryptocephalinae except Clytrini. Monrós (1949) gave a good description of the anatomy of *Mylassa* and showed that it is certainly not synonymous with *Cryptocephalus* (Seeno and Wilcox 1982, following Chapuis 1874, who followed Suffrian 1866!). The suggested resemblance between *Mylassa* and Australian Cryptocephalina (Monrós 1949b) is not supported morphologically, especially in the anatomy of the mouthparts and male and female genitalia.

Acolastus shares several important attributes with Clytrini and may be the latter's sister-group. The most notable similarity (and probable synapomorphy) is in the complex sclerotisation of the rectum. Otherwise *Acolastus* shows little external similarity to Clytrini, having prominent convex eyes, reduced lateral pronotal borders and so on, but these features may simply be autapomorphies. The difference between *Griburius* and *Metallactus* is based on non-discrete variation in the prosternal process, therefore these genera are probably synonymous (as suggested by Jacoby (1908)). However I am unwilling to make this synonymy without comparing the type species. A possible phylogeny of the genera of Pachybrachini examined here would be : *Mylassa* + ((*Pachybrachis* + *Ambrotodes* + *Griburius* + *Metallactus*) + (*Acolastus* + Clytrini)). Published descriptions of the four remaining genera of Pachybrachini not examined here, *Mastacanthus* Suffrian (1852; also Chapuis 1874), *Sternoglossus* Suffrian (1866; also Chapuis 1874), *Falsopachybrachys* Pic (1947) and *Thelytrerotarsus* Weise (with three subgenera, see Berti and Rapilly 1973; Lopatin 1979, 1982b, 1983), suggest that these unequivocally belong to the *Pachybrachis* + *Ambrotodes* + *Griburius* + *Metallactus* clade.

The supposed Australian member of this tribe, '*Diandichus*', is closely related to *Aporocera* (Cryptocephalini). The superficially similar genera *Arnomus* and *Semelvillea* definitely belong to Cryptocephalini (*qq. v.*). The only Australian representatives have therefore been two species of *Metallactus* which were introduced into South Queensland as biological control agents and have apparently failed to become established (Julien 1978).

8.4.7 Achenopini

No positively identified material of the monotypic 'tribe' Achenopini was examined in this study of the Cryptocephalinae. *Achaenops*, founded on a single species, was described by Suffrian (1857), who noted its general similarity in compact body form to *Lexiphanes* and *Coenobius*, but separated *Achenops* from these by its broadly separated unexcavated eyes, obtuse thoracic hind-angles and lack of teeth on pronotal hind margin. Suffrian suggested that these characteristics placed *Achenops* between Pachybrachini and Cryptocephalini, although it showed no similarity in body form to the former. This view was supported by Chapuis (1874).

Suffrian's description is insufficient for placement of *Achenops* in the classification given here. The rounded pronotal hind angles would exclude it from Cryptocephalini, and exclusion is supported by the lack of pronotal teeth. Eye-shape and the other characteristics given by Suffrian (1857) are not diagnostic of any particular group but would also favour Pachybrachini. I believe that when *Achenops* is re-examined it will prove to belong to either Pachybrachini or Cryptocephalina, with my preference for the latter because its structures have probably been misinterpreted.

For this study I originally examined specimens of *A. nigrolineatus* Bryant, which unquestionably belongs to Pachybrachini. However, Bryant was notorious for casual association of species with genera and I decided to ignore this material in all analyses because it was unlikely to be congeneric with the type species.

8.5 Cryptocephalini

I have already noted that the Cryptocephalini were frequently non-monophyletic in numerical analyses. The hypothesis of non-monophyly is rejected here because synapomorphies are available for the group and because no more plausible solution to the phylogeny of Cryptocephalinae is available. The proposed phylogeny for the subtribes of Cryptocephalini is illustrated in Fig. 955.

Monophyly of the Cryptocephalini is based on the following synapomorphies : adult with crenulate posterior margin to pronotum (with a few presumed reversals) (Figs 107-108, 479); larva with frontal setae in 2+2 or 2+2+2 arrangement (not *Aprionota*) (Figs 27-40); and possibly pupa with elytrothecal lobe (Figs 289, 292, 296), but the pupae of Stylosomina, Platycolaspina and Coenobiina are unknown. There are three possible challenges to the monophyly of Cryptocephalini : (i) Chlamisini should be included, near to *Ditropidus*; (ii) Pachybrachini should be included, as in all modern classifications (Seeno and Wilcox 1982); (iii) Cryptocephalini is a paraphyletic basal lineage, with both Clytrini and Chlamisini being derived from cryptocephaline ancestors. Evidence for (i) was discussed and refuted in section **8.4.3**. Evidence for (ii) was discussed and refuted in sections **8.4.3** and **8.4.6**. Evidence for (iii) is largely lacking, but is implicit in Kasap and Crowson's discussion of larval characters. Refutation may be through wide distribution of plesiomorphic states (from outgroup) of characters in Chlamisini, Clytrini, Pachybrachini (for example tibial spurs, separation of first and second tergites, simple kotpresse in Chlamisini, lack of pronotal teeth) together with the synapomorphies defining Cryptocephalini *sensu stricto* (for example pronotal teeth, frontal-seta configuration in larvae).

There are two distinct divergent lines in the Cryptocephalini. Stylosomina and Platycolaspina appear to form one lineage and Coenobiina, Ditropidina and Cryptocephalina the other. The relationship between these two lineages is unclear. They differ so markedly in body form that it is difficult to see any association. Comparison with the outgroups might suggest that the compact body form of the second lineage is the plesiomorphic state (if homologous with *Megalostomis*, *Griburius* and Chlamisini for example), or that the looser form of the first lineage is plesiomorphic (homology with *Clytra* and *Acolastus*). Neither larval nor adult characters provide any clear cut synapomorphies between the group Stylosomina + Platycolaspina and any one of the other groups. The kotpresse of *Stylosomus* is unique but that of *Platycolaspis* and allies is similar to *Ditropidella* (Ditropidina) whereas that of *Semelvillea* and *Arnomus* is similar to *Stegnocephala* (Cryptocephalina) and *Coenobius* (Coenobiina)! *Semelvillea* and *Arnomus* are superficially remarkably similar to species of *Aporocera* (Cryptocephalina; they have been identified as *Aporocera* species in collections), but I believe this to be convergent as such a relationship is not supported by characters of the first instar larva, adult prothorax, male genitalia or kotpresse. In many ways the genus *Platycolaspis* provides an intermediate link between *Semelvillea* and *Atenesus*.

8.5.1 Stylosomina and Platycolaspina

Stylosomina and Platycolaspina were frequently closely associated, but not necessarily monophyletically, in the numerical systematics studies reported in previous chapters (Figs 927, 929, 931, 936, 942, 943, 946). I recognise both as monophyletic sister-groups, as analysed in ALA(v-vi) (Figs 947-949). The proposed phylogeny of the genera of Stylosomina and Platycolaspina is illustrated in Fig. 949.

The monotypic Stylosomina share the following synapomorphies with at least some Platycolaspina : eye evenly and strongly convex, canthus not developed (Figs 66-70) (except *Semelvillea waraganji*); pronotal corner setae on 90° projections (Figs 475, 477); tergites weakly sclerotised, soft and flexible (also two Coenobiina, five Ditropidina and two Cryptocephalina); loss of abdominal pleurites (Fig. 568) (not *Atenesus*); spermatheca with elongate collum (Figs 751-756; not markedly so in *Arnomus* and *Semelvillea*); kotpresse with lateral extensions (Fig. 820) (with *Platycolaspis*, *Leasia*, *Atenesus*); tuberculation of epicranium of larval head capsule (Figs 17-18) (*vide* Medvedev and Zaitsev 1978) (with some *Semelvillea* and *Arnomus*) and lack of epicranial keel (with *Platycolaspis*, *Leasia* and *Atenesus*). In Stylosomina the procoxal cavities are closed by insertion of the prosternal process into the hypomeron (Figs 114, 474), as in *Semelvillea acaciae*, but in *S. nothofagi* and *Arnomus* the two structures merely touch (Figs 476, 478) and in the other genera the procoxal cavities are open (Figs 111-113). In Stylosomina and Platycolaspina the aedeagus is symplesiomorphic, with dorsal and ventral setae (Fig. 637), and there is no abruptly declined scutellum (Fig. 139), although it is reduced to a small tubercle in Stylosomina (Fig. 505). Stylosomina are small beetles (< 3mm) like *Platycolaspis* and *Leasia*. They differ from the Platycolaspina in several ways, including presence of distinct pronotal teeth (Fig. 114) (a plesiomorphy), although these are suggested in *Atenesus*, divided kotpresse sclerites (Fig. 820) and lack of a scutellum (Fig. 505) (autapomorphies).

The similarities listed above are considered sufficient to consider these two groups as sister-taxa, but insufficient to merge them in any taxonomic category.

The phylogenetic closeness of Stylosomina to Platycolaspina is of considerable biogeographical interest. *Stylosomus* is distributed from the Mediterranean basin through the Himalaya to West China, whereas Platycolaspina are restricted to Australia and New Zealand.

Chapuis (1874) placed Stylosomina in Cryptocephalini + Pachybrachini, but suggested that they were intermediate between Clytrini and Pachybrachini. Sharp (1876) allied *Arnomus* and *Stylosomus* and suggested that these were basal groups in the Cryptocephalini + Pachybrachini, without providing reasons.

8.5.2 Stylosomina

The Stylosomina were generally isolated as a taxon in the numerical analyses, sometimes as sister-group to all remaining Cryptocephalini (AL(i), AA(iv)), but more often related to a portion of the Cryptocephalini which included some or all of the Platycolaspina (for example AL(ii), ALA(i-v)).

The tribe consists of the small Eurasian genus *Stylosomus*. In adult characters *Stylosomus* is very distinct with many autapomorphies, for example lack of scutellum (Fig. 505) and presence of divided but laterally expanded transverse kotpresse sclerites (Fig. 820). Other differences from Platycolaspina include : subapical antennomeres with well-defined pits for basiconic sensilla (Fig. 358); pygidium half exposed in male; sternites V and VI fused (also *Semelvillea nothofagi*). The polarity of the first two states is uncertain. The larva (Zaitsev and Medvedev 1978) is unridged on the head but microtuberculate on the whole epicranium and the setal pattern is unremarkable and similar to *Cryptocephalus*. The adult of *Stylosomus* has been distinguished from other Cryptocephalinae by the combined lack of canthus, pronotal teeth and scutellum. The canthus is also lacking from Platycolaspina and there are very distinct elongate pronotal teeth present, similar to those of *Aporocera* (*Diandichus*) (Fig. 114).

The other genera hitherto placed in Stylosomini (Seeno and Wilcox 1982), *Arnomus* (Sharp 1876) and *Atenesus* (Weise 1923), show some similarity to *Stylosomus* but share more apomorphies with genera of Platycolaspina.

8.5.3 Platycolaspina.

The Platycolaspina were rarely monophyletic (AA(iv), ALA(v)) in the various analyses, being completely dissociated (AA(ii)), serially associated (AL(i)), or mixed with *Stylosomus* (AL(ii), AA(i), ALA(iv)) or Clytrini (ALA(i)). When monophyletic the genera separated into two groups : *Arnomus* + *Semelvillea* and *Platycolaspis* + (*Leasia* + *Atenesus*) (ALA(vi)). This phylogeny is followed here (Fig. 949).

All genera share the following probable apomorphies : basiconic antennomere sensilla scattered, not concentrated in apical discs (Figs 88-92); hind margin of pronotum flat or bordered, without teeth (Figs 161-170), except teeth faintly present in *Atenesus*; abdomen covered by elytra, at least in males (Figs 149-150, 307-308). These synapomorphies are based on rather weak characters but they hold together two groups of genera which do not fit easily into any other association with members of the other four tribes. The genus *Platycolaspis* is somewhat intermediate between the two groups, but is more strongly associated by synapomorphy with *Leasia* and *Atenesus*.

8.5.3.1 *Atenesus*, *Leasia* and *Platycolaspis*

These genera of small (most <3mm) black or brown beetles share the following possible synapomorphies : short antenna; open procoxal cavity (Figs 111-113, 125-126); densely strigose mes-epimeron sculpture (Figs 125-126); stilleto-type ejaculatory guide (Fig. 638) (not all *Atenesus* spp.; Fig. 630); spermatheca with elongate collum (Figs 752-756; also *Stylosomus*); modified kotpresse with laterally extended transverse sclerites (Figs 828-830). The larva combines lack of a ridge or tuberculation on the head capsule (Figs 15, 30-32, 197, 200, 202, 204) (except *Platycolaspis* with tubercles along frontal sutures), with a plesiomorphic mandible type (Figs 198, 201, 203, 205). The originally monotypic genus *Leasia* only differs from *Agetinella* by secondary male sexual characters and the two genera are therefore synonymised, *Leasia* having priority (see chapter 9).

The genera *Leasia* and *Atenesus* are closely related, especially as seen in the adults, with the following synapomorphies : adult : basal margin of pronotum narrowly produced medially, the lobe semicircular or triangular (Figs 162-166); lobe of hypomeron much shorter than gap between it and prosternal process (Figs 111-112); elytral epipleura abruptly attenuate (Figs 149-150); abdominal spiracles fused with tergites; larva : head capsule atuberculate (Figs 30, 32); distance Dts1-2 less than distance Dts2-3 (Figs 207, 254). *Leasia* species have the following probable synapomorphies : adult : head and pronotum densely and evenly isodiametrically microsculptured (Fig. 67); dorsal punctures fine; antennae shorter than 1.5 head width; posterior lobe of pronotum triangular; apical angles of scutellum rounded or obtuse (Figs 167-170); larva : setae Fs5-6 papillate, narrow (Figs 200, 202). *Atenesus* species are not so well-defined synapomorphically, but have the following characteristics : adult : apical antennomeres rugosely sculptured, with setae and sensilla set in pits and ridges between (Fig. 89); long thin setae present on internal margin of lacinia; abdominal pleurites free (plesiomorphy); apex of median lobe of aedeagus either strongly produced or upturned (Figs 625-636), compared with *Leasia* and *Platycolaspis*; larva : setae Aes1, Aes3-4, Fs1-3 not papillate but only slightly clavate at apex (Figs 46, 204); spiracle plates with <10 cells (Fig. 58); The distinctive deeply cleft labrum of *Atenesus cassiae* (Fig. 66) is unfortunately not diagnostic for the whole genus.

Platycolaspis shares some apomorphies with *Arnomus* and *Semelvillea* : adult : lateral abdominal lobe unsclerotised dorsally; larva : Aes1 papillate and broad (Fig. 31), femora spiculate (Fig. 255). It also shares some apomorphies with only *Semelvillea* : claws appendiculate; basal border of sternite III curving posteriorly before reaching lateral margin, larval tarsungulus angulate at base. *Platycolaspis* is included with *Leasia* and *Atenesus* because of the shared synapomorphies with these and lack of synapomorphies with both *Arnomus* and *Semelvillea*. Autapomorphies for *Platycolaspis* include the open wing cell Rt.

Leasia and its synonym *Agetinella* were described in the Clytrini and Eumolpinae respectively (Jacoby 1907, 1908). *Platycolaspis* was also placed in the Eumolpinae (Jolivet 1908). Monrós (1951b) made a morphological study of *Leasia* with the bizarre conclusion that it did not even belong to the Chrysomelidae and this conclusion has been maintained (Jolivet 1957; Seeno and Wilcox 1982). The Australian Eumolpinae were last revised in 1915, but *Platycolaspis* and *Agetinella* were only mentioned (Lea 1915a) and both remain in Eumolpinae (Seeno and Wilcox 1982). The original description of

Atenesus noted its similarity to *Stylosomus*, but that the scutellum was visible and the upper surface glabrous (Weise 1923).

8.5.3.2 *Arnomus* and *Semelvillea.*

These two genera were always paired in numerical analyses, usually in proximity to other Platycolaspina and to Stylosomina.

Arnomus and *Semelvillea* have many shared features including the following apomorphies : adult : all sides of pronotum distinctly and usually broadly margined (Figs 307, 893, 897, 898); dorsal transverse sclerite of kotpresse either obliquely directed basally or with a lobe of this shape (Figs 821-827); larva : mandible with tooth5 absent or barely expressed (Figs 194, 227); epicranium angulate or keeled (Figs 16-18); surface of tibia and femur spiculate (Figs 196, 253); venter of tarsungulus angulate. Symplesiomorphies or non-polarised character states include : apex of prosternal process convex (Figs 109-110, 475, 477); epipleuron gradually attenuated to apex (Fig. 307); abdominal spiracles free (Fig. 568); ejaculatory guide well-developed, convoluted (Figs 603, 607, 613, 617, 624); dorsal and ventral rectal sclerites not extending beyond sides of rectum (Figs 821-827); sharply pointed rectal sensilla. The two genera are superficially very similar to some *Aporocera* species, but differ considerably in larvae, male and female genitalia and kotpresse.

There may be some argument for uniting this obvious taxon pair as one genus. I have seen all described species of *Arnomus* and describe eight species of *Semelvillea* (chapter 9) and the two groups have several constant character differences but these may all be autapomorphic for *Semelvillea*. *Semelvillea* has larger eyes, with slight canthus (Figs 894, 896, 899; except S. nothofagi, Fig. 69), prosternal process strongly narrowed medially (Figs 109-110, 475), scutellum elongate (Figs 893, 897, 898), sutural locking mechanism evanescent before apex (Figs 893, 897, 898), claws appendiculate and apex of aedeagus produced and usually with long setae (Figs 157-158, 600-615). In *Arnomus* the eyes are smaller and without a canthus (Fig. 334), the prosternum broad (Fig. 477), the scutellum shorter (Fig. 308), the suture complete (Fig. 308), claws simple and apex of aedeagus simple (Figs 622-623). Sclerotisation of the kotpresse is reduced, possibly autapomorphic, in all *Arnomus* spp (Fig. 827). The larval head capsule of *Arnomus* sp. (Figs 18, 35) is similar to that of *Semelvillea acaciae* (Figs 17, 33), but the epicranial sculpture may be plesiomorphic (also present in *Stylosomus*) and the spiracles of *Semelvillea* are different (plesiomorphic in *Arnomus*).

When describing the genus *Arnomus*, Sharp (1876) suggested it was allied to *Stylosomus* and should be placed "at thebeginning" of the Cryptocephalini, without providing any reason for this hypothesis. The widely separated coxae, cited as a difference between the two genera, are present in both (Figs 114, 477).

8.5.4 Coenobiina, Ditropidina and Cryptocephalina

The three subtribes Coenobiina, Ditropidina and Cryptocephalina were never resolved as a monophyletic group in numerical analyses but were either paraphyletic (AA(iv)) or polyphyletic (AL(i),(ii), AA(i),(ii), ALA(i),(iv),(v)), usually by inclusion of members of Platycolaspina and Stylosomina. When the three subtribes were deliberately made a monophyletic group the resultant tree was many steps longer than the minimum-length tree for the same data set (ALA(v)). This is hardly convincing evidence for their monophyly! Nevertheless there is no better evidence for a different arrangement of the five subtribes of Cryptocephalini, nor for the combination of any of these subtribes with another tribe of Cryptocephalinae. The proposed phylogeny of the three subtribes is illustrated in Fig. 955.

The compact, squat, members of the Cryptocephalina, Coenobiina and Ditropidina contain the bulk of species of Cryptocephalini. Of these subtribes, the Coenobiina and Ditropidina are both distinct, synapomorphically defined, monophyletic groups but each may lie within the Cryptocephalina rendering the latter paraphyletic. The three subtribes share the following probable synapomorphies to the exclusion of Stylosomina and Platycolaspina : posterior margin of eye smoothly or abruptly truncately flattened (the eye is never hemispherical and if apparently evenly convex is only so in species with very small weakly convex eyes; Figs 71-74, 335-350); scutellum abruptly elevated (Figs 137-138, 141, 143, 506, 512, 513, 519); basal flange of mesonotum below scutellum angulate, bilobed or truncately produced (Figs 506-519); at least half of pygidium exposed (not some Australian species, for example *Aporocera* (*Diandichus*) *analis*, *Cadmus* (*Brachycaulus*) *ferrugineus*, state present in *Stylosomus*); larval foreleg with sensillum Ptsm1 closest to seta Dats1 (Figs 260-263) (not *Ditropidus* sp. 865, *D. pilula* or *D.* sp.862); moniliform larval spiracles present on abdomen (Figs 59-60) (several exceptions in Ditropidina and Cryptocephalina). The presence or absence of abdominal moniliform spiracles varies between closely related species in Cryptocephalina but the abdominal spiracles are always cribriform in Platycolaspina. The presence of interlocking teeth at the base of the elytral suture could also be a synapomorphy for Coenobiina, Ditropidina and Cryptocephalina (teeth are completely absent from Platycolaspina and Stylosomina), but only a few Australian Cryptocephalina show this state. One character-state which I overlooked is the presence of almost right-angled projections at the sides of the dorsal surface of the posterior foramen of the prothorax (Figs 480, 483, 494, 495), but these are weakly expressed in some Australasian species (Fig. 497). It appears to be synapomorphic for Ditropidina, Coenobiina and Cryptocephalina. The distribution of most of the attributes listed above is confused in non-Cryptocephalini so it is not possible to conclusively state polarities but these are probable apomorphies. I am unable to find any characters which define any other combination of the five tribes as a monophyletic group.

Adults of Coenobiina and Ditropidina superficially appear to be closely related and the Coenobiina have until now always been associated with *Ditropidus* and allies. Probable synapomorphies for their combined monophyly are : prosternal process parallel sided and laterally ridged (Figs 106-108, 479, 482); middle of the prosternal anterior border truncate or even convex (not used as a character in analyses; Figs 106-108), in contrast to Cryptocephalina (Figs 105-107); stepped scutellar base (Fig. 506) (not present in *D.* sp. 865, Fig. 510, and scutellum absent in *Adiscus*, Fig. 508) and the narrow-lobed pronotal base (Figs 106-108) (not *Coenobius*, which at least lacks a truncate lobe, Fig. 479). These two features may be correlated. The aedeagus in both groups is similar with one to a few long dorsal setae, laterally placed (Figs 154-156; not listed as a character and dorsal setae absent in *Adiscus*). The parallel ridged form of the prosternal process in the group of genera *Lexiphanes*, *Stegnocephala* (Fig. 492) and *Diachus* (Fig. 117) is apparently homoplasious because the whole process is of different shape, being basally contracted. The larvae of Coenobiina and Ditropidina are completely different, although only one species of Coenobiina is known. The distinct 2+4 frontal setal pattern of *Aprionota* may be plesiomorphic (Fig. 208) and the distinct mandibles of Ditropidina are certainly autapomorphic (Figs 228-232). Sensillum Fsm1 is always adjacent to seta Fs2, but this relatively weak state is also present in *Aporocera* [*Loxopleurus*] sp. nr *inconstans*. Neither larval type has cephalic keels, strong tuberculation or pitting, but the legs show little resemblance. I think there are sufficient differences between the two groups to maintain them as separate subtribes while acknowledging that they form a monophyletic unit.

The subtribe Monachina Chapuis 1874 (name preoccupied by Monachina Gray 1869 in Pinnipedia) is synonymised here with Cryptocephalina. The type genus of Monachina Chapuis is *Lexiphanes* which is phylogenetically close to *Cryptocephalus*. Both adult and larva of *Lexiphanes* lack any of the autapomorphies of either Ditropidina or Coenobiina. The Cryptocephalina share the compact body structure of Ditropidina and Coenobiina, except in a few aberrant Australian forms, such as *Aporocera* (*D.*) *analis* Chapuis. Taxa such as *Diandichus* provide exceptions to nearly every generalisation one can otherwise make about Cryptocephalina, but at the same time are definitely members of this group through their close relationship with other more typical Australian taxa. A possible synapomorphy for Cryptocephalina is the truncate basal lobe of the pronotum with larger teeth at corners but this is absent from *Aporocera* (*Diandichus*) and a few other Australian Cryptocephalina.

Previous classifications of the Cryptocephalini have placed the Coenobiina, Ditropidina and some genera with short antennae together in 'Monachini' (Chapuis 1874, Seeno and Wilcox 1982), the remainder forming Cryptocephalini. This distinction based on antennal length is vague and has led to genera like *Melixanthus* being placed in either group and the misidentification of *Coenobius* species (Weise 1903). LeSage (1984a, 1986) showed that the larvae of *Lexiphanes* and *Cryptocephalus* are almost identical.

The classification of the subtribes of Cryptocephalini presented here remains challengable but there are some very obvious close relationships between genera within each subtribe. Identification of these monophyletic groups helps in recognition of overall phylogeny. Recognised monophyletic groups of genera are listed below under their appropriate subtribal designation.

8.5.5 Coenobiina

The numerical analysis of the five species included in adult studies made the Coenobiina monophyletic and sister-group of *Lexiphanes* (AA(i)). The other analyses, using only *Aprionota,* gave the same result or made it sister-group to all other Cryptocephalini (ALA(v)). The association of Coenobiina and *Lexiphanes* was at least partly due to shared parallel keels on the prosternum (character A66 state (1)) which I now believe to be homoplasious. Subparallel keels are present on the prosternum of *Lexiphanes*, *Stegnocephala* and *Diachus* (all Cryptocephalina), but they are contracted at base because of the quite different shape of the prosternal process; a feature which was not utilised as a character. In the study of all five taxa the African and Pacific species were separated as two monophyletic groups (AA(i)). The proposed phylogeny of the genera is shown in Fig. 956.

The subtribe Coenobiina is a distinct group on external and internal morphology but the species are generally very small (mostly 1-3 mm) and may be confused with Ditropidina. The following probable adult synapomorphies are present : canthus deeply angulate and eyes very close together giving characteristic wedge shaped frons (Fig. 335) (similar to *Ditropidella*); eyes dorsally flat and head capsule completely retractable into prothorax (Fig. 64); frons grooved between antennal sockets; antennae without sensillate circular depressions (Figs 82-84); mandibular setae apparently absent (Figs 413-416); submentum without basal angles (Fig. 453); claws appendiculate; ejaculatory duct short, strongly sclerotised and very thick (Figs 642-645); vaginal palp characteristically narrow with relatively thick sclerotised apical edge (Figs 727-728); spermatheca reduced to bulbous pump-like structure with short duct (Figs 764-766). The kotpresse varied greatly in structure in my small sample, but all species except *Aprionota* [*Pycnophthalma*] *tutuilana* (extremely reduced; Fig. 832) had the ventral transverse sclerite produced basally which is a possible symplesiomorphy. A few of the above attributes are found in non-Coenobiina, but rarely in Ditropidina. Possible larval apomorphies are the development of broad papillate setae, otherwise only present in Cryptocephalina, and seta Des1 papillate (also some Cryptocephalina), but it is probably unwise to list apomorphies on the basis of a single species. A probable larval plesiomorphy is the distant position of Aes4 from the frontal suture.

The analyses separated the African and Australasian species. Possible synapomorphies for the African species : segment 2 of labial palp longer than 3 (cf. Fig. 453); pronotal teeth longer than broad; subscutellar lobe of mesonotum bilobed; external margin of tibiae widely excavate; apex of ♀ tergite VIII deeply excised. Possible synapomorphies for the Australasian species : scutellum elongate, rectangular or triangular (Figs 137, 507); pygidium with a strong transverse biconvex ridge (compare Figs 570 and 571).

Three genera are recognised here : *Aprionota* (Australasian species), *Coenobius* and *Isnus* (African species). I include *Pycnophthalma* within *Aprionota* because the two quite different type species represent extreme points in a morphological cline which has its greatest diversity in Fiji. For similar reasons, it is possible that further study would show that *Coenobius* and *Isnus* should be synonymised. The myrmecophilous *I. petasus* Selman (1962) probably belongs to Coenobiina but should be redescribed because the original description does not include any tribal or generic characters. It is the only known myrmecophile in the Cryptocephalini.

Isnus (Weise 1898) was described for small 'Monachini' with transverse antennal club segments, triangular basal pronotal lobe and close but not holoptic eyes. Weise (1903) noted differences between the African and Asiatic species of *Coenobius* and it is possible that the Asiatic species he mentioned belong to *Aprionota*. He also noted that some *Coenobius* species did not key out in 'Monachini' *sensu* Chapuis 1874 because of their long antennae, weak posterior pronotal lobe or truncate prosternal process. The form of the spermathecal pump and the ejaculatory duct define the Coenobiina and show that antennal length, eye shape and pronotum shape are variable characters in this subtribe.

Aprionota and *Pycnophthalma* were both described from single species from Samoa (Maulik 1929). *Pycnophthalma* was intended to receive the bulk of Australasian species of *Coenobius*, but Maulik did not differentiate the two genera. *Aprionota* was compared with *Ditropidus*, but not, remarkably, with *Pycnophthalma*. Here *Aprionota* is made the senior synonym of *Pycnophthalma*, by page priority. *Aprionota* clearly belongs to Coenobiina and is not a synonym of *Ditropidus* (Gressitt 1956). Furthermore, *Aprionota* includes all (!) of the Coenobiina, Ditropidina and Cryptocephalina described from Fiji (Bryant and Gressitt 1957), the *Coenobius* of Micronesia (Gressitt 1955; including *Cephalocryptus*), and most of the Australian species described in *Coenobius* by Lea (1920a, b). Probably many of the New Guinean species described in *Elaphodes*, *Ditropidus* and *Coenobius* (Gressitt 1965) belong in *Aprionota*. The range of morphological diversity in the sample of western Pacific Coenobiina available to me mirrors the morphological diversity of Ditropidina or Cryptocephalina,except that there is no significant secondary sexual dimorphism.

The larva of only one species is available, *A. inconstans* (Lea), which limits the credibility of the larval definition. This larva shows an interesting mixture of autapomorphic and plesiomorphic states. The scatoshell of *A. inconstans* is unique amongst the Camptosomata in having short cross-ridges between the evenly formed spiral ridges (Fig. 173). The pupa is unknown.

8.5.6 Ditropidina

The Ditropidina were almost always monophyletic in numerical analyses, but the internal phylogenies showed great variation in structure. As a whole the Ditropidina were sister-group to : almost all other Cryptocephalini and Pachybrachini (AL(i)), but paraphyletically with Cryptocephaline A; all other Cryptocephalini except Coenobiina (AL(ii)); *Melixanthus* (AA(i)); Coenobiina + *Lexiphanes* (AA(iv)); Coenobiina, Cryptocephalina and Pachybrachini (ALA(i)); Coenobiina and Holarctic Cryptocephalina (ALA(iv)); and Stylosomina, Platycolaspina and Cryptocephalina minus *Lexiphanes*. In studies which included *Adiscus*, this genus was sister-group to the remaining Ditropidina. The numerical studies suffered from lack of range to encompass all variation of the 250+ species in the subtribe and this lack was manifested in two ways : some peculiar species or species-groups were omitted which may have had some supraspecific validity and intermediate forms were not included allowing some terminal taxa to be artificially discretely different (for example *Ditropidus* [*Prasonotus*] *submetallicus*). The proposed phylogeny of the genera of Ditropidina is illustrated in Fig. 956.

Monophyly of the Ditropidina is not supported by universal adult synapomorphies which include *Adiscus* and the larva of *Adiscus* is unfortunately unknown. *Adiscus* and Ditropidina are almost certainly sister-groups. It is therefore reasonable to assume that attributes shared between *Adiscus* and at least some other Ditropidina, but not Coenobiina or Cryptocephalina, are synapomorphic. Combination of these states with the larval synapomorphies of available Ditropidina gives the following list of synapomorphies : adult : hind margin of pronotum toothed and produced as a narrow triangle (Figs 107-108; only weakly so in some taxa, for example *Ditropidus* [*Tappesia*] *saundersi*); scutellum fusiform to ovoid, broadest near middle (absent from *Adiscus*, almost quadrate in *D.* [*Tappesia*] *saundersi* and circular in two Coenobiina); scutellar microchaetae arranged in a narrow strip (Fig. 138; also *Melixanthus* and not *D. sp. WA*); larva : mandible characteristic, with a strong central tooth on the internal edge (Figs 228-232); sensillum Csm1 dorsal to seta Cs1 (Figs 212, 215, 218, 220) (not *Ditropidus* [*Polyachus*] sp. 865); triangular epipharyngeal sclerotisation present (*vide* Kasap and Crowson 1976, Fig. 14); apex of labrum rounded to shallowly concave; prothoracic spiracles at least twice as large as abdominal spiracles. In the kotpresse of both *Adiscus* and other Ditropidina there is no basal median extension of the ventral transverse sclerite (Figs 834-841), as seen in most Coenobiina (Figs 831 and 833) and some

Cryptocephalina (Figs 842, 845, 847), but the sclerites are otherwise variable. Plesiomorphic attributes in Ditropidina which are unique in the Cryptocephalini include presence of lateral lobes on metendosternite (*Adiscus* only) and larval frontoclypeal suture internally thickened.

The eyes of *Adiscus* are similar to Hoarctic Cryptocephalina (for example *Melixanthus*, Figs 348, 350) in shape and size but such a relationship is rejected by the different epipleura (Fig. 559), basal pronotal lobe (Fig. 489), antenna (Fig. 363), prosternal process (Fig. 489) and other features.

8.5.6.1 *Adiscus*.

The genus *Adiscus* is the sister-group to the remaining Ditropidina. Synapomorphies for *Adiscus* include : longitudinal grooves and ridges on prosternal process (Fig. 481); no externally visible scutellum (Fig. 508); cell 2A extremely small compared with 1A; no dorsal aedeagal setae (Fig. 646); vaginal palp deeply internally lobed (Fig. 729); ventral transverse sclerite of kotpresse divided and not reaching sides of rectum (Fig. 834). *Adiscus* also has some interesting plesiomorphic traits, such as retention of lateral metendosternite lobes (Fig. 538) and multiple digitiform sensilla on the maxillary palp. The elongate flat eyes with relatively broad and shallow canthus may be plesiomorphically shared with Holarctic Cryptocephalina, or may be autapomorphic amongst Coenobiina and Ditropidina and a result of the extreme reduction in size of the head capsule and its retraction into the pronotum. *Adiscus* is a south and south-east Asian genus with no Australian species and the larva and pupa are unknown.

8.5.6.2 Other Ditropidina

In all PAUP phylogenetic analyses the Ditropidina excluding *Adiscus* were represented by at least seven species. In the larval analysis AL(i) (in which the sister-group of ditropidine taxa was most of Cryptocephalini) the seven Ditropidina were not monophyletic (Fig. 925). In the adult analysis AA(i) the 16 species were monophyletic and *Adiscus* was the sister-group (Fig. 933). *Ditropidus* [*Prasonotus*] *submetallicus* and

Ditropidus sp. nr *antennarius* were successive sister-groups of the remaining species. The two *Ditropidella* species were paired, with *Ditropidus* sp. WA as sister-group. The three *Ditropidus* [*Elaphodes*] species were widely separated. The pattern of variation of characters like sensory antennal segment number, shape of epipleuron and dorsal vestiture did not match the cladistic distribution of taxa. In AA(ii) (sister-group of ditropidine taxa Lamprosomatinae, Chlamisini, Coenobiina and part of Cryptocephalina) the seven species were arranged as a 'Hennigian comb' (Fig. 937) with, successively, *Ditropidus* [*Polyachus*] sp. 865 and *P. submetallicus* as the most basal species and with the two *Ditropidella* species paired. The combined data analysis ALA(ii) (Fig. 944; sister-group of ditropidine taxa Holarctic Cryptocephalina and Coenobiina) of seven taxa gave a similar clade to AA(i), with *D. submetallicus* and *D. antennarius* successive sister-groups of the remaining species and *Ditropidus* sp. FO and the two *Ditropidella* species in the same clade.

Analysis ALA(vi) was an attempt to determine phylogeny using selected characters with the Coenobiina as outgroup. The minimum-length tree (Fig. 950), with a relatively low CI, gave *Adiscus* as sister-group to all other Ditropidina as expected, followed by *Scaphodius*, *Ditropidus* [*Bucharis*] *suffriani* and *D.* [*Prasonotus*] in sequence. However this tree was only one step shorter than many others with quite different arrangements of Ditropidina above the branch to *Adiscus*. Therefore I do not regard these numerical phylogenies as more than guides for the following discussion.

The Ditropidina excluding *Adiscus* are monophyletic and have the following synapomorphies : fusion of sternites V and VI (Fig. 573) and loss of lateral lobes of metendosternite (Fig. 541). Some of the larval character states used for Ditropidina may only apply to the Ditropidina excluding *Adiscus*.

The many so-called genera in this part of the Ditropidina were originally separated by very minor variations in shape of the prosternal process, antennal segments and pronotal borders, or by secondary sexual characters. The following available names have been applied to taxa included in this section of Ditropidina : *Bucharis*, *Ditropidus*, *Elaphodes*, *Euditropidus*, *Nyetra*, *Pleomorpha*, *Pleomorphus*, *Polyachus*, *Prasonotus*, *Scaphodius, Tappesia* (Seeno and Wilcox 1982). *Tappesia* is included in Ditropidina for the first time, although Baly (1877c) clearly related it to *Elaphodes* in his original description and it was described as a species of *Elaphodes* by Lea (1921b). *Pleomorpha* and *Ditropidus* have always been placed in synonymy since the original description of *Pleomorpha* and their type species are similar. The characters separating the remaining taxa from *Ditropidus* are of two types, with either graded or discrete states.

The graded characters (antennal length, prosternal length and shape, structure of basal pronotal lobe) may have been discrete for the small sample of species available to early authors but are no longer workable. *Bucharis* was separated from *Ditropidus* by having an undivided basal pronotal lobe but Lea (1921c) noted overlap in the generic characteristics of *Bucharis* and *Ditropidus*, effectively synonymising the two, although he did not examine type species. The sample of Ditropidina illustrated here (Figs 119, 481, 482, 485-487, 489, 491), which includes the type species of *Bucharis* (Fig. 486), shows that the ventral groove of the posterior lobe may be of variable shape and may cut into the posterior margin to various degrees. *Elaphodes* and *Ditropidus* were originally separated by relative length of antennal segments (Chapuis 1874, Lea 1920a, b, 1921a, b, c), but this changed to the single criterion of presence or absence of dorsal pubescence (Gressitt 1965). There is certainly a trend towards species either having relatively long antennae and pubescence or short antennae and no dorsal pubescence. However, the long antennae of typical *Elaphodes* (Fig. 87) may be found in glabrous *Ditropidus* species (Fig. 362) and many *Ditropidus* with short antennae are pubescent. The genera *Pleomorphus*, *Prasonotus*, *Scaphodius* and the *Ditropidus* + *Elaphodes* combination were only separated by shape of the prosternal process (Chapuis 1874). These differences in shape are also unworkable as monothetic characters. For example, compare the supposedly diagnostic elongate prosternal process of *Prasonotus* (Fig. 108) with that of *Ditropidus* (Fig. 107). The posterior margin of the prosternal process is concavely excavate to varying degrees in almost all Ditropidina and I am unable to separate triangular (*Pleomorphus*) from semicircular (*Prasonotus*) excavations. Furthermore the supposedly diagnostic straight-edged process of *Scaphodius* is really slightly concave (not figured), but this shape of process does occur in a few *Ditropidus* species including *D.* [*Tappesia*] *saundersi* (slightly convex; Fig. 482).

Polyachus and *Euditropidus* were created for species with an extra antennal club segment (Chapuis 1875a; Lea 1920a), which is a discrete character state. In Ditropidina the club segments are distinguished by presence of a sensory pit of basiconic sensilla which may be present (*Polyachus* and *Euditropidus*; Fig. 85) or absent (Fig. 87) on antennomere 6. This character is sexually dimorphic and overlooked in some morphologically diverse species hitherto placed in *Ditropidus* (Fig. 362), *Polyachus* and *Elaphodes*. Furthermore, some species described in *Elaphodes* have six-segmented antennal clubs in both sexes. The distribution of states of this character suggests that it is only of limited use and the type species of *Euditropidus* and *Polyachus* are otherwise hardly distinguishable from 'typical' species of *Ditropidus*. The prevailing number of sensory segments in *Ditropidus* is five.

Male secondary sexual characters vary greatly in the Ditropidina, as they do in all Cryptocephalinae. Thus there are many species with enlargement or modification of the mandibles and other mouthparts, which is usually associated with increased head width (Figs 340-342). Some males have enlarged forelegs or enlarged antennae (Fig. 362), but modifications to the abdomen appear to be absent. Such secondary sexual characters are scattered throughout the Ditropidina. For example, enlarged mandibles without clypeal modification are found in some *D.* [*Elaphodes*] species, a red and green species-group based on *D. ruficollis*, and the quite unrelated yellow and black species-group based on *D. dimidiatus*. Lateral projections on the clypeus are found in *Scaphodius*, *D. cornutus* and members of the *D.* [*Polyachus*] *bicolor* species-group. Various secondary sexual characters are therefore frequently convergent in Ditropidina and should be used to describe species-groups with caution.

A further indication of the limited value of the traditional characters is that one species (*D. maculicollis*) has been independently described in three different genera (*Ditropidus*, *Polyachus* and *Euditropidus*). The sexes of the *Ditropidus antennarius* species-group would be placed in quite separate sections of this assemblage because of their dimorphic antennae.

This large group of taxa, Ditropidina minus *Adiscus*, has generally been considered as a single unit, although *Ditropidus* [*Prasonotus*] has been included in the Cryptocephalina (Lea 1904) and *Ditropidus* [*Tappesia*] *saundersi* has been put in Cryptocephalina by cataloguers (Clavareau 1913; Seeno and Wilcox 1982). It is essentially Australian with a few species in New Caledonia, New Guinea and a few islands west of New Guinea. The only New Zealand species, described in *Scaphodius* (Sharp 1881), is a *Ditropidus*. It was described from a single specimen which remains the only specimen of Ditropidina recorded from New Zealand and was therefore probably either incorrectly labelled or an accidental introduction. Many species have been described in this section of the Ditropidina from Fiji (Bryant and Gressitt 1957) and Vietnam (Kimoto and Gressitt 1981) but these are almost certainly all Coenobiina. Some New Guinean species described in *Elaphodes* and *Ditropidus* (Gressitt 1965) also belong in Coenobiina; Gressitt's descriptions of these genera are incorrect. The vast bulk of species are therefore Australian and have been fairly thoroughly revised (Lea 1903a, 1920a,b, 1921a, b, c; Weise 1903, 1908, 1916, 1923) within the early classification of Chapuis (1874). Lea and Weise commented on the discrimination of genera but made no phylogenetic observations. In dealing with individual species, a lack of distinction was noted between *Ditropidus* and *Bucharis* (Lea 1921c; Weise 1923), *Ditropidus* and *Prasonotus* (Lea 1921c) and *Ditropidus* and *Elaphodes* (Lea 1920a,b) and five genera were recognised (Lea 1920a). When inadvertently describing *Tappesia saundersi* (as *Elaphodes multimaculatus*) Lea (1920a) noted similarities to other *Elaphodes* species. Lea noted that *Euditropidus* was only separable from *Ditropidus* by the extra sensory antennomere (Lea 1920a) and that in using sensory antennomeres as a generic character he was following the precedent of Baly and Chapuis.

The main problems arising from the present study are that it difficult to recognise morphologically discrete groups and to create monophyletic groups without leaving a paraphyletic residue. The latter problem is partly due to difficulties in polarising characters but also due to the small size of the monophyletic species groups which do not leave a synapomorphic residue. Three genera are recognised, *Scaphodius*, *Ditropidella*, *Ditropidus*, with the genus *Ditropidus* holding the vast majority of species.

8.5.6.3 *Scaphodius*

In analyses *Scaphodius* was resolved as the sister-group of *D. saundersi*, in AA(i), or all other Ditropidina except *Adiscus*, in ALA(v).

This is a monophyletic group of about 15 species. *Scaphodius* was revised by Fauvel (1907), who included three species. Here it incorporates the monotypic genus *Nyetra* (which was distinguished by male secondary sexual characters; Baly 1877a), because there is a range of (undescribed) intermediates. *Scaphodius compactus* Sharp, described from New Zealand, is an ordinary species of *Ditropidus*. Conversely, the species of *Ditropidus* described from New Caledonia (Fauvel 1907), and probably the species of *Lexiphanes* (=*Monachus*) (Montrouzier 1861), belong to *Scaphodius*. The densely longitudinally strigose pronotum of *S. strigicollis* is found in four other species but the males of the non-strigose species in *Scaphodius* have elongated mandibles and often other bizarre modifications to the mandibles and clypeus.

Scaphodius is considered a valid genus, confined to New Caledonia and the Loyalty Islands. The following possible synapomorphies are present : male with elongate mandibles (at least as long as eyes) and clypeal border produced in middle (Figs 341-342), or at sides; antennae long and thin (segments elongate); eyes small, not excavate internally, convex (Figs 341-342); head relatively broad, pronotum not strongly constricted anteriorly; pronotum anteriorly produced, hooding head; hind-angles of pronotum projecting posteriorly; elytra puncture-striate or with smooth interspaces between finely and densely punctured strial grooves; front legs of male often enlarged; claws appendiculate; median lobe of aedeagus elongately produced (Fig. 661). The elytral epipleuron is always feebly lobed and the dorsal transverse sclerites of the kotpresse extend beyond the rectum (Fig. 635). The maxillary palp is plesiomorphic, with more than five digitiform sensilla in a row. The larva is unknown, but a female specimen of an undescribed species has a scatoshell attached to the abdomen. This scatoshell is remarkably similar to that illustrated for *Aporocera* (*Diandichus*) (Fig.2) and may be synapomorphic for *Scaphodius* within the Ditropidina.

I have collected material of an undescribed species of *Ditropidus* in Western Australia superficially similar to *Scaphodius strigicollis*. This species (*Ditropidus* sp. 1041) has small shallowly excavated eyes, a densely strigose pronotum and appendiculate claws but the head is narrow with flat eyes, the pronotum without posteriorly projecting hind-angles and the body shape is quite different. Some species of *Ditropidus* [*Elaphodes*] are similar to the female of *Scaphodius* [*Nyetra*] *forcipata* but always have an angulate canthus, confused elytral punctation and a straight clypeus if the mandibles are enlarged (the mandibles are never elongate).

Scaphodius is a distinct monophyletic group of species. Giving it generic rank is partly influenced by its biogeography, but *Scaphodius* appears to have no Australian or New Guinean members and it is difficult to determine its closest relatives. The scutellum and prosternum/mesosternum junction are typical of *Ditropidus*. The eye shape, elongate antennae, produced pronotum, appendiculate claws and dorsal pubescence (in some species) suggest that the nearest living relative of *Scaphodius* may belong to *D.* [*Elaphodes*], as intimated by analysis AA(i).

8.5.6.4 *Ditropidella*

This taxon was included in analyses as two species for which larvae and both sexes were available. These species (*Ditropidella* spp. 5 and 738) were always paired in analyses (AL(i), AA(i),(iv), ALA(iv),(v),(vii)) and always placed as a sister-group to one or two species well within the clade of Ditropidina which were usually *Ditropidus* sp. WA and/or *D.* sp. 438. The analyses therefore indicated monophyly but not rank.

This genus includes approximately 15 species (four described) which would hitherto have been placed in *Ditropidus* but show distinct adult and larval features : adult : size small (< 3mm); canthus less than 90° and eyes large and close (Fig. 339); frons usually produced medially (Fig. 339); gena long, impunctate; clypeal region between and below antennae with triangular demarkation (Fig. 339); pronotum very transverse; anterior border of pronotum strongly raised and constricted (collared); posterior lobe of pronotum raised and posterior angles produced (Fig. 488); elytra with strongly punctate striae and convex intervals; ventral transverse sclerite of kotpresse with lateral extensions and dorsal transverse sclerite small, not laterally extended (Fig. 839); larva : internal mandibular tooth weak and basal process obtusely rounded (Figs 219, 221); seta Aes1 distant from frontal suture (Figs 218, 220); seta Aes2 papillate (Figs 218, 220); one or more apical foreleg setae spatulate (Figs 257-258); distance Vts3-4 less than 0.5 length of either. In *Ditropidella* the adult antennae may have five (Fig. 364) or six (some males) sensory segments. A few species are longitudinally strigose on the pronotum like*Scaphodius striaticollis.*

Ditropidella appears to be monophyletic and well-defined as both adult and larva. In the adult the eyes, pronotal shape, elytral striae and small compact shape are similar to those of *Aprionota* species. If the genus *Adiscus* is ignored as an extremely autapomorphic sister-group, use of the Coenobiina would suggest that *Ditropidella* is the sister-group of the remaining Ditropidina; the eyes and pronotal characters would become probable plesiomorphies. However I suspect that the facial similarity is convergent, because the outline of the fronto-clypeal border and position of the antennae relative to the eyes is different in the two groups (contrast Figs 335 and 339). If the two groups are similar through convergence the nearest relative of *Ditropidella* is probably to be found among the small oval species of *Ditropidus* in south-eastern Australia, some of which have a raised posterior pronotal lobe and strongly striate elytra.

8.5.6.5 *Ditropidus* sensu lato including *Elaphodes*, *Euditropidus*, *Bucharis*, *Pleomorpha*, *Pleomorphus*, *Polyachus*, *Prasonotus* and *Tappesia*

Removal of the more distinct monophyletic groups listed above leaves a large number of species which form a probably paraphyletic group without any strong unifying characteristics, which would have to be either polythetically defined or further dismantled. Adults and larvae appear to be plesiomorphically defined. In adults, the eyes and head capsules are almost always of intermediate shape between *Scaphodius* and *Ditropidella* (Figs 336-338, 340). The antenna (Figs 86-87, 362), prosternum (Figs 107-108, 482, 490), pronotal posterior lobe (Figs 107-108, 482, 485-487, 491), scutellum (Figs 138, 509-510), male (Figs 650-659) and female (Figs 769-771, 773-776, 778-780) genitalia and kotpresse (Figs 836-838, 840) are all variable but without the combination of attributes characteristic of *Scaphodius* and *Ditropidella*. The larvae have simple tibial setae (Figs 217, 259-260), a prominent basal projection on the inner margin of the mandible (Figs 213, 216, 228-232), Aes2 simple, not papillate (Figs 212, 215; one exception) and Aes1 close to the frontal suture (Figs 212, 215).

These species of Ditropidina do not form well-defined monophyletic groups, or form monophyletic groups which are very small or separated from other taxa by one or two characters. Only a few adult characters vary in a discrete way, for example claw shape, and all possible permutations of these characters seem to exist. Larval characters, such as setal morphology, vary discretely but do not seem to be strongly genetically constrained. Therefore the whole group is treated as a single unit. This is a conservative approach, but at least the taxa are defined in a subtribe for future workers to disentangle if they see fit. In this large group I include the type species of *Bucharis*, *Ditropidus*, *Elaphodes*, *Euditropidus*, *Pleomorphus*, *Polyachus*, *Prasonotus* and *Tappesia*. Intermediate species can be found which link each of these although there is great morphological diversity. The account below gives a summary of the larger or more distinct monophyletic species-groups, their possible apomorphic character states and their possible relationships.

8.5.6.5.1 *Ditropidus* [*Prasonotus*] *submetallicus* species-group

The species *Ditropidus* [*Prasonotus*] *submetallicus* was used in all analyses. It was generally resolved at or near the base of each clade. For larval characters I studied *D. submetallicus* and *D.* [*Pleomorphus*] sp. 522 which is the same as a species labelled as *Pleomorphus* in the Chapuis collection.

This is a small group of about 15 species which is difficult to define. The type species of *Prasonotus* is quite distinct in surface sculpture, colour and size. It is obviously closely related to the other species hitherto placed in *Prasonotus* (for example *P. ruficaudis*) which in turn grade into the oval species of *'Pleomorphus'* and certain oblong species of *Ditropidus s. str.* (for example *D. anthracinus*) The species-group is weakly defined by the following combination of possible synapomorphies : adult : body elongate, somewhat parallel-sided (Fig. 310); relatively long antennae with elongate segments; junction of thorax and elytra flat in side view (Fig. 310); prosternal process quadrate to elongate, the apex bilobate (Fig. 108), the lobes overlapping the mesosternal process at sides, the visible portion of the mesosternal process quadrate to slightly transverse (Fig. 522) and convex; epipleuron sinuately lobed, with the posterior part of the lobe more abruptly bent (Fig. 310); larva (head capsule Fig. 212) : frons coarsely sculptured; tubercles adjacent to frontal suture on frons and top of epicranium; seta Aes1 papillate; seta Aes3 papillate and clavate; upper frontal setae papillate and clavate; tibiae spiculate. In the adult the head is inclined internally and has small eyes (length much less than distance between them) and a very short clypeus (Fig. 65), the posterior pronotal lobe is always large, the sides of the pronotum are usually explanate, the hind angles posteriorly produced (Fig. 108) and the claws are simple. Similar species include : *D. aurichalceus* with small eyes and the same prosternum and mesosternum, but short antenna, less sinuate epipleuron and appendiculate claws; *D. tarsatus*, dorsally flat, eyes small and prosternal process deeply arcuate, but mesosternum flat and transverse, epipleuron less sinuate and antennae short. The larva is similar to those of *Ditropidus* [*Elaphodes*] *cervinus* species-group and *D. semicrudus*.

'Prasonotus' is not well-defined and is therefore given species-group status within *Ditropidus*. The original genus *Prasonotus* was not consistently interpreted, reflecting the weak defining characters (*Prasonotus festivus* was also described as a species of *Ditropidus*). Here the original concept of *Prasonotus* is expanded to include most *Pleomorphus* species and a few described in *Ditropidus*. The supposed difference

between *Prasonotus* and *Pleomorphus* (degree of excavation of prosternal process) is trivial, although *'Pleomorphus'* species are more ovoid and flatter dorsally.

8.5.6.5.2 *Ditropidus* [*Elaphodes*]*cervinus* species-group *sensu lato*

Elaphodes cervinus was included in all analyses and *E. aeneolus* and *E. pilula* in AA(i) and ALA(v), in the latter united as one taxon. The analyses were inconclusive and in AA(i) the three species were widely separated.

The genus *Elaphodes* was supposed to comprise those Ditropidina with elongate antennae with five sensory segments (Chapuis 1874). Later authors defined *Elaphodes* by presence of pubescence (Lea 1921; Gressitt 1965) and all the species discussed below are pubescent. It is almost impossible to define a genus *Elaphodes*, unless only the two or three species sharing the combination of character states found in the type species are considered. This group differs by only single character state changes from numerous other species. The shape of the spermatheca (Figs 769, 773, 776) and the aedeagus (Figs 651-653) are variable in the species described in *Elaphodes*, even in the *cervinus* species-group. The 'genus' is therefore treated as a series of loosely defined species-groups in this work.

The type species (*cervinus*) is quite distinctive and has the following characteristics : form relatively elongate; covered with recumbent scale-like pubescence; eyes small, widely separated and slightly convex with greater than 90° canthus; fronto-clypeus relatively long; antennal scape long and thin, and antennae relatively elongate (Fig. 87); middle of front margin of pronotum produced, slightly 'hooding' head; elytra non-striate; epipleura almost evenly tapered to apex; tibiae relatively thin; tarsal claws appendiculate. These attributes are shared with *D.* [*E.*] *aeneolus*, and at least two other species. This small group of species forms *Ditropidus* [*Elaphodes*] *cervinus* species-group *sensu stricto*.

Other species which have been described in *Elaphodes*, or are undescribed but similar, lack one or more of the above attributes and appear to link 'typical' *Elaphodes* with other *Ditropidus* including the type of *Tappesia*.

However, the majority of species hitherto placed in *Elaphodes* (including *pilula*)show a different set of features : form more globular; setae variable; eyes average sized, canthus much more than 90°; antennal scape shorter and broader and antennae broader; fronto-clypeus very short; pronotum not produced; elytra striate; epipleura crossed at base or at least basally lobed; tibiae broader; claws simple. At least 15 species more or less fit this description, with some variants (*E. oblongus* with non-striate elytra; *E. epilachnoides* with tapering epipleuron; *E.* sp. (undescribed) with deep canthus). In one species (undescribed) both sexes have six sensory segments and in another (undescribed) the male has six sensory antennal segments and both sexes have tuberculate elytra. A variation of this type is represented by *E. coccinelloides*, with only erect pubescence on non-striate elytra and appendiculate claws.

A third type related to *D.* [*Elaphodes*] is represented by six species with the following attributes : male with enlarged head, especially mandibles and labrum; covered in scale-like setae; eyes small and slightly convex, canthus about 90°; fronto-clypeus very short; antennae with six sensory segments in both sexes; pronotum produced, 'hooding' head; elytra densely punctured, striae fine or absent; epipleura evenly narrowed; claws simple. Six species belong to this group, one of which (undescribed) has only five sensory antennal segments in both sexes.

A fourth type is similar to the second in head characters, but is oblong and has the front of the pronotal disc highly arched and the posterior lobe strongly raised, rugosely striate elytra, front legs visibly longer than other legs and simple claws. Two species (undescribed) conform to this description, except that one has legs of equal size.

Tappesia was erected (Baly 1877c) for an elongate species which has small, non-emarginate and rather convex eyes (Fig. 336), a slightly convex apex to the prosternum (Fig. 482), undivided pronotal posterior lobe (Fig.482) and an almost quadrate scutellum (Fig. 509), but there are other undescribed species which link this to the various '*Elaphodes*' types described above. In these species the pronotal lobe is slightly divided, the eyes more deeply excavate, the scutellum more ovate and the apex of the prosternum slightly concave, but the shape, surface sculpture and vestiture is similar.

The larvae of *'Elaphodes' aeneolus*, *cervinus* and *pilula* were examined. These larvae share some probable apomorphic (but not unique) states, for example, deep excavation of internal mandibular surface below tooth 5 (Figs 216, 229, 230), seta Aes1 simple (Figs 12, 215) and spiculate tibiae (Figs 217, 259; possibly plesiomorphic). The frons microsculpture and the morphology of Aes3 is variable. In general they are similar to the larva of *D.submetallicus*. The smooth scatoshell of *D. cervinus* with its flask-like chamber (Fig. 177) is unusual but the other species of *'Elaphodes'* (*aeneolus* and *pilula*) show the normal ditropidine type (see Figs 175-176).

Elaphodes, in the original sense of Suffrian (1859) and Chapuis (1874), has not been consistently interpreted. A few species with 'long' antennae have been placed in *Ditropidus* and many species with 'short' antennae have gone into *Elaphodes*.

8.5.6.5.3 *Ditropidus* [*Polyachus*] *pallidipennis* species-group

An undescribed species of this group (*Ditropidus* sp. 865) was included in analyses and was variously placed, but often with *D.* [*Euditropidus*] *variabilis*, which it does not resemble.

This is a group of only three species. The following possible apomorphies are present : eyes small but with a canthus; fronto-clypeus elongate, particularly in the male (Fig. 337); posterior margin of pronotum very weakly lobed (Fig. 485); posterior margin of prosternum strongly raised (Fig. 484); epipleuron not or shallowly lobate; claws appendiculate. The antennae have either five or six sensory segments and the elytra may be glabrous or pubescent. The spermatheca of *D.* sp. 865 is unusually thin and sinusoidal (Fig. 770), a shape shared with *D.* [*T.*] *saundersi* and *D. cervinus* species-group. The larva has tibial spiculae plus simple seta Aes1, as in *Ditropidus cervinus* species-group, and the head capsule setae are relatively long.

This group is defined by a single autapomorphic state, the elongate fronto-clypeus. Without this state the species resemble *D.* [*Polyachus*] *geminus*, which in turn resembles more typical species of *Ditropidus s. str.* The species on which this group is founded, *pallidipennis*, was originally described as a species of *Ditropidus* (Chapuis 1875) and redescribed as a species of *Polyachus* (Lea 1920).

8.5.6.5.4 *Ditropidus antennarius* species-group

Two closely related species of this group were used in analyses, the larval and adult species being different. *Ditropidus 'antennarius'* was variably placed in the various minimum-length trees.

This apparently monophyletic group of about 10 species is characterised by the following possible synapomorphies : dorsum entirely reddish-yellow, or with black markings; male antennae very elongate, with six expanded segments (female with five) (Fig. 362); eyes relatively large with narrow deep canthus; clypeus very short; elytral margin swollen at base of epipleuron whichis lobed and crossed at base (Fig. 560). The larva has no unusual features, but the scatoshell is smooth and chambered (Fig. 174), similar to *D.* [*E.*] *cervinus*. The only attribute unique to this species-group is the long male antenna; for example the swollen and crossed epipleuron is present in several globuar species of *Ditropidus* including *D.* [*Euditropidus*] *variabilis* which has six sensory antennomeres in both sexes. The *D. antennarius* species-group is defined by one character state and may be non-monophyletic due to undetected reversal. The species in this group are extremely similar and all the available names have been placed in synonymy, probably erroneously.

8.5.6.5.5 Further differentiation in *Ditropidus*

Other unusual types of *Ditropidus* are exemplified by the following : *Ditropidus canescens* (with strong keel at hind angles of pronotum); *Ditropidus fasciatus* species-group (dark metallic species with recumbent white scales on pronotum at least); *Ditropidus coriaceus* species-group (minute, more or less impunctate, densely microsculptured, legs thin); *Ditropidus cornutus* species-group (male mandible swollen and clypeus lobate); *Ditropidus laminatus* species-group (quadrate, eyes close, frontoclypeus long, elytron deeply canaliculate); *Ditropidus mirus* (head and pronotum pubescent, front legs enlarged, head swollen with large mandibles in male); *Ditropidus nigricollis* species-group (thorax densely longitudinally strigose (fine and parallel), hind margin hardly produced). These are examples of taxa around which species-groups could be based. Many more could be picked from the 250+ species of *Ditropidus*.

The male secondary sexual characters are not particularly useful for delimiting monophyletic groups because they seem to be frequently reversed or convergently derived. For example, very similar enlarged mandibles occur in *D. fugitivus* (Fig. 340), *D. mirus* and *D. vulpinus* which otherwise appear to belong to different species-groups, yet all have closely related species which lack male enlarged mandibles.

8.5.7 Cryptocephalina

The Cryptocephalina, as defined here, were rarely monophyletic in phylogenetic analyses (AL(ii)). They were usually resolved as paraphyletic, with the inclusion of Coenobiina (AL(i)), or polyphyletic (AA(i), (ii), (iv), ALA(i),(ii),(iii)). In the large data set analyses the species of *Cryptocephalus* were sometimes resolved separately, in paraphyly.

In the classification presented here the Cryptocephalina, excluding *Mylassa* (Pachybrachini) and *Tappesia* (Ditropidina), are considered to be monophyletic. The results of the analyses described above are ignored. The possible synapomorphies for the Cryptocephalina are : hind margin of pronotum produced as a broad truncate lobe which has enlarged central and lateral teeth (not *Aporocera* (*Diandichus*) *analis* and *A.* [*Loxopleurus*]*pauperculus*); loss of dorsal aedeagal setae; scatoshell commonly coarsely constructed (Figs 178-179, also Erber 1988). There are exceptions but such taxa are otherwise normal Cryptocephalina. The Cryptocephalina universally lack the apomorphies of Ditropidina and Coenobiina such as the stepped scutellum and parallel-sided prosternal process of adults and in larvae either the frontal seta pattern of Coenobiina or the mandible type of Ditropidina. Almost all species have rounded anterior rectal sensilla.

The Cryptocephalina may be divided into two distinct groups which may be monophyletic and are almost allopatric in distribution : (i) Eurasian, African and American species; (ii) Australian and south-east Asian species.

8.5.7.1 Holarctic, African, Asian and American taxa.

These were never resolved as a monophyletic group in analyses and the species of *Cryptocephalus* were sometimes placed in paraphyly. There are 11 genera (Seeno and Wilcox 1982), of which two are monotypic and four were not included in this study. It is not possible to present a phylogeny of the genera because of the small sample of genera and species used here but the possible relationships of each genus are briefly discussed below. Only the larvae of *Cryptocephalus* and *Lexiphanes* are known therefore it is not possible to make comparisons of larvae between genera. LeSage (1986) suggested that the presence of papillate pronotal setae in late instars was characteristic of *Cryptocephalus* but this is also a feature of some species of *Aporocera* and *Cadmus.*

This group of non-Australian genera is probably monophyletic but is largely plesiomorphically defined. If the outgroup for character polarity is Coenobiina + Ditropidina + Australian Cryptocephalina, then possible synapomorphies are : eyes flat, narrow and with a broad, shallow canthus (Figs 74, 343, 346, 348, 350; in *Diachus* (Fig. 73) the eyes are broader without a canthus, and *Stegnocephala* (Fig. 344) and a few *Cryptocephalus* (Fig. 345) may have broad eyes with a deep or narrow canthus); hind angles of pronotum produced posteriorly (Figs 311-313, 492-493; also in a few Ditropidina and Coenobiina); loss of mesonotal patches of microchaetae (Figs 511-516; weakly present in a few species (Fig. 514), absent from *Melatia*); larva : sensillum Aesm2 in front of Aes2 or between Aes1 and Aes2. Members of the group share similar eyes, antennae (Figs 365-366), prosternal process (Figs 116-117, 492-493), kotpresse (Figs 842-847; dorsal and ventral sclerites present, ventral sclerite always reaching sides of rectum but not extending beyond) and larvae (eg. frontal setae 2+2+2, Fig. 40), but almost all these features are plesiomorphic relative to the Australasian taxa. The scutellum is usually triangular or if truncate the angles are rounded (Figs 143, 311, 313, 511-516; also *Melatia*). The aedeagi (Figs 662-667) and spermathecae (Figs 781-785) are morphologically as diverse as those of Australian Cryptocephalina. In the following discussion the genera are briefly reviewed to indicate both their close relationship to each other and their distinction from the Australasian taxa. The former American genera of 'Monachini' (*Lexiphanes*, *Heptarthrius* and *Stegnocephala*) are included here because they are related to Nearctic *Cryptocephalus* and allies, and quite different from Ditropidina and Coenobiina.

This group of taxa is dominated by the genus *Cryptocephalus* which, with approximately 1800 described species, is one of the world's largest genera. It is therefore difficult to make conclusions about the status and morphological variation of *Cryptocephalus* from the detailed examination of three (four larval species) Old World and one New World species! However, because it is so large there is a reasonable amount of literature including detailed descriptions of adult and larval morphology (see references in Chapters **4** and **6**). The adult of *Cryptocephalus* is plesiomorphically defined; it lacks all of the autapomorphies defining the following genera. The larval head capsule keel may be present or absent in *Cryptocephalus*, but when present it is smooth, not crenulate, and set well back from the frontal sutures (e.g. see LeSage 1986). The position of sensillum Aesm2 is apparently synapomorphic for *Cryptocephalus* species : in front of Aes2 or between Aes2 and Aes1.

All attempts to create subgenera have used relatively small groups of Old World species and primary or secondary male sexual characters. These subgenera (listed in Appendix B) have not had wide application and have been discredited by some of their authors. From evidence of male genitalia (Burlini 1955; Lopatin 1965; Mohr 1966; Berti and Rapilly 1979) and external morphology I do not consider that the seven subgenera of *Cryptocephalus* listed by Seeno and Wilcox (1982) represent cladistically significant groups of generic rank. The present study and examination of literature suggest that the primary division of *Cryptocephalus* may be between New World and Old World species.

Bassareus was separated from Nearctic *Cryptocephalus* by possession of a few, not necessarily homologous, male secondary sexual characters (LeConte 1880) and is otherwise very similar to the *calidus* and *venustus* species-groups (White 1968) of the latter. These species-groups include the Nearctic species of *Cryptocephalus* studied here and by LeSage (1986). *Bassareus* was included in the synonymy of *Cryptocephalus* by Chapuis (1874). *Bassareus brunnipes* and *C. venustus* have a few probable synapomorphies including colour pattern (White 1968), form of occipital carina (Fig. 346) and shape of spermathecal appendix (Figs 783-784). The eye shape, antenna, female prothorax and abdominal lateral lobes are almost identical. The inclusion of *Bassareus* with the Nearctic *Cryptocephalus calidus* and *venustus* species-groups may make a monophyletic group. If *Cryptocephalus* is split into New World and Old World species-groups, as seems possible from a phylogenetic viewpoint, the former could take the name *Bassareus*.

There are approximately 100 species of *Lexiphanes*, the type genus of Monachini *sensu* Chapuis, and all are American. Chapuis (1874) suggested that *Lexiphanes* was intermediate between Cryptocephalini and Chlamisini because of the short antennae and compact body form. The few North American species were revised by Balsbaugh (1966) who figured the aedeagus and spermatheca, but did not comment on the systematic placement of the genus. Balsbaugh also showed that the diagnostic feature used by North American workers (Arnett 1971), the appendiculate claw, is variable. The immature stages of one species have been described and show great similarity to North American *Cryptocephalus* (LeSage 1984a). Larvae of North American *Cryptocephalus* and *Lexiphanes* show the following in common, to the exclusion of other *Cryptocephalus* : Aes2 broad and papillate (also all *Aporocera* and *Cadmus*, simple in other Cryptocephalus and Ditropidus); Aes1 and Aes 2 similar sized (also most *Aporocera* and *Cadmus*, dissimilar in all *Cryptocephalus* and Ditropidina). These characters are at least slightly correlated and the sample size is small therefore similarities or differences may not be significant. *Lexiphanes* and *Stegnocephala* were originally separated by a minor non-discrete variation in the prosternal process (Baly 1877a), as in many of the genera synonymised with *Ditropidus*. The two species of these genera examined here have differences in eye shape, distribution of aedeagal setae and number of sensory antennomeres, which may be considered significant at generic level. These genera share many attributes with Nearctic *Cryptocephalus* (head capsule including eyes, prothorax and mesonotum are almost identical in shape) and it is possible that together they are a monophyletic group separate from Old World *Cryptocephalus* species and *Melixanthus*. This possibility needs to be tested with a much larger sample of taxa.

The genus *Diachus* is well-defined autapomorphically. The type species, *Diachus auratus*, has an indistinct crenulate pronotal margin (Figs 121, 123) which is only evident under high magnification. This species has several unusual autapomorphies, for example simple eyes, canaliculate gland on frons (Fig. 73), row of tubercles on pronotal base (Fig. 123), shape of spermatheca (Fig. 781), but is otherwise evidently close to *Lexiphanes* and Nearctic *Cryptocephalus* (in shape of prosternal process (Fig. 117), scutellum (Fig. 143) and other structures).

Triachus is a tiny example of the *Lexiphanes* type with a few distinctive features which may be attributed to its small size or may not be significant (five sensory antennomeres). Male and female specimens were examined but not included in analyses.

Lexiphanes, *Stegnocephala*, *Diachus* and *Triachus* may be more closely related to Nearctic *Cryptocephalus* than to Old World *Cryptocephalus* species.

The Old World genus *Melixanthus* is probably monophyletic but seems to be very close to Old World species of *Cryptocephalus* and many species may be misplaced in either genus. Reineck (1913c) has distinguished the two genera by the possession of more deeply excavate eyes (Figs 348, 350), shorter antennae and toothed claws in the former, but it is evident from the figures that the first two characters are not appropriate. Some authors have used only the length of the antennae to separate the genera (Gressitt and Kimoto 1961). The subgenus *Anteriscus* of *Melixanthus* (Weise 1906; Reineck 1913c; not recognised by Seeno and Wilcox 1982), represented here by the type species *M. erythromelas* (Suffrian), is separated by its longer antennae from *Melixanthus s. str.* (Reineck 1913c), represented here by type species *M. intermedius* Suffrian (Figs 348, 350). *Melixanthus intermedius* is distinguished by its transversely ridged and weakly sclerotised kotpresse, but the body form and kotpresse are similar in these two species and subgenus *Anteriscus* is not considered valid. Weise (1923) suggested that *Anteriscus* was a junior synonym of *Idiocephala* (here synonymised with *Aporocera*), but gave no reason for this curious action. Possible synapomorphies of *Melixanthus* species are : metendosternite narrowly but strongly produced anteriorly (Fig. 543); claws appendiculate; venter of rectum with longitudinal ridges (Figs 846-847). The presence of microspiculae on the mesoscutum may be plesiomorphic (Fig. 514). The larva is unknown. As it stands at present *Melixanthus* represents all the relatively small species of *Cryptocephalus* in Africa and Asia with short antennae and appendiculate claws. *Melixanthus* and the Old World *Cryptocephalus* species may form a monophyletic group.

The descriptions of *Jaxartiolus* species (Lopatin 1963; 1976) show that this genus is only distinguished from Palaearctic *Cryptocephalus* by a single character autapomorphy, reduced lobation of the third tarsal segment. This genus should probably be sunk under *Cryptocephalus*.

I have not seen material of *Heptarthrius* Suffrian, *Protinocephalus* Reineck and *Lophistomus* Weise but from their descriptions these genera belong to the Cryptocephalina as defined here. Adults of *Heptarthrius* are like large *Lexiphanes* with the enlarged forelegs of some *Ditropidus* and the short but elongate antennae of *Elaphodes* (Chapuis 1874). The prosternum is grooved like that of *Adiscus*. However the triangular scutellum and broadly truncate posterior margin of the pronotum show that this belongs to Cryptocephalina, and it is presumably close to *Lexiphanes*. *Protinocephalus*, with large head and untoothed pronotal margin (Reineck 1913b), and *Lophostomus*, with enlarged mandibles (Weise 1896), are otherwise typical *Cryptocephalus* which show the usual extreme secondary sexual autapomorphies convergently derived in many clytrine and cryptocephaline genera. Reineck notes the closeness of *Protinocephalus* to southern African *Cryptocephalus* species.

None of the taxa belonging to this section of the Cryptocephalina are native to Australia but one species, *Diachus auratus*, has recently been recorded (Reid 1988).

8.5.7.2 Australasian Cryptocephalina

The Australasian Cryptocephalina were usually resolved as a monophyletic group in the numerical analyses (AL(i),(ii), ALA(i),(ii),(iii),(iv)), the exceptions involving isolation of *Aporocera* (*Diandichus*) *analis* and/or *Melatia* (*M. glochidionis* + *solomonensis*) (AA(i),(ii),(iv)) in paraphyly. When *Melatia* was included in analysis it was always resolved as a separate monophyletic entity from all other Australasian species. In the study of Australasian taxa with *Cryptocephalus* + *Melixanthus* as outgroup (ALA(vi)), *Melatia* was resolved as the sister-group of all remaining taxa. When the Australian taxa were resolved as monophyletic the internal structure of the clade was variable but usually had *A.* (*Diandichus*) and *Aporocera pauperculus* as near basal groups. *Diandichus analis*, the species of *A.* (*Diandichus*) used in adult analyses, is certainly peculiar compared to the other taxa analysed, but other members of the subgenus are less divergent and there appears to be an almost continuous spectrum of variation connecting *D. analis* to more typical *Aporocera* species (see below under *Diandichus*). The proposed phylogeny of the genera and subgenera of Australasian Cryptocephalina is illustrated in Fig. 957.

The group 'Australasian Cryptocephalina' is considered monophyletic. It has the following possible synapomorphies : canthus narrow but long, internal angle less than 90° (Figs 71-72, 347) (a few small species may almost lack a canthus but have relatively convex eyes); posterior of eye flat but abruptly truncated before epicranium ; antennae without sensillate circular depressions (Figs 93-96, 367); inner edge of galea with subapical patch of short, inwardly curved setae (not *A.* (*Diandichus*) or *A.* [*Loxopleurus*] sp. 1049); submentum medially divided (Fig. 457) (not *M. glochidionis* or *A. pauperculus*); angle between scutellum and mesoscutum at least 30° (Fig. 519) (in almost all taxa the angle is much greater; some *Cryptocephalus* and *Melixanthus* species approximate this angle); base of inner face of vaginal palp (hemisternite) with an internal projection (Figs 739-740) (not *Melatia glochidionis*, *A.*(*Diandichus*), *A.* [*Cryptocephalus*] *bihamatus*); ventral transverse sclerite either absent or reduced to small transverse patches (Figs 848-851) (*Melixanthus intermedius* is similar with the transverse sclerite almost unsclerotised but it is distinctly thickened at the edges). In addition the occipital carina is never present. The larval head capsule (Figs 46-49, 222) shows the following probable synapomorphies (larvae of *Melatia* are unknown) : seta Aes2 broad and papillate (not four species) and similar size to Aes1 (not five species) (also North American *Cryptocephalus* and *Lexiphanes*); sensillum Aesm1 in front of or level with Aes1 and further from epicranial suture (eight exceptions); upper frontal setae in 2+2 pattern (not *Aporocera* [*Loxopleurus*] *atra* nor a teratological specimen of *A.* (*Diandichus*) sp. 435 (Fig. 38)); distance Fs2-Fs2 equal to or less than Fs3-Fs3.

Historically the Australasian Cryptocephalina have been treated in various ways : separated from other Cryptocephalina as a group of many genera (Saunders 1842-1847; Baly 1877a); with many genera, but including *Cryptocephalus* (Suffrian 1859; Lea 1904); or with few genera but including *Cryptocephalus* (Chapuis 1874; Weise 1923; Gressitt 1965). Assignment of species to genera has been almost random (Lea 1904) and many species have been described in two or more genera Because of this confusion the following account makes little reference to the historic treatment of the genera. In this study I have found no evidence that *Cryptocephalus* occurs in Australia or New Guinea. The superficial similarity of some Australian taxa to Chlamisini has led to suggestions that Chlamisini may be derived from *Cadmus* (*Lachnabothra*) (Chapuis 1874), or that *Cadmus* (*Brachycaulus*) is a relatively primitive taxon in the Cryptocephalini (Kasap and Crowson 1976), although the latter view was partly based on a larval misidentification. These hypotheses are rejected by the phylogeny proposed here.

The analyses supported a division of the Australasian Cryptocephalina into two monophyletic groups : *Melatia* (primarily non-Australian species) and other taxa (primarily Australian) (Fig. 957).

8.5.7.3 *Melatia*.

The species *Melatia* [*Cadmus*] *glochidionis* and *solomonensis* were the sister-group of all remaining Australasian Cryptocephalina in adult data analyses, or were associated with them by paraphyly. They were also consistently separated from

Cryptocephalus and *Melixanthus*. The two species chosen for the numerical analyses represent a group of about 30 species described from the Moluccas, New Guinea and Solomon Islands (Baly 1865; Bryant 1943; Gressitt 1965). One of these species (*M. glochidionis*) is newly recorded here from Australia. The species have been placed in *Cadmus*, *Cryptocephalus* and *Lachnabothra* (Gressitt 1965), but they do not belong to these genera. No larvae were available for this group.

Melatia can be defined by the following possible synapomorphies : relatively small and convex eyes with triangular canthus (Fig. 347) (*C.* (*Brachycaulus*) is similar); lacinia broad and rounded (Fig. 445); prosternal process transverse and truncate to slightly convex (Fig. 496); mesoscutum without median longitudinal ridge anterior to scutellum and without lateral patches of microchaetae (Fig. 517); outer margin of tibiae longitudinally grooved, lateral lobe at base of abdomen with angulate apex (Fig. 575). The elytra are frequently tuberculate (Gressitt 1965, under *Cadmus*). The scutellum is triangular or if truncate the angles are rounded. Members of one group of species, including *M. glochidionis* and *M. metallicus,* have considerably reduced pronotal teeth (Fig. 496) and a very large triangular scutellum (Fig. 517).

Melatia is the sister-group of other Australasian Cryptocephalina and is therefore useful as an unequivocal outgroup. However, the species included in *Melatia* are morphologically diverse, including tuberculate drab pubescent species like many *Cadmus* and brightly coloured glabrous species like *Aporocera* (all '*Cadmus*' and some '*Cryptocephalus*'in Gressitt 1965, see Appendix B).

8.5.7.4 Remaining Australasian Cryptocephalina (*Cadmus* and *Aporocera*)

Several analyses (AL(i), AA(i),(ii), ALA(ii),(vi)) included a large number of Australian Cryptocephalina in order to test the previous classification and look for other possible phylogenies of the Australian species. These are described in detail here. The relatively conflicting and unresolved results of these analyses are reflected in the proposed phylogeny (Fig. 957).

Adult analysis AA(i) included a broad range of taxa with representatives of all the described genera and a large number of characters. The Australian species were only monophyletic with the exclusion of *Aporocera* (*Diandichus*) *analis* and two different minimum-length trees are illustrated in Figs 934 and 935. All minimum-length trees shared the same general structure. The single species, *A.* [*Loxopleurus*] *pauperculus*, *Cadmus pacificus* and *A.* [*Rhombosternus*] *jocosus* were successively sister-taxa to all remaining species in the clade. The majority of coarsely punctured pubescent or crenulate species (*C.* (*Brachycaulus*) *ferrugineus* and allies) were resolved as monophyletic, but not *Cadmus australis* which was coupled with *Aporocera* [*Cyphodera*] *chlamydiformis* elsewhere in the clade. Four of the species with antennal slots on the pronotal margin (*A.* [*Schizosternus*] *albogularis* and allies) were resolved monophyletically, but not *A.* [*Cryptocephalus*] *bihamatus* and *A.* [*Cryptocephalus*] *jacksoni* which were separately placed. The remaining species were mixed, without a discernible pattern.

Analyses AL(i), AA(ii) and ALA(ii) were based on the same limited set of species which included examples of most of the Australian genera (Figs 926, 938, 945). In the adult analysis AA(ii) the Australian species were only monophyletic by the exclusion of *A.* (*D.*) *analis*. The larval analysis AL(i) showed little sorting of species into groups that could be related to adult morphology, for example the taxa of the apparently monophyletic groups *C.* (*Brachycaulus*) + *C.* (*Lachnabothra*) + *Cadmus* s. str. and *A.* [*Schizosternus*] + *A.* [*Euphyma*] were separated. Therefore characters which were useful for delimiting synapomorphic larvae, such as individual setal morphology, presence or absence of a cephalic ridge or epicranial microsculpture did not match the variation of adult characters. The adult clade AA(ii) paired *C.* (*L.*) *hopei* with *C.* (*B.*) *ferrugineus* and *A.* (*S.*) *albogularis* with *A.* (*E.*) *flaviventris* but separated *Cadmus australis* from *C.* [*Paracadmus*] *luctuosus* and both of these from *C.* (*B.*) *ferrugineus*. The adult clade had *A.* [*Loxopleurus*] *gravatus* as the sister taxon to all others. When adult and larval data were combined, the minimum-length tree showed a combination of the features of the adult and larval clades. For example, the pairing of *C.* [*P.*] *luctuosus* with *A.* [*Cadmus*] *aurantiacus* and *C.* (*B.*) *ferrugineus* with *C.* (*L.*) *hopei*, as in AA(ii), and the splitting of *A.* [*S.*] *albogularis* and *A.* [*E.*] *flaviventris*, as in AL(i).

Analysis ALA(vi) with MACCLADE was undertaken to find the most parsimonious cladogram for carefully selected Australasian Cryptocephalina taxa with adult and larval characters, using *Cryptocephalus* and *Melixanthus* as the outgroup. A strict consensus of the five minimum-length trees confirmed the position of *Melatia* as sister-group to all other taxa but did not resolve the remaining taxa into a phylogeny appropriate for the traditional classification. The original nomenclature is used in the following descriptions because the taxa were chosen to test the traditional classification (*sensu* Lea 1904). The group of taxa (*Aporocera* = *Aporocera*, *Chariderma*, *Chloroplisma*, *Cryptocephalus bihamatus*, *Diandichus*, *Euphyma*, *Idiocephala*, *Loxopleurus*, *Mitocera*, *Ochrosopsis*, *Rhombosternus*, *Schizosternus*) representing smooth, glabrous and non-tuberculate species is not resolved and is paraphyletic. The group of taxa (*Cadmus* = *Brachycaulus*, *Lachnabothra*, *Cadmus*, *Prionopleura*) representing coarsely punctured, usually pubescent and tuberculate species forms a monophyletic clade. Its sister-groups are taxa (*Cyphodera, Cadmus perlatus*, *Ochrosopsis apicalis*) of glabrous tuberculate species without coarse punctation. The sister-group for all other Australian taxa is *Loxopleurus pauperculus*. These taxa were rearranged with MACCLADE to make monophyletic clades of : *Idiocephala* + *Schizosternus* + *Euphyma* + *Cryptocephalus bihamatus* (ie. smooth species with grooves in front margin of prosternum); *Aporocera* + *Chariderma* + *Chloroplisma* + *Loxopleurus* + *Mitocera* + *Ochrosopsis* + *Rhombosternus* (smooth species without prosternal grooves); *Diandichus* + *Loxopleurus pauperculus* (smooth species with even and long pronotal teeth, elongate scutellum and dense microsculpture); *Ochrosopsis apicalis* + *Cyphodera* + *Brachycaulus posticalis* (tuberculate species with thin legs and not coarsely punctured). The coarsely punctured, pubescent and tuberculate species group was retained. The length of the tree with this arrangement of taxa was 11 steps longer than the minimum-length tree for the same data set . Other combinations of these taxa to make similar monophyletic groups gave equally long or longer trees (see Section **7.2.6**). This experiment with parsimony suggests that *Cadmus* is probably monophyletic but *Aporocera* is not.

The Australasian Cryptocephalina excluding *Melatia* are considered monophyletic, with the following synapomorphies : lateral lobes of mesoscutellum with round or oval microchaetal patches (Figs 141, 518-519; not *Cadmus* (*Brachycaulus*) and *A.* [*L.*] *gravatus*); female with internal surface of apex of tergite VIII setose (only few setae in some species). The scutellum is rarely triangular (almost always apically truncate, Figs 127, 141, 314-330, 518-519) and most species have lost the irregular interlocking teeth at the base of the elytral suture. This large group includes individual species described from southern Burma, Borneo and Timor and a few from New Guinea, but the vast majority are Australian. All Australian species previously described in genera of Cryptocephalini (*sensu auctt.*) belong here except for *Tappesia* (*vide* Ditropidina). The Fijian species of '*Loxopleurus*' (Bryant and Gressitt 1957) all belong to Coenobiina (*q.v.*).

The following generic names have been considered valid at some time for this section of the Cryptocephalina : *Aporocera*, *Brachycaulus*, *Cadmus*, *Chariderma*, *Chloroplisma*, *Cryptocephalus*, *Cyphodera*, *Diandichus*, *Dicenopsis*, *Euphyma*, *Idiocephala*, *Lachnabothra*, *Loxopleurus*, *Melinobius*, *Mitocera*, *Ochrosopsis*, *Paracadmus*, *Prionopleura*, *Rhombosternus*, *Schizosternus*. All species from Australia described in the Holarctic genus *Cryptocephalus* have been mis-placed, therefore all Australian species belong to endemic Australasian genera. Most of the genera were founded on single species. Most authors have accepted the validity of some genera but there has never been agreement on which genera are valid.

The discussion of difficulties in defining genera in the Ditropidina (section **8.5.6.5**) could equally apply here. The standard classification of the numerous Australian genera (Lea 1904) was based on a combination of the work of Saunders (1842-7), Suffrian (1859), Chapuis (1874) and Baly (1877a), who gave definitions for all the genera. The characters used by these authors for generic separation were : antennal length and shape including segment proportions, tuberculation of pronotum, shape of lateral pronotal margins, shape of apex of prosternal process, inflation of male hind femora, shape of metapleuron, shape of scutellum. For several genera different definitions are given by each author. These largely graded characters may have sufficed for the small samples of species available to early authors but they were already unworkable for Lea (1904), who nevertheless perpetuated their use.

Most of the large number of genera proposed for this group cannot be justified by synapomorphic discretely varying characters but, conversely, few adult characters are discretely variable and larval characters are discretely variable but reversal or convergence is common. Species-groups which are well-defined (for example those representing *Brachycaulus*, *Lachnabothra*) appear to be terminal clades well within the broad range of taxa. Thus, in the genus *Cadmus* as defined here, the former genera may be related as follows : the sister-group of *Brachycaulus* is probably *Prionopleura*, *Prionopleura* grades into *Cadmus*, the sister-group of all of these is possibly *Cadmus pacificus* species-group and/or *Lachnabothra*, and the sister-group of all of these is, dubiously, the *Ochrosopsis apicalis* species-group and/or the *Brachycaulus posticalis* species-group.

The practical problem with a weak phylogeny is not identification but nomenclatural stability, therefore I have taken a conservative approach and 'lumped' all available names into two polythetically defined genera, *Cadmus* and *Aporocera*, which may be monophyletic, or at least substantially so. *Cadmus* represents a collection of fairly well-defined species-groups, most of which have available generic names which are retained as subgenera. *Aporocera* represents a much looser (and larger) assemblage which is much less well understood and which has few discretely defined groups, most of which are only defined by secondary male sexual characters. I recognise only two subgenera, one of which is biologically distinct. The larval characters did not discriminate between *Cadmus* and *Aporocera* nor between their constituent subgenera and are therefore not included in the discussions of genera and subgenera given below.

8.5.7.5 *Cadmus* (including the type species of : *Brachycaulus*, *Cadmus*, *Lachnabothra*, *Paracadmus* and *Prionopleura*, and the *Cadmus pacificus*, *Ochrosopsis apicalis* and *Brachycaulus posticalis* species-groups)

This is a large polythetically defined group which may not be monophyletic. The problem subgenera are *Brachycaulus*, *Cadmus* s.str. and *Aorocarpon* (qq.v.) each of which is well-defined but has at least superficially similar species in *Aporocera*, although the similarity is probably convergent. *Cadmus* species are almost entirely confined to the south and east of Australia; only two undescribed species occur in the centre and north.

Possible synapomorphies are : metallic and interference colours (blue, green, purple) absent from all species; male antennae very long (Figs 315-316, 318) proportionately much longer than female antennae (not *Brachycaulus* or *Cadmus* sp.A, Figs 314, 317); pronotum densely punctured and usually pubescent; lateral pronotal margins at least feebly crenulate or uneven (Figs 314-317; not *C. pacificus*); anterior angles of pronotum produced beyond prosternum (not *C. pacificus*); scutellum punctate (not *Cadmus* s. str., Fig. 141), longitudinally ridged or at least medially convex, basally notched (Figs 317-318, 518); elytra rugosely punctate (not some *Cadmus* s. str.); elytra usually covering entire abdomen (Figs 314-315, 317); tibiae usually conspicuously expanded to apex (Figs 314-317); male with excavate apical ventrite; aedeagus tending to form apical and/or ventral medial keel and paired apical fenestrae (Figs 675-677, 916-920). The colour range is black, brown, red and yellow, ie. colour is due to varying amounts of black pigment. Many species are tuberculate on the elytra and often also on the pronotum (Figs 304, 308, 906-911). In all species the prosternum is flat or abruptly reflexed at the apical margin (Figs 314-315, 317), never gradually raised anteriorly from the middle. The transverse dorsal rectal sclerite is only present in *Cadmus* s. str. (Fig. 849). The broad, usually apically truncate or convex prosternal process and the pubescent or strigose and usually keeled scutellum may be plesiomorphic because these states are characterisitc of *Melatia*. Many of the species are large for the Cryptocephalini (> 8mm). No larval attributes were found to distinguish *Cadmus* from *Aporocera*.

8.5.7.5.1 Subgenera *Cadmus s. str.* and *Brachycaulus*.

These morphologically diverse groups seem to form a monophyletic unit.

They share the following synapomorphies : surface of head and pronotum deeply and rugosely punctured, with dull, narrow interspaces; lateral margins and sides of anterior margin of pronotum strongly and fairly evenly crenulate (Figs 314-317). The scutellum varies from medially sharply keeled with sunk pubescent pits either side to convex with a few scattered lateral punctures. The aedeagi (Figs 670, 674-677) and spermathecae (Figs 789, 791-793) are also variable.

8.5.7.5.2 *Cadmus s. str.* (including *Paracadmus* and *Prionopleura*)

This group is equivalent to the combination of *Cadmus*, *Paracadmus* and *Prionopleura*, all sensu Baly (1877a,b). The scutellar keel, used by Baly to separate *Cadmus* and *Prionopleura*, seems to go through a sequence from being sharp and narrow with setose punctures on either side to being absent, although the scutellum is at least convex and impunctate along the midline.. Baly also used dorsal pubescence, but this is variable. *Cadmus* was distinguished by Suffrian (1859) and Chapuis (1874) by the supposedly truncate shape of the prosternal process and *Paracadmus* was distinguished by the bilobate process (Baly 1877b), but Lea noted the variability of this character. There are approximately 35 species, mostly in south-eastern Australia.

Diagnostic and possibly synapomorphic attributes are : male antennae approximately body length and narrow (Figs 315-316), female antennae less than half body length and expanded (not *C. australis* and allies, or *C.* sp.); scutellum quadrate and convex, or truncate-triangular and longitudinally keeled; elytra not tuberculate, but may be canaliculate; second tarsal segment of middle and hind legs elongate or quadrate (Figs 315-317). The antennae of the type species *C. australis* are long but broad and similar in both sexes. *Cadmus* sp. A is an undescribed arid zone species with autapomorphic expanded head and mandibles (in both sexes), short, broad antennae and canaliculate elytra (Fig. 317). It may be the sister-group of *Brachycaulus* but, apart from the short antennae and broad tarsi, lacks any of the synapomorphies of that subgenus.

Some species of *Cadmus* s. str. (eg. the type species, *C. australis*) are similar to species I have placed in *Aporocera* which were originally described in *Cadmus* and *Ochrosopsis*. The members of this group (*A.* [*Ochrosopsis*] *australis* species-group; Fig. 325) have the following features in common with *C. australis* : yellow, brown or black coloration, never metallic; pronotal front angles produced; front margin of prosternum abruptly raised; apex of prosternal process convex, broad; scutellum quadrate, almost impunctate, glabrous; male with concavity in apical ventrite. In *A. stratioticus* the pronotum is densely, rugosely punctured, the antennae are elongate and black tipped (like *C. excrementarius*, *C. crucicollis*) and the lateral margins of the pronotum are uneven. An undescribed species is similar to *stratioticus* but has crenulate lateral pronotal margins, although the crenulations are much longer and flatter than in *Cadmus australis*. In *Aporocera stratioticus* and the other species the scutellum is very shallowly notched at the base and the aedeagus has a simple apex. If these species were included in *Cadmus* many species of the *A. australis* species-group would have to be admitted and this species-group appears to grade into more typical *Aporocera*, through *A.* [*Cryptocephalus*] *sticticus* and allies. This may be an argument for abandoning the separation of *Cadmus* and *Aporocera* altogether, which I am not prepared to do at present.

The smooth, chambered scatoshell of C. *litigiosus* is unusual (unique in the Cryptocephalina) (Fig. 180). It may also characterise the type species of *Cadmus*, *C. australis*, because these species are morphologically extremely similar (allopatric geographical races). Other species of *Cadmus* s. str. have roughly surfaced scatoshells (Fig. 179).

8.5.7.5.3 Subgenus *Brachycaulus*

This distinctive monophyletic species-group has been consistently interpreted since the original description of *Brachycaulus* (Fairmaire 1843), although it was synonymised with *Cadmus* by Chapuis (1874). Kasap and Crowson (1976) suggested that the prosternal grooves were a plesiomorphic feature and misidentified the larva.

There are approximately eight species some of which are very widely distributed and may be species-complexes.

Brachycaulus has the following possible autapomorphies : eyes relatively small, canthus small and vertex large (Fig. 314); antennae short (Fig. 314); pronotum bituberculate in both sexes (tubercles large and evenly rounded) (Fig. 314); prosternal process convex, with pair of longitudinal median ridges or central area rectangularly raised; scutellum not ridged but convex, pubescent or glabrous; elytra with large tubercles near scutellum (Fig. 314); apex of aedeagus relatively simple, with setae minute or absent (Figs 670, 674); apex of spermathecal receptaculum rounded (Figs 792-793). Most species have the anterior pronotal border strongly reflexed and grooved to receive the antennae and transverse second tarsal segments on the mid and hind legs. One species (*crassicostatus*) has greatly reduced posterior pronotal teeth. The small eyes, short antennae and simple aedeagus may be plesiomorphic (by comparison with *Melatia*), but *Brachycaulus* species are otherwise morphologically very similar to *Cadmus* s. str. If *Brachycaulus* or *Brachycaulus* + *Cadmus* s. str. is the sister-group of all remaining *Cadmus* and *Aporocera*, then *Cadmus* is paraphyletic. Since an equally good case could be made for *Lachnabothra* or *Cadmoides* or *Aorocarpon* as the most basal group, I prefer to keep all these taxa united under *Cadmus*.

Aporocera tasmanica is superficially similar to *Brachycaulus* (swollen pronotal disc, densely rugosely punctured upper surface, size and colour pattern similar to *B. minor*), but is non-tuberculate and has large deeply excavate eyes, long antennae, simple prosternum and thin legs.

8.5.7.5.4 Subgenera *Lachnabothra* and *Cadmoides*

The closest relative of the *Lachnabothra* species-group is not obvious, but there is some resemblance to the *Cadmus pacificus* species-group. Both share the following possible apomorphies : antennae strongly sexually dimorphic (as described for *Cadmus*); recumbent pubescence on pronotum, radiating from centres around the pronotal disc and similar pubescence on scutellum; pronotal punctation dense but not rugose; lateral pronotal margins very thin and uneven but at most feebly crenulate; prosternum clothed with dense, long pubescence; short elytra exposing pygidium (Fig. 318). However, differences between the two groups include tuberculation, projection of anterior angles of pronotum, structure of scutellum, sculpture of the mesepimeron, structure of aedeagus and development of cephalic keel in larva. Therefore it is also quite likely that these are not sister-groups.

8.5.7.5.5 Subgenus *Lachnabothra*

This apparently monophyletic group of species is difficult to define monothetically because there are many reversals of characters. Some species are similar (dorsum almost glabrous, scutellar keel, elytral tubercles) to species of *Aorocarpon*. *Lachnabothra* includes at least 20 species, which were studied in some detail to gain an understanding of interspecific variation in the Australian Cryptocephalina. It was found that even the aedeagus shows such a range of morphological variation that no apomorphic feature is universal (Figs 916-919). The ovipositor, spermatheca and spermathecal duct (Figs 921-922) show a more limited range of variation but do not provide synapomorphies. In the larva the apex of the labrum is variable (Fig. 276), but the larval foreleg has the bases of setae Vts3-4 adjacent (Fig. 278) (also found in *Cryptocephalus moraei*, Fig. 263).

The species have the following combination of possible apomorphies : strongly sexually dimorphic in length and shape of antenna and shape of pronotum (except one species, in which male has female antenna and female has male pronotum), with male antenna approximately body length, female less than half body length (compare Figs 901-902 with 904); male pronotum at least slightly bituberculate or medially longitudinally grooved (Figs 906-907); female pronotum uneven, with basal (two) and lateral shallow impressions; pronotal pubescence in rosettes (one species almost glabrous); sides of pronotum feebly crenulate or uneven; scutellum truncate-triangular and longitudinally ridged (Fig. 318); elytra tuberculate (Figs 318, 908-909); male with excavate last sternite; aedeagus (Figs 916-919) ventrally keeled (not three species), subapically dorsally keeled (except one species) and apex of lobe with transparent patches (except one species). The six species for which mature larvae, pupae or unemerged adults have been observed have scatoshells with elongate spurs around the entrance and these larvae pupate at the top of plant stems (the scatoshell spurs appear to anchor the scatoshell). Late-instar scatoshell morphology and pupation site may be synapomorphic for the whole genus.

An undescribed species of *Aorocarpon* is very similar to *Lachnabothra*, but is dorsally glabrous, with non-dimorphic antennae (Figs 903, 905) and tarsi (Fig. 914) and the aedeagus (Fig. 920) and vaginal palp (Fig. 923) are unlike any species of *Lachnabothra*. The tuberculate pronotum is of different form from *Lachnabothra* (Fig. 908) but the elytral tubercles are similar (Fig. 911). This species may be the sister-group of *Lachnabothra*, or a species of *Lachnabothra* with many reversals, or simply convergently or plesiomorphically similar. It is placed in *Aorocarpon* because it lacks all of the synapomorphies of *Lachnabothra* but is similar to *Cadmus* (*Aorocarpon*) *apicalis* and *posticalis* .

8.5.7.5.6 Subgenus *Cadmoides*

This monophyletic group is at least superficially similar to some species of *Cadmus s. str.*in scutellum and surface sculpture. It includes approximately 10 species.

The species have the following possibly apomorphic characteristics : dorsal punctures fine, pubescent, interspaces densely microreticulate; pronotal pubescence in rosettes but less marked than *Lachnabothra*; apex of prosternal process convex; anterior angles of pronotum not produced beyond prosternum; mesepimeron pubescent; scutellum quadrate and at least laterally punctate and pubescent; elytral striae confused or double punctured; aedeagus simple, with very few apical setae (Fig. 671).

The three named species (Appendix B) were described as species of *Cadmus s. str.* or *Cryptocephalus.*

8.5.7.5.7 Subgenus *Aorocarpon*

This subgenus comprises two species-groups (*A.* [*Ochrosopsis*] *apicalis* s-g. and *A.* [*Brachycaulus*] *posticalis* s-g.) which are morphologically diverse and may not be monophyletic in combination. Some species appear to be intermediate between *Cadmus* and *Aporocera* and others are at least superficially similar to subgenera *Lachnabothra* or *Brachycaulus*. There are approximately 10 species.

All the species have the following combination of possible apomorphies: dorsal surface tuberculate or at least uneven : tuberculation or uneveness of pronotum similar to female *Lachnabothra* or *Brachycaulus* or some *Cadmus s.str.*; pattern of tuberculation or uneveness on the elytra similar to *Lachnabothra*; mesepimeron pubescent or densely strigose; scutellum longitudinally ridged or convex, punctate or strigose and truncate-triangular; tibiae at most slightly expanded to apex; tarsi elongate. The pronotal punctation of these species is generally sparser than other species of *Cadmus* and one species (undescribed) is almost impunctate but densely strigose. All species have the antennae not notably dimorphic, the front angles of the pronotum projecting beyond the prosternum and the lateral and apical margins of pronotum simple but sometimes uneven. The larvae of *A. apicalis*, *pauxillus* and *posticalis* show no particular attributes.

Members of the *A. posticalis* species-group have a strongly bituberculate pronotum and dull, densely strigose or pubescent dorsal surface (autapomorphies). In the *A. apicalis* species-group the pronotum is slightly bituberculate or uneven and has an irregular impunctate ridge from behind the middle to the base. One species in the latter group is very similar to *Lachnabothra* (*qv.*).

The four described species of *Aorocarpon* were described (including synonyms) in *Brachycaulus*, *Cadmus*, *Loxopleurus*, *Ochrosopsis* and *Rhombosternus*! For example, Lea (1904) described *A. posticalis* in *Brachycaulus* because of the bituberculate pronotum. However it lacks the rugose sculpture, small eye, short antenna, pronotal crenulations, prosternal grooves, broad legs, or reduced aedeagal setae of that subgenus.

Aporocera [*Cyphodera*] *chlamydiformis* (Fig. 326) and an unnamed species of *Aporocera* (Fig. 328) are similar to this group. In common with *Aorocarpon* they have a strongly swollen pronotal disc, front angles of pronotum produced, elytral tubercles. These species have the following attributes of *Aporocera* : upper surface shining and glabrous, sparsely but strongly punctured; anterior half of prosternal process gradually elevated from middle; prosternal process concave; lateral margins of pronotum simple; mesepimeron normally microsculptured, glabrous; scutellum smooth, impunctate; aedeagus simple. The eyes of *Aporocera* sp. A are greatly enlarged like many other *Aporocera* species but unlike those of *Cadmus*. Both species appear to belong to *Aporocera* and may not even be sister-species.

8.5.7.6 *Aporocera* (including type species of *Aporocera*, *Chariderma*, *Chloroplisma*, *Cyphodera*, *Diandichus*, *Dicenopsis*, *Euphyma*, *Idiocephala*, *Melinobius*, *Mitocera*, *Ochrosopsis*, *Rhombosternus* and *Schizosternus*, and other species-groups)

The remaining species of Australian Cryptocephalina are difficult to define as a monophyletic group and may be residual. They were not resolved monophyletically in the computer-based analyses. *Aporocera* species lack the possibly plesiomorphic keeled and/or pubescent scutellum of almost all *Cadmus* and rarely have slight lateral pronotal crenulation. Most aspects of morphology (e.g. size, eye shape, antennae, prosternal process) are much more variable in *Aporocera* than *Cadmus* but tuberculation is very rare and conspicuous dorsal pubescence is absent. Most species are shining and relatively sparsely punctured, and metallic colouration is common. Most of the genera named from species in this group are monotypic due to autapomorphies, or are impossible to substantiate. Undescribed species include even more bizarre forms (Figs 328-330).

Perhaps the only synapomorphy is therefore loss of scutellar punctation and pubescence, but this also true of several *Cadmus* species. Only two subgenera are recognised, *Aporocera s. str.* and *Diandichus*. *Aporocera* and *Diandichus* are separated for practical and *a priori* reasons. It is possible to morphologically define the group of species named *Diandichus*, some attributes may be plesiomorphic compared with *Aporocera* and the species have a distinct biology. However, the two subgenera are only weakly distinguished.

8.5.7.6.1 *Aporocera s.str.*

The type species, *Aporocera apicalis* (Fig. 319), has expanded antennal segments but is otherwise typical of the vast majority of the 200+ species in this group. The subgenus *Aporocera* is almost certainly rendered non-monophyletic by the exclusion of *Diandichus*, and probably more so by the separation of some of the groups constituting *Cadmus*.

Typical members of *Aporocera* are illustrated (Figs 319-325). There is great morphological variation in *Aporocera* but little of it can be discretely characterised. As in *Ditropidus* (section **8.5.7.5**) monophyletic groups of species are very small, autapomorphically defined or separated from other taxa by combinations of few, non-unique character states. Larval characters also seem to be useless for distinguishing species-groups.

Some species are close to *Diandichus* (for example *Aporocera* sp. 1049) but differ through having simple lateral pronotal margins (not crenulate or broadly explanate), broader scutellum, shorter clypeus, shorter legs. The similarity of *Aporocera* [*Cyphodera*] to *Cadmus* (*Aorocarpon*) has already been noted, as also the similarity of some *A.* [*Ochrosopsis*] *australis* species-group to *Cadmus* s. str., and the similarity of *A.* [*Idiocephala*] *tasmanica* to *Brachycaulus*. *Aporocera* [*Cryptocephalus*] *serenus* has feebly crenulate lateral pronotal margins.

Some of the more distinct species-groups are briefly indicated below, although they may not be monophyletic.

8.5.7.6.2 *Aporocera* [*Schizosternus*] *albogularis* species-group

This group (formerly the genera *Schizosternus* and *Euphyma*) is defined by the presence of both laterocentral and lateral antennal slots in the anterior margin of the prosternum (Fig. 499), in what are otherwise typical species of *Aporocera*. It includes *A.* [*Loxopleurus*] *libertinus*, *A.* [*Euphyma*] *flaviventris* and *A.* [*Idiocephala*] *consors*. This is a group of about 20 species which shows too much variation to be monophyletic. There is some intraspecific variation in development of the antennal slots.

8.5.7.6.3 *Aporocera [Cryptocephalus] bihamatus* species-group

This is certainly a monophyletic species-group with several synapomorphies. It has a possible sister-group in *A.* [*Cryptocephalus*] *ornatipennis* which is a typical member of *Aporocera* except that it shares the abdominal hollow, prosternum and transverse scutellum of *A. bihamatus*. The sister-group of *A. bihamatus* species-group + *A. ornatipennis* may be part or all of the *A.* [*Ochrosopsis*] *australis* species-group.

There are four species with the following synapomorphies : male with apical antennomeres flattened and twisted (Fig. 329); front margin of prosternum reflexed and concave; scutellum transverse (Fig. 329); male with excavated apical ventrite; male with paired processes on ventrites (Fig. 329). In one species (undescribed) the male has inflated (almost toothed) hind femora (Fig. 329), but is otherwise typical.

8.5.7.6.4 *Aporocera [Ochrosopsis] australis* species-group

This may be a monophyletic group but the species are structurally variable. The approximately 20 species are all yellow to straw coloured with piceously stained punctures, have a convex apex to the prosternal process and a quadrate or transverse scutellum. The type species of *Ochrosopsis*, *O. australis*, is illustrated (Fig. 325). The small species in this group (*A. melanocephalus* and allies) are similar to typical *Aporocera* but some large species are superficially like *Cadmus* species and have been referred to under *Cadmus s. str.* *Aporocera australis* species-group may be related to *Cadmus s. str.* either through symplesiomorphy (both groups being basal in their respective lineages), or synapomorphy, but with *Melatia* as outgroup symplesiomorphic similarity of *Cadmus s. str.* and *Aporocera australis* species-group is unlikely. This problem needs to be pursued further. The species-group is particularly well represented in northern Australia and has one species in Timor (*wallacei*) and another in New Guinea which is shared with northern Australia (*poeciloderma*).

8.5.7.6.5 *Aporocera* [*Cadmus*] *pauperculus* species-group

The only species is minute (< 2.5mm) and may therefore only be different for allometric reasons. It is similar to typical *Aporocera* (cylindrical body, oblique pronotal grooves, epipleural lobes) but differs by : small size; dense microsculpture; scutellum with deep basal notch but elongate rectangular shape; base of pronotum almost straight; aedeagus without apical setae (Fig. 678). In common with *Diandichus* it has : dull, densely microreticulate upper surface; posterior margin of pronotum not produced, with long teeth; elongate narrow scutellum.

This may be either a small form of *Diandichus* or of more typical *Aporocera.* The attributes which identify it with *Diandichus* may be due to extreme reduction in size; biologically it differs from this subgenus. I have therefore placed *A. pauperculus* in *Aporocera.*

8.5.7.6.6 Further differentiation in *Aporocera s. str.*

Several books could be filled under this heading. The following examples illustrate some of the great range of morphological variation : *Aporocera* [*Cryptocephalus*] *albopictus* species-group (three species with antennomeres 3-5 broadly expanded in both sexes); *A.* [*Cyphodera*] *chlamydiformis* (with grossly inflated central pronotal tubercle; Fig. 326); *A.* sp. (Cania Gorge) species-group (five species with combination of strongly swollen pronotal disc, relatively wide head and short, thin legs; Fig. 327); *A.* sp. (undescribed, Kalgoorlie) (male with massively inflated head, toothed fronto-clypeus and elongate mandibles, female normal; Figs 330, 349). *Aporocera* sp. (Cania Gorge) species-group appears to be biologically distinct their hosts are *Melaleuca* and *Callistemon*, a host association so far unique in the Cryptocephalina.

I am not willing to create new names for any of the above because these taxa are essentially small autapomorphic units within *Aporocera.*

8.5.7.6.7 Subgenus *Diandichus*

Diandichus was formerly a monotypic genus described in the Pachybrachini (Chapuis 1874) and, although Baly later removed it to the Cryptocephalina (Baly 1877a), it is placed in Pachybrachini in the recent checklist (Seeno and Wilcox 1982). *Diandichus analis* is one of the most distinct species of Australian Cryptocephalina (figured in Chapuis 1876a). It belongs to a group of six species with the following possible synapomorphies : upper surface densely microsculptured (Fig. 127); eyes bulging laterally, with deep and narrow canthus; clypeus long with sides parallel-sided; lateral margin of pronotum broadly explanate and feebly crenulate; no oblique pronotal grooves; base of pronotum evenly rounded and elongately toothed (Fig. 127); prosternal process narrow and elongate, width less than half width of procoxa (not *absonus*); scutellum narrow, very elongate, base notched (Fig. 127); epipleura evenly attenuated, not sinuately lobed; female hollow very large and deep (Fig. 152); larva : apex of galea with elongate flattened basiconic sensilla; distance Dts1-2 less than Dts2-3; scatoshell with rows of elongate spines (Fig. 2). *Diandichus* also has the following features : antennae as long as body, with scattered basiconic sensilla (Figs 93-94); mesepimeron impunctate; elytral punctures confused; legs elongate, especially tarsi. The larval head capsule has large frontal tubercles but is otherwise unremarkable (Figs 37-38).

Diandichus analis is extremely distinctive, but other species of subgenus *Diandichus* are similar to Western Australian species which I have placed in *Aporocera* (for example *A.* sp. 1048 and *A.* sp. 1049) which grade into more typical *Aporocera*. *Diandichus* and *A.* sp. 1049 and allies share the following : narrow, elongate scutellum; eyes deeply excavate with narrow canthus; female egg-hollow large and deep; elytra long, covering pygidium. *Diandichus* species differ by the combination of bulging eye shape, long parallel-sided clypeus, narrow prosternal process, and explanate lateral pronotal borders. The scatoshells of *A.* spp. 1048 and 1049 are simply ridged. *Diandichus* species are unusual in the Australian Cryptocephalina because they all feed in *Acacia* flowers, but the similar Western Australian species *A.* sp. 1049 is also unusual, feeding on *Hibbertia* flowers. *Acacia* and *Hibbertia* are unrelated plants but both have yellow flowers. All the above evidence suggests that although *Diandichus* is distinct, it may be derived from within *Aporocera.*

8.6 Observations on character variation within the proposed classification

The phylogenies proposed in the preceeding sections and the classification presented in Chapter 9 are the result of the study of character variation. It may seem tautologous, therefore, to use this classification to discuss character variation and evolution. However, the classification is not based on any one character system. The following discussion examines certain characters or character complexes and the extent to which they vary in the classification. An understanding of the variation in some important characters was facilitated by species level studies of adults and larvae (if available) of all Australian Chlamisini, Platycolaspina, *Cadmus* subgenus *Lachnabothra* and *Aporocera* subgenus *Diandichus*, that is, approximately 70 species in all. Finally, the phylogeny of the Camptosomata is compared with a non-morphological data set, the karyology.

As an explanation for the non-universal distribution of character states in clades I have generally assumed that reversal is evolutionarily simpler, more likely and more frequent than independent acquisition of the same structure. However, if homoplasy is common it would be impossible to distinguish the process of reversal from convergence in taxon evolution.

8.6.1 Scatoshell

Scatoshell production and morphology is reviewed by Erber (1988). The following is based on his review and my observations. There seems little doubt that attachment of the scatoshell to a substrate is plesiomorphic for the Camptosomata, as it is found in Lamprosomatinae, Chlamisini and Clytrini. This habit has been lost in Pachybrachini, Cryptocephalini and some Clytrini. A rough relatively fibrous and unstructured scatoshell surface may also be plesiomorphic and is characteristic of Lamprosomatinae and Chlamisini. Clytrini, Pachybrachini and most Cryptocephalini have spiral arrangements of ridged plates. Various secondary modifications of scatoshell shape are convergent and widespread in Clytrini, Pachybrachini and Cryptocephalini.

Enlargement of the scatoshell by the larva is plesiomorphic in Lamprosomatinae and Chlamisini; material is added at the orifice and the original scatoshell remains as a nipple on the end of the larval case. In Clytrini, Pachybrachini and Cryptocephalini the larva adds material along a ventral slit as well as the orifice, eventually obliterating the original scatoshell.

Variation in scatoshell structure appears to be related to variation in morphology of the female rectum. The ability to make a spirally walled scatoshell may be correlated with development of a dorsal longitudinal fold in the rectum (some Pachybrachini, all Cryptocephalini), or a complete transverse dorsal sclerite (some Pachybrachini, all Clytrini). The size and shape of the individual plates used in scatoshell construction is probably correlated with variation in flexure of the dorsal fold. There is no correlation between vaginal palp shape and scatoshell structure in the Australian Cryptocephalina, which show a great range of variation in both structures.

8.6.2 Larva

8.6.2.1 General morphology

The evolution of larval development in a case apparently occurred only once (ancestor of Camptosomata) and has resulted in relative stasis of the thoracic and abdominal structures. The plesiomorphic bicameral spiracles were replaced by cribriform spiracles after divergence of the Lamprosomatinae. Cribriform spiracles are associated with larvae in humid micro-environments (Crowson 1981; inside the scatoshell?). Moniliform spiracles may have appeared in the ancestor of Cryptocephalini (they are in all subtribes except Stylosomina), but there is either much reversal or convergence. Both moniliform and cribriform spiracles are found in different species of *Lachnabothra* and on different parts of the body in *Semelvillea* species and there seems to be no correlationnbetween spiracle type and habitat. The number of pairs of eggbursters is presumably primitively three, but this is reduced to two in *Oomorphus*, *Neochlamisus*, most Platycolaspina, all Ditropidina and most Cryptocephalina. The abdominal eggburster is present in *Pachybrachis*, but was overlooked by LeSage (1985a; I have examined his material). The eggbursters are always small and presumably functionally unimportant because the chorion is so thin.

8.6.2.2 Head capsule

Surface microsculpture of the head capsule is absent from Eumolpinae, Lamprosomatinae and Chlamisini and posteroventral tuberculation is present in all Clytrini, Pachybrachini and Cryptocephalini. Pitting of the epicranium is presumably convergent in Clytrini and Cryptocephalina. The thickened operculate type of head capsule with a ridge or angulate rim at the edge of the epicranium has evolved in three quite separate lineages : Pachybrachini, Platycolaspina and Cryptocephalina. In the Cryptocephalina it has probably evolved at least twice and perhaps many times. The epicranial ridge is present in about half the species of each of *Cryptocephalus* and the Australian taxa but the different positions of the frontal sutures and setae Aes1-3 relative to the ridge in the two groups suggest separate origins of this feature. The operculate capsule is not confined to arid zone species and may therefore have a defensive rather than microclimatic function. Fusion of the labrum to the clypeus is not reversed in Camptosomata and is a good synapomorphy for them. The dorsal epipharyngeal setae are synapomorphic and not reversed in Cryptocephalinae.

Reduction of antennal segments from three to two is convergent in *Lamprosoma*, Chlamisini and Clytrini. The plesiomorphic mandible type for Cryptocephalinae, which has a long straight edge and overlapping tooth internally, is convergently modified in Pachybrachini and Ditropidina.

The number and position of head setae is remarkably stable in the Cryptocephalinae. Papillation of the setae is probably a synapomorphy for Clytrini, Pachybrachini and Cryptocephalini. However the shape and position of individual setae varies greatly and these states are frequently convergent. For example, Aes1 is either simple or papillate in Platycolaspina and Ditropidina, and Des1 becomes part of the row of setae adjacent to the frontal sutures in several unrelated Australian Cryptocephalina. The pattern of upper frontal setae is relatively stable within higher taxa. The 2+4 system is possibly plesiomorphic within Cryptocephalinae and is characteristic of Chlamisini, Clytrini, Pachybrachini and Coenobiina, although the last group may be convergent. The 2+2 system is convergent in some Platycolaspina and in Australian Cryptocephalina.

8.6.2.3 Legs

The number and position of setae and sensilla is relatively stable in Clytrini and Cryptocephalini. 'Additional' ventral tibial setae in Chlamisini and Pachybrachini may be convergent or plesiomorphic although the number is variable in Chlamisini. Spatulate tibial setae have independently evolved in the completely unrelated groups Chlamisini and *Ditropidella*. These are similar to the adult tarsal adhesive setae used for gripping leaves (Figs 147-148) and Chlamisini feed on living foliage (LeSage 1984b), therefore it is possible that *Ditropidella* larvae have a similar biology. However, the larvae of *Lexiphanes* also feed on living foliage but lack setal modifications on the legs (LeSage 1984a).

8.6.3 Pupa

Only a few observations may be made about the distribution of pupal characters. Setae of Camptosomatan pupae are reduced in size and distribution. Urogomphi have been independently lost in Clytrini and some Cryptocephalina. The fleshy protuberances of tergites VI and VII may be convergent in Chlamisini and Cryptocephalini or may be more widespread and related to the similarly placed spines in eumolpine larvae. The apical elytrothecal lobes are possibly synapomorphic for Cryptocephalini but are not mentioned in the description of *Lexiphanes* (LeSage 1984a).

8.6.4 Adult

8.6.4.1 Colour and surface sculpture

Colour was not used as a character, but there is an obvious relationship between brightness of colour and lack of visible pubescence (there is usually at least a minute setal 'stump'in each puncture). Pubescent species are dark and often rugosely sculptured. Species with dorsal bright coloration are not dorsally pubescent. Visible pubescence is scattered throughout all the supraspecific taxa studied. Densely microsculptured species are also dull or dark coloured and frequently pubescent. Surface sculpture, pubescence and colour are at least partially correlated characters and should be used cautiously in phylogenetic studies of this group. Generally these characters are of little use in the Cryptocephalinae because they are conspicuously variable in otherwise well-defined species-groups.

8.6.4.2 Male secondary sexual characters

The possible functions of male secondary sexual characters in Cryptocephalinae were discussed by Medvedev (1962a). Enlargement of the male mandibles (and consequently the head capsule) occurs in a few species of genera of Lamprosomatinae (Monrós 1956a; Medvedev 1962a), Chlamisini (Monrós 1951a; Karren 1972), Clytrini (Fig. 303; Jacoby 1908b; Monrós 1953b; Mohr 1966), *Leasia* (Fig. 408), *Ditropidus* (Figs 309, 340), *Scaphodius* (Figs 341-342) and *Aporocera* (Figs 330, 349). Absence of enlargement in closely related species of at least some of these taxa suggests that male mandible enlargement is not a good criterion for defining genera. Enlargement of the fore legs of males is also sporadic but widespread in the Camptosomata and is characteristic of all Pachybrachini except *Mylassa*, in which there are other leg modifications (Fig. 305; Monrós 1949b). Enlargement of the hind femora occurs in some *Lachnabothra* species (Fig. 915) and an undescribed *Aporocera* (Fig. 329). All of the male secondary sexual attributes described above are probably concerned with male rivalry for females. Other secondary sexual characters include the development of ventral tubercles on the metasternum (Fig. 912) or sternites (Fig. 574), which may have a pivotal function on stems in fights between rival males, or may lock into the gap between apex of elytra and pygidium as described for *Cryptocephalus* (Medvedev 1962a). All of the male secondary sexual attributes described above are probably concerned with male rivalry for females (Thornhill and Alcock 1983). Many of the species in Australia with strong sexual dimorphism are relatively rare (the species of *Aporocera* with massive mandibles (Fig. 330) and enlarged hind femora (Fig. 329) are each known from two specimens; *Lachnabothra* species are rare). In confinement males of Cryptocephalini are very aggressive and will bite off each other's antennae. Rival male *Labidostomis* (Clytrini) use the base of the mandibles to grip the antennae at which point the held individual gives up (Medvedev and Pavlov 1988). Loss of antennae presumably leads to inability to find females therefore evolution of large mandibles may be directly related to mate competition. Evolution of antenna size may also be affected by male sexual behaviour, but larger antennae have more sensilla for finding females.

Ventral abdominal tubercles may also act as a secondary 'lock and key' mechanism against the apex of the female dorsum (Medvedev 1962a; Medvedev and Pavlov 1988). Medvedev showed that the male tubercle may be applied to the concavity between the elytra and pygidium of the female and that the male apical abdominal hollow accommodates the pygidial surface. The male abdominal hollow is common in Australian Cryptocephalina (many *Cadmus*, some *Aporocera*), but is deep and armed with lateral spurs in some species and may therefore have another function.

8.6.4.3 Mouthparts

The mouthparts were studied in detail but hardly used in the derivation of phylogeny. I had hoped to find the kind of useful variation found in other Coleoptera (for example Staphylinidae; Ashe 1984), but discovered remarkable uniformity in the mouthparts of Camptosomata. This is probably not surprising, since all the species studied here eat leaves or flowers (not pollen). Variable characters varied within supraspecific taxa (for example epipharyngeal basiconic sensilla Figs 368-396; mandibular shape Figs 397-425; division of submentum Figs 448-457).

8.6.4.4 Prothorax

The procoxal cavity was primitively closed by the insertion of the hypomeron into the prosternal process, as found in Eumolpinae and Lamprosomatinae. All members of the Cryptocephalinae have the prosternal process slotted into the hypomeron or open procoxal cavities. Reversal of the locking mechanism is likely to have involved an intermediate state with open cavities. Open procoxal cavities are only present in some members of the unrelated Clytrini and Platycolaspina, but in both groups they are most likely to have been derived convergently from an ancestor with the reversed mechanism, because other members of these groups, and their sister-groups, show the derived closure state.

Adult Eumolpinae and Camptosomata lack surface defence glands (Deroe and Pasteels 1980), therefore it is not surprising that their normal defence mechanism, 'drop-off' and thanatosis, has led to the convergent development of ventral antennal grooves. Convergence of the lateral prosternal process grooves in the Camptosomata is debatable (Kasap and Crowson 1976), because they are present in relatively plesiomorphic taxa, the Lamprosomatini, Chlamisini and *Adiscus*. Deep antennal grooves are absent in Sphaerocharitini, Pachybrachini, Clytrini and Cryptocephalini except *Adiscus* and appear to be of different origin in *Oomorphus* and *Chlamisus* (Figs 101-102), therefore the grooves are probably convergent in each taxon. Other, obviously analogous but not homologous, grooves are present in *Ischiopachys* and several Australian Cryptocephalina.

8.6.4.5 Elytral tuberculation

In the camptosomata, elytral tuberculation is largely confined to Australasian Cryptocephalina and is possibly convergent in *Melatia*, *Cadmus* and *Aporocera*. Convergence may seem unlikely because of the similar distribution of the tubercles, but it is possible that tuberculation only occurs in certain parts of the elytral interstriae, perhaps in areas between the tracheae, punctures and other 'organs'. If this is true then a tendency towards tuberculation would repeat a similar pattern in unrelated taxa, given that the internal elytral morphology was similar. This (untested) hypothesis is comparable to the explanation for similar wing spots in various unrelated butterflies.

8.6.4.6 Aedeagus

The aedeagus has been illustrated for numerous species of *Cryptocephalus* (for example, see Burlini 1955; Mohr 1966; White 1968; Berti and Rapilly 1979; Lopatin 1982a). It is clear from these studies that aedeagal morphology may help to define some species-groups but that it is an organ with a fairly limited range of variation so that similar but complex shapes recur in unrelated species. This is especially obvious when the aedeagi of the Australian Cryptocephalina are compared with those of *Cryptocephalus*. Many of the aedeagi of Australian species are simply bent, dorso-ventrally flattened tubes with a triangular tip and a variable-sized apical orifice. Such aedeagi are of little use for phylogenetics, being too similar morphologically. Other aedeagi are quite bizarre in shape, for example in *Lachnabothra* species (Figs 916-919). This bizarreness may be almost facsimilied by unrelated species, for example the aedeagi of *Lachnabothra* species are almost identical to those of Iranian *Cryptocephalus* species (Berti and Rapilly 1979). Aedeagal shape may be simple or complex within genera (*Atenesus*; Figs 625-636). The ejaculatory guide may also vary greatly (*Semelvillea*; Figs 603, 607, 613, 617) and is difficult to see and describe. The aedeagus is too variable within certain morphological restraints to be of great use at generic level.

The presence or absence of setae at the apex of the aedeagus is useful at tribal or subtribal level but the actual distribution of the setae is difficult to categorise and was not used in this study. The setae have been lost in some species of Cryptocephalina.

8.6.4.7 Spermatheca

This organ is remarkably conservative in morphology throughout the Camptosomata, as it is in Chrysomelidae generally (Suzuki 1988). Apart from the synapomorphic pump-like structure of Coenobiina, peculiarity of structure is rare and scattered.

Correlation between length of the spermathecal duct and length of the ejaculatory duct was absent in the taxa studied. Both ducts were long.and coiled in only 9 of the 29 species with at least one duct long and coiled.

8.6.4.8 Kotpresse

The kotpresse is a complex character system with considerable variation and therefore ideal for phylogenetic study. The plesiomorphic sclerite system for Cryptocephalinae appears to be one complete transverse ventral sclerite and a split transverse dorsal sclerite, together with at least a pair of lateral sclerites. This system is present in Chlamisini, Platycolaspina, Coenobiina, Ditropidina and Cryptocephalina. It has been convergently reduced to almost nothing in *Aprionota tutuilana*, *Melixanthus intermedius* and the Australasian Cryptocephalina. Lateral extensions to the ventral and dorsal sclerites have probably independently evolved in Pachybrachini + Clytrini, Platycolaspina + Stylosomina and Ditropidina. Secondary sclerotisation occurs widely and convergently in different subtribes of Cryptocephalini.

8.6.4.9 Karyology.

I did not use karyological data in this study but information is available for some groups. The following discussion summarises these data and relates them to my own studies. The mechanisms of chromosomal evolution in Chrysomelidae and the associated terminology are discussed in detail by Virrki (1984) and Petitpierre and Segarra (1985).

Karyology represents a different character system from life-stage morphology, but it has only two characters : number of chromosomes and type of sex chromosomes. Hence there is the possibility of considerable convergence if evolutionary changes are frequent. Known chromosome numbers and meioformulae have recently been summarised for all Chrysomelidae (Petitpierre, Segarra, Yadav and Virrki 1988) which show great diversity. Within the Camptosomata, these authors provide information (number of genera and species in brackets) for Chlamisini (2:2), Pachybrachini (2:7), Clytrini (6:12) and Cryptocephalini (1(*Cryptocephalus*):29). The karyology of 39 species of Eumolpinae is also described.

Some interesting observations may be made from these data. Two species, *Diapromorpha turcica* (Clytrini) and *Platycorinus peregrinus* (Eumolpinae), show intra-specific variation in both chromosome number and sex chromosome type and this emphasises that only tentative phylogenetic conclusions may can be made from karyology. It appears probable that the plesiomorphic condition in the Chrysomelidae is 16 (n=7) chromosomes with the X_{yp} sex-determining system (Petitipierre 1988). This 'parachute' system associates the male heterosomes by the nucleolus or telometric heterochromatin (Virrki 1984). The modal meioformula for Eumolpinae is $7+Xy_p$. All Pachybrachini have 7+Xy except *Metallactus* with 7+X. The chromosome number is frequently doubled in some Chrysomelidae and most *Cryptocephalus* have $14+Xy_p$ or $14+Xy_r$ but there is considerable variation, from $7+Xy_p$ to $19+Xy_p$. The meioformulae of Chlamisini and Clytrini show great variation but no obvious relationship to $7+Xy_p$ or $14+Xy_p$. The meioformulae of Clytrini are 10+Xy, 10+X+y, 11+Xy, 11+X+y, $11+Xy_p$ and 19+Xy. The meioformulae of Chlamisinae are $9+X_1X_2Y$ and 8+neoXY. Meioformulae for Lamprosomatinae are unfortunately not available.

Petitipierre (1988:146) describes the similar meioformulae of Pachybrachini and Eumolpinae as convergent (because "both taxa [are] well separated in all taxonomic arrangements") and suggests that $9+Xy_p$ is the ancestral formula for Chrysomelidae. He also suggests that the shared X+y system between Megalopodinae and a few Clytrini is evidence for a relationship between these "closely related" subfamilies.

My interpretation of the same data, obviously based on *a priori* knowledge of the morphology of the taxa, is that Pachybrachini show the plesiomorphic meioformula for Cryptocephalinae, some *Cryptocephalus* species (a possible but unlikely monophyletic group) have undergone chromosome fission to give n=14 and the meioformulae of Clytrini and Chlamisini are not phylogenetically useful at present. The X+y mechanism of Megalopodinae and some Clytrini is also found commonly in Alticini and is presumably convergent in each group.

The time has come to draw in the reins of my inspiration and to stop for a moment along the way, as when one looks at a woman's vagina; it is wise to look over the ground I have covered, and then, having rested my weary limbs, to soar off with a bold leap. To cover such a stretch in a single breath is by no means easy; one's wings get very tired, flying high, without hope and without remorse ....

Chants de Maldoror, Lautréamont, 1869 (transl. P. Knight).

Chapter 9 : Identification and classification of the Camptosomata in Australia and the south-western Pacific region

The following survey includes keys and diagnostic descriptions for all supra-specific taxa in Australia, Fiji, Micronesia, New Caledonia, New Guinea, New Zealand, Samoa and Tonga, but is written largely from an Australian viewpoint. New taxa are given more comprehensive treatment. Suprageneric diagnoses appropriate for the world fauna are suggested in Chapter **8**. The species of the genera occuring in the region are listed in Appendix **B** and this appendix includes details of nomenclatural changes.

Non-Australian taxa are indicated by an asterisk.

9.1 Diagnosis of Camptosomata.

The Camptosomata are reasonably well defined on larval characters but adults may be difficult to separate from some Eumolpinae. The following attributes are almost universally present. In adults : apical aedeagal setae (except a few *Aporocera* and *Cadmus*); loss of articulation of vaginal palp and ovipositor not telescopic; loss of spiculum gastrale in female. There is no development of a subcubital fleck. In eggs and first instar larvae : egg completely coated by glandular/excremental mixture (scatoshell), either attached to leaf by chorionic stalk or dropped; larva case-bearing, and therefore body C-shaped to allow passage of faecal matter; labrum fused to clypeus; labio-maxillary complex elongated, flattened and strongly sclerotised. In pupae the possible synapomorphies are entirely short setae, and absence of setae from legs.

9.2 Keys to the genera of Camptosomata in Australia and the south-west Pacific region

In each couplet characters are listed in order of diagnostic value *and* visibility. Additional characteristics are given in brackets to aid in recognition of one half of a couplet; in these cases the other half of the couplet should be assumed to be variable.

Some taxa, polythetically defined, may be diagnosed by possession or lack of combinations of attributes.

9.2.1. Adults

1. Upper surface smooth and prosternum with deep lateral antennal slots (Fig. 102); ventrites VI and VII free, not connate; hypomeron inserted into prosternal process; (size 1.2-2mm; form hemispherical; antenna short (c. head width); pygidium at most with only apex exposed by elytra); [Lamprosomatinae] .... **Oomorphus*

\- Without antennal slots at sides of prosternal process or if so, upper surface tuberculate; ventrites VI and VII connate; prosternal process inserted into hypomeron or procoxal cavities open; (rarely hemispherical) [Cryptocephalinae] 2

2(1). Scutellum trapezoid, widest at apex (Fig. 502); prosternal process with lateral antennal slots (Fig. 103); basal margin of pronotum bisinuate; sternites IV to VI telescoped into III (Fig. 564) (form cylindrical; coarsely tuberculate and microsculptured; head deeply inserted into prothorax; eye with well-developed canthus; pygidium completely exposed; Figs 857-892) .... *Chlamisus*

\- Scutellum otherwise; prosternal process without antennal slots; basal margin of pronotum rarely bisinuate; sternites IV to VI not telescoped into III 3

3(2). Procoxal cavity externally open (Figs 104, 111-113, 468-469); hind margin of pronotum bordered or untoothed (Figs 161-170, 304) 4

\- Procoxal cavity closed; hind margin of pronotum usually unbordered and toothed 7

4(3) Prosternal process narrow, concave and sunk between coxae, not expanded at apex; hind angles of pronotum rounded (Fig. 304); antenna serrate (Fig. 356), length approximately equal to head width (Fig. 304) .... *Aetheomorpha*

\- Prosternal process broader, expanded at apex (Figs 111-113); hind angles of pronotum prominent (Figs 111-113); antenna longer, not serrate (Fig. 357) 5

5(4). Lateral margins of pronotum broadly explanate, posterior margin almost straight (Fig. 161); apex of elytral suture evanescent; hypomeron lobe longer than distance between it and prosternal process (Fig. 113) .... *Platycolaspis*

\- Lateral margins of pronotum simple, narrow (Figs 162-164); elytral suture complete to apex; hypomeron lobe shorter than this distance (Figs 111-112) 6

6(5). At least head and pronotum strongly and evenly isodiametrically microsculptured (Figs 67, 163-166); posterior lobe of pronotum usually triangular (Figs 163-166); scutellum with rounded apex (Figs 130, 167-170) (dorsal punctures finer; antenna shorter) .... *Leasia*

\- Dorsum without regular microsculpture (Figs 66, 162); posterior lobe of pronotum rounded (Fig. 162); scutellum with truncate apex (Fig. 129) (dorsal punctures coarser; antenna longer) .... *Atenesus*

7(3). Pronotum with row of small tubercles parallel to posterior border (Fig. 123); prosternal process constricted at base, parallel-sided in apical half and apex concave (Fig. 117); scutellum triangular and flat (Fig. 143); canthus shallow (Fig. 73) .... *Diachus*

\- Pronotum without a row of small tubercles; prosternal process either entirely parallel sided or expanded towards apex (Figs 106-110, 115); without the other combination of characters 8

8(7). Posterior margin of pronotum smoothly bordered, without trace of teeth (Figs 109-110, 306-308) (posterior pronotal lobe shallow and truncate) 9

\- Posterior margin of pronotum unbordered (Figs 309-330), usually entirely toothed (may be reduced to a pair of small angular projections on either side of middle, Fig. 117) 11

9(8). Front femur enlarged and ventrally keeled (Fig. 306); length of elytron 1.5 x length of pronotum (Fig. 306); antennal basiconic sensilla in circular pits (Fig. 78) .... *Metallactus*

\- All femora similar sized (Figs 308, 893); length of elytron less than twice length of pronotum (Figs 308, 893, 897, 898); basiconic sensilla not in pits (Fig. 92) 10

10(9). Sutural locking mechanism evanescent before apex (Figs 893, 897, 898); prosternal process elongate and greatly expanded apically (Figs 109-110, 475-476); claws appendiculate .... *Semelvillea*

\- Sutural locking mechanism complete to apex (Fig. 308); prosternal process transverse and not greatly expanded at apex (Figs 477-478); claws simple .... **Arnomus*

11(8). Prosternal process broad and flat, sides approximately parallel and ridged (Figs 106-108); scutellum always small, flat, usually fusiform or elongate rectangular, rarely oval or quadrate (Figs 137-138, 506-510); anterior of scutellum stepped to accomodate pronotal lobe (not usually externally visible); posterior lobe of pronotum narrow, triangular or rounded (Figs 106-108, 309-310, 482, 485-489) (maximum size 6mm) 12

\- Prosternal process without parallel, ridged, sides (Figs 115, 496, 498-499); scutellum usually much larger, posteriorly raised, never fusiform, not stepped (Figs 141, 517-519); posterior lobe of pronotum broad and truncate or absent (Figs 314-330) (antennal basiconic sensilla not in circular pits) 15

12(11). Antennal basiconic sensilla not in circular pits (Figs 83-84); canthus deep, triangular, with horizontal upper margin and antennae inserted high on frons with a row of impressed punctures or a groove between them (Figs 64-335); pygidium with a transverse biarcuate ridge (Fig. 571) (eyes large, touching or almost so) .... *Aprionota*

\- Basiconic sensilla in circular pits at apices of segments (Figs 85-87, 362-364); canthus rarely deep, upper margin not horizontal and antennae inserted lower on frons, without groove between (Figs 65, 336-342); pygidium simple 13

13(12). Eyes large, close, with deep angulate canthus (Fig. 339); clypeal area well-marked, triangular (Fig. 339); gena long, impunctate; posterior lobe of pronotum raised and posterior angles produced (Fig. 488);elytronstrongly puncture-striate with convex intervals (size < 3mm) .... *Ditropidella*

\- Eyes smaller, canthus shallower (Figs 65, 335-338, 340-342); clypeal area not triangularly delimited; gena usually shorter or punctate; posterior lobe of pronotum rarely raised (Figs 309-310, 484);elytronrarely puncture-striate with convex intervals 14

14(13). Eye relatively small, convex, without a canthus (Figs 341-342); antennal segments thin and elongate; male with elongate mandibles (at least as long as eye) and laterally or centrally produced clypeus (Figs 341-342); pronotum not strongly constricted anteriorly; elytral epipleuron slightly lobate, not crossed at base; claws appendiculate .... **Scaphodius*

\- With three or less of the above characters in combination; very rarely without a canthus; pronotum more strongly constricted apically .... *Ditropidus*

15(11). Eye relatively small but convex with deep triangular canthus (Fig. 347; the species illustrated has the largest eye to temple ratio); temple relatively large; scutellum triangular, apex sometimes rounded but never truncate, usually flush with elytra (Fig. 517); mesoscutum without lateral patches of microchaetae and without a longitudinal keel along midline (Fig. 517); external edge of tibia with a longitudinal groove or pair of ridges (not *M. solomonensis*) (antenna usually about half body length, never more than 2/3) .... *Melatia*

\- Eye usually larger, less convex and canthus lobate and internally rounded if deep (Figs 71-72, ; temple relatively smaller; scutellum rarely triangular, if so apex truncate, always projecting above elytra (Figs 314-330); mesoscutum almost always with lateral patches of microchaetae and with a longitudinal ridge along midline (Figs 141, 518-519); tibia without external grooves or a pair of ridges 16

16(15). Pronotal disc with a pair of large usually blunt tubercles which are rarely reduced to slight angulation of the sides of the disc (Figs 314, 906-908); scutellum laterally punctate or densely longitudinally strigose; elytra tuberculate, at least near scutellum (Figs 314, 909-911) 17

\- Pronotal disc simple, or with several small tubercles, or a single central tubercle (Fig. 326), or with front half strongly gibbous (Figs 327-328); scutellum variable; elytra rarely tuberculate 19

17(16). Lateral margins of pronotum and sides of anterior margin strongly and fairly evenly crenulate (Fig. 314); disc of prosternal process longitudinally raised, usually with a pair of ridges; eye relatively small (Fig. 314), with shallow canthus; antenna 1/2-2/3 body length (Fig. 314); second tarsal segment transverse to quadrate (Fig. 314) .... *Cadmus* sg. *Brachycaulus*

\- Lateral and anterior margins of pronotum simple or lateral margins slightly uneven (Fig. 318); prosternal process flat; eyes relatively larger, with a deep lobate canthus; antenna 2/3 length of body or longer (Fig. 318); second tarsal segment elongate 18

18(17). Antenna as long as or longer than body (Fig. 318), last segment dark tipped or inflated (except one species with short pale antennae; Figs 901-902); pronotal pubescence recumbent and radiating from lateral and basal depressions (except one species with sparse erect pubescence); prosternal process densely pubescent, surface not visible; scutellum strongly raised (Figs 909-910) with median longitudinal keel and radiating pubescence on either side .... *Cadmus* sg. *Lachnabothra*

(males, plus female of one species with reversed characters)

\- Antenna less than body length, last segment undifferentiated (Fig. 903); pronotal pubescence variable; prosternal process not densely pubescent;

scutellum without longitudinal keel and lateral pubescence ....
.... *Cadmus* sg. *Aorocarpon* (part)

19(16). Scutellum with a median longitudinal keel (Figs 317-318, 518) and/or large lateral punctures; pronotum densely or rugosely punctured, usually visibly pubescent [*Cadmus*] 20

\- Scutellum without median keel (Fig. 519) or lateral punctures (or a few minute ones present); pronotum rarely densely or rugosely punctured, not pubescent [*Aporocera*] 23

20(19). Elytra tuberculate (as in Figs 318, 909-910); scutellum keeled, truncate-triangular (Fig.318) (pronotal lateral margins uneven or simple, not strongly crenulate) 21

\- Elytra non-tuberculate, or canaliculate; scutellum usually quadrate, keel variable (Figs 315-316) 22

21(20). Pronotum clothed in recumbent pubescence radiating from lateral and basal depressions; scutellum with lateral radiating pubescence and strong central keel; prosternal process densely pubescent ....
.... *Cadmus* sg. *Lachnabothra* (females)

\- Upper surface glabrous or almost so, without such recumbent pubescence; scutellar keel less prominent; prosternal process not densely pubescent
.... *Cadmus* sg. *Aorocarpon* (part)

22(20). Lateral margins of pronotum and sides of anterior margin visibly and fairly evenly crenulate (Figs 315-317); anterior angles of pronotum produced beyond prosternum(Figs 315, 317); head and pronotum densely and rugosely punctured, often glabrous; scutellum often ridged (Figs 317, 518), if not usually glabrous .... *Cadmus s. str.*

\- Lateral and anterior margins of pronotum simple, borders thin; anterior angles not produced; head and pronotum densely but relatively finely punctured and pubescent; scutellum unridged, punctate and pubescent ....
.... *Cadmus* sg. *Cadmoides*

23(19). Scutellum elongate, narrow (Fig. 127); upper surface densely microsculptured (Fig. 127); clypeal area quadrate, parallel-sided; eye strongly laterally convex; lateral margins of pronotum explanate; basal margin of pronotum evenly rounded or feebly produced; prosternal process narrow and elongate, width less than half width of procoxa (not *absonus*) .... *Aporocera* sg. *Diandichus*.

\- At least without the combination of long parallel-sided clypeus, laterally bulging eye, explanate lateral pronotal margins and narrow prosternal process; but otherwise variable (e.g. Figs 319-330) .... *Aporocera s. str.*

9.2.2 First instar larvae (larvae of *Aetheomorpha*, *Diachus*, *Melatia*, *Metallactus* and *Scaphodius* unknown)

1. Spiracles biforous (Figs 56, 264) (all setae simple) .... *Lamprosomatinae

\- Spiracles cribriform (Figs 57-60, 265-272) [Cryptocephalinae] 2

2(1). Tarsungulus short, ventrally bluntly toothed and protibia with more than four, spathulate, ventral setae (Fig. 240); (epicranium not ridged (Fig. 186); antenna two segmented, sensory appendage conical; setae not papillate) .... *Chlamisus*

\- Tarsungulus longer, not toothed and protibiae with four or rarely five ventral setae, rarely one or two clubbed (Figs 251-263) 3

3(2). Antenna 2 segmented, sensory appendage globular or flattened (Figs 189, 192) (epicranium not ridged (Figs 10-11); frons not microtuberculate; frontal setae in 2+4 pattern) .... Clytrini

\- Antenna 3 segmented, sensory appendage conical (Figs 18, 200, 212) 4

4(3). Mandible with strong non-overlapping tooth on middle of internal edge (Figs 226, 228-232) 5

\- Mandible with less prominent, usually overlapping tooth in apical third of internal edge (Figs 227, 233-238) (mandibular setae simple) 7

5(4). Frontal setae in 2+4 configuration (as in Figs 25-26, 192); mandibular seta Ms1 papillate (Fig. 226) .... Pachybrachini

\- Frontal setae in 2+2+2 configuration (Figs 27-28, 215), or rarely 2+2 (Fig. 212); mandibular setae simple (Figs 228-232) 6

6(5). At least one apical tibial seta spathulate (Figs 257-258); seta Aes1 much more distant from frontal suture than Aes2 (Figs 218, 220) (internal mandibular tooth relatively small; frons non-tuberculate) .... *Ditropidella*

\- Tibial setae simple (Figs 259-260); setae Aes1 and Aes2 at similar distance from frontal suture (Figs 212, 215) .... *Ditropidus*

7(4). Frontal setae in 2+4 configuration (Fig. 208); all frontal and upper epicranial setae broad and papillate (Fig. 208); frons and epicranium non-tuberculate; mandible with extra external tooth (Fig. 209) .... *Aprionota*

\- Frontal setae in 2+2 or 2+2+2 configuration (Figs 30-40); if frontal and epicranial setae papillate, then at least upper frons microtuberculate; mandible without extra tooth (Figs 227, 233-238) 8

8(7). Frons and upper epicranium non-tuberculate, or with a few scattered tubercles along epicranial side of frontal suture (Figs 30-32); epicranium without ridge or angulation (Figs 14-15) (frontal setae in 2+2+2 configuration; Aes2 much longer than Aes1) 9

\- At least upper frons with tubercles (Figs 33-40); edge of epicranium usually ridged or angulate (Figs 16-22) 11

9(8). Head setae slightly expanded at apex, not papillate (Figs 14, 32, 204); spiracles minute (Figs 58, 269); mandibular teeth relatively broad (Fig. 205) .... *Atenesus*

\- At least some head setae clearly expanded at apex and papillate (Figs 197, 200, 202); spiracles larger; mandibular teeth finer (Figs 198, 201, 203) 10

10(9). Epicranium with a few tubercles along frontal suture (Fig. 31); distance between Dts1 and Dts2 much more than Dts2-Dts3 and femora spiculate (Fig. 255) .... *Platycolaspis*

- Epicranium smooth (Fig. 30); distance Dts1-Dts2 much less than Dts2-Dts3 and femora smooth (Fig. 254) .... *Leasia*

11(8). Tibiae and femora spiculate (Figs 196, 253); internal tooth of mandible weak, not overlapping (Figs 194, 227); (upper epicranium tuberculate or smooth) 12

- Tibiae and femora smooth (Figs 261-262); internal tooth of mandible well-developed, clearly overlapping edge (Figs 233-237) (upper epicranium pitted or smooth) 13

12(11). Thoracic spiracle moniliform, abdominal spiracles cribriform; Aes1 and Aes2 similar sized (Figs 16-17, 193) .... *Semelvillea*

- All spiracles cribriform; Aes2 much longer than Aes1 (Fig. 35) .... **Arnomus*

13(11). Frontal setae in 2+2+2 configuration and distance Fs2-Fs2 much greater than Fs3-Fs3 (Fig. 40); seta Des1 never forming part of Aes1-4 row (Fig. 22); epicranial ridge, if present, posterior to Aes row (Fig. 40) .... Nearctic Cryptocephalina (including *Diachus*?)

- Frontal setae in 2+2 configuration and distance Fs2-Fs2 equal to or less than Fs3-Fs3 (Figs 36-39, 222); Des1 commonly close to or part of Aes1-4 row (Figs 19-21); epicranial ridge, if present, aligned with Aes row (Figs 39, 222) .... *Aporocera* and *Cadmus* (not distinguishable)

9.3 SUBFAMILY ***Lamprosomatinae** Lacordaire.

TRIBE **Lamprosomatini** Lacordaire

The subfamily Lamprosomatinae is a small group of 12 genera and 200 species which are primarily Neotropical (Monrós 1960*b*). Two species of Lamprosomatini are recorded for the region, and both belong to the genus *Oomorphus* in the tribe Lamprosomatini. *Oomorphus* belongs to the tribe Lamprosomatini. The diagnosis is given here is based on the work of Monrós (1956a; 1958a) and the three species used in this study, because the local species were not examined.

Diagnosis

Adult : body almost hemispherical with flat venter; procoxal cavity closed by insertion of hypomeron into prosternal process (Fig. 467); sides of prosternal process with deep antennal slots (Fig. 102); lateral margin of epipleuron angular; clavate protarsal setae of female on segments 1 to 3; hind margin of apical abdominal sternite and internal apex of elytron crenulate (Fig. 563); sternites separated into three regions by longitudinal lateral ridges (Fig. 563); abdominal ventrites free not connate (Fig. 563); sternite VIII of female broad and setose (Fig. 717); vaginal palp with stylus present but fused to coxite ventrally (Fig. 717); ventral transverse sclerite of kotpresse absent (Figs 808-809); hollow of apical sternite of female very shallow or absent.

Further characteristics of the three Lamprosomatini studied here which may be more widely applicable include : antennae without well-defined sensory areas on segments (Fig. 77); simple broadly curved to shallowly angular posterior pronotal margin (Fig. 102); prothoracic furca large and angulate, with a basal lobe (Fig. 467); mes-epimeron densely strigose; lateral angles of mesoscutum simple, not enclosing a deep hollow; scutellum triangular and flat; metendosternite with very thin lateral processes and tendon arms not fused and produced (Fig. 530); if cell 2A present, greater than or equal to size of 1A (Fig. 553); basal lateral process of abdomen composed of both sternite and pleurite (Fig. 563); pygidium at most with only apex exposed by elytra; ejaculatory guide absent (Figs 584-585); venter of kotpresse with scattered sensilla in both anterior and posterior halves (Figs 808-809).

First instar larva (based on *Lamprosoma* and *Oomorphus concolor*): without papillate setae (Fig. 185); head capsule smooth, without pits or tubercles and epicranium not ridged (Fig. 24); mandible with blunt tooth half way along internal edge and with three apical teeth (Fig. 224); mandibular setae not aligned towards apex (Fig. 224); epipharyngeal setae internal (Fig. 185); spiracles biforous (Fig. 264).

The two species are placed in *Oomorphus*. This is a widespread genus with a European type species.

9.3.1 *Oomorphus* Curtis

Diagnosis

The following diagnosis of *Oomorphus* is from Monrós (1956a) : antennae longer than prosternal process, with segment 8 obviously narrower than 7 and 9; claws not appendiculate; eyes entire or slightly internally sinuate, without a wide groove along the internal border. *Guggenheimia* Monrós (Sumatra) only differs from this by a wider internal eye groove and deeper canthus (Monrós 1956a).

The New Caledonian species are small, 1.2-1.9mm and dark brown, black or metallic green. They are illustrated by Monrós (1958a). The biology of the New Caledonian species is unknown.

The larva of *Oomorphus concolor* illustrated here is very different from the larva of *Lamprosoma* and the peculiar head capsule may be autapomorphic rather than applicable to the genus as a whole. One plesiomorphic difference is the presence of three antennal segments in *Oomorphus*.

Discussion.

The subfamily Lamprosomatinae has a curious distribution. Most species are Neotropical, there are a few in southern Africa and India, and a minor radiation in Japan and Taiwan. I have no evidence that members of this subfamily occur in Australia, despite recent references (Seeno and Wilcox 1982; Kimoto 1988). The species were relatively recently catalogued by Monrós (1960b) who listed two species of *Oomorphus* from New Caledonia and *Guggenheimia* Monrós and *Oomorphoides* Monrós (appendiculate claws) from Sumatra. It is possible that species have yet to be collected in the far north of Australia, but Lamprosomatinae are also unknown from Java to New Guinea (Gressitt 1965).

9.4 SUBFAMILY **Cryptocephalinae** Gyllenhal

Diagnosis

Adult : form rarely hemispherical, venter usually convex; procoxal cavities externally open behind or closed by the insertion of the prosternal process into the hypomeron (Figs

468, 471); reduction of anal veins from four to three (Figs 554-558); clavate protarsal setae of female confined to segment 3 (Fig. 147); fusion of sternites VI and VII (Figs 565-576); reduction of pleurite in lateral lobe of sternite III; hind margin of apical abdominal ventrite never crenulate; female with a well-marked hollow in the middle of apical ventrite (Figs 151-153); aedeagal ejaculatory guide present (Fig. 586); complete loss of distinct stylus on vaginal palp (Fig. 718); development of ventral and dorsal transverse rectal sclerites in kotpresse (Figs 810-851).

First instar larva : head capsule with papillate or clavate setae (Figs 25-40); external epipharyngeal setae (Fig. 193); mandible with tooth on internal edge which either overlaps the edge or is large and triangular (Figs 225-238); mandibular setae aligned towards apex; spiracles cribriform or moniliform (Figs 265-272).

Four tribes are represented in the region : Chlamisini, Clytrini, Pachybrachini and Cryptocephalini.

9.5 TRIBE **Chlamisini** Gressitt.

There are about 11 (Seeno and Wilcox 1982) genera and 400 species of Chlamisini worldwide. The tribe is pantropical with its greatest diversity in the neotropics (*vide* Monrós, 1951, for distribution map, but note that species in New Guinea and Australia are not indicated). Three species are native to New Guinea, two native to Australia and one has been deliberately introduced from Brazil.

Diagnosis

Adult : canthus well-developed, eyes deeply excavate (Fig. 63); antennae short, less than 1.5 times head width (Fig. 858); disc of pronotum usually strongly raised as a single or paired swelling (Figs 858, 866, 872); hind margin of pronotum bisinuate, medially produced, unbordered; prosternal process with lateral antennal slots; scutellum trapezoid, broadest at apex, abruptly raised from mesoscutum; elytra ridged or tuberculate; anal wing venation with less than four anal veins, anterior anal vein free; abdominal sternites IV-VI telescoped into III. The species in the western Pacific region have the apical half of the elytral suture strongly serrate.

First instar larva : antenna with two segments and conical sensorium (Fig. 186); vertex between Les3, labium and stemmata smooth, unsculptured; no papillate setae present, although frontal setae Fs1-3 may be clavate (Fig. 186); frontal setae in 2+4 arrangement (Fig. 186); tarsungulus short and strongly curved, with broad basal lobe (Fig. 240); more than 5 ventral protibial setae and at least a pair clubbed (Fig. 240); all spiracular plates compound cribriform (Fig. 265).

All the species are placed in *Chlamisus* for reasons given in Chapter 8.

9.5.1 Genus ***Chlamisus*** Rafinesque

The type species of this tropicopolitan genus is North American. The following description is for the six species in the region. The three species in Australia are illustrated in Figs 857-892 and the introduced species was recently described (Karren 1989).

Diagnosis

Adult (see Figs 857-892) : size small, 2.5-4mm; dull brownish-yellow to black, strongly punctured and microsculptured; body cylindrical, apices truncate; head flat, sunk into and flush with prothorax; antennae with 4-8 sensory segments; front angles of pronotum strongly produced, almost encircling head ventrally; at least front margin of pronotum strongly bordered; disc of pronotum strongly raised, may be bituberculate; elytral suture strongly serrate in apical half; elytra coarsely reticulately ridged or tuberculate; sides of elytra strongly ventrally lobed, fitting flush against length of sternite III; epipleura not lobed; pygidium with broad shallow lateral grooves. Shape of antennae, pronotum, abdominal sternite III, legs, aedeagus and spermatheca variable.

First instar larva (only first instars of *C. mimosae* were available, see Figs 186-188, 239-240) : setae Fs1-3 clavate; Aes2, Aes3, Fs5 and Fs6 much longer than other head setae; mesothoracic spiracle very large, forming a free-standing ventrally directed lobe, apical cells much finer than basal; fore tibia with three pairs of ventral setae, five spatulate, and three spatulate apical dorsal setae.

Host plants : an adult and larvae of one Australian species have been collected on *Amyema*. Gressitt (1965) records one species on *Rhododendron* in New Guinea. The introduced species is a biological control agent for *Mimosa pigra* (Karren 1989).

9.6 TRIBE **Clytrini** Lacordaire.

SUBTRIBE **Clytrina** Lacordaire

The Clytrini is a fairly large tribe of about 62 genera (Seeno and Wilcox 1982) and several hundred species. All Eurasian species belong to subtribe Clytrina. There are only two or three species in the region.

Diagnosis

Adult : antenna short, approximately width of head, and serrate (Fig. 304); both mandibles internally toothed (Figs 402-403); lacinia strongly sclerotised; hind margin of pronotum simple, bordered, broadly and truncately produced in middle (Fig. 304); hind angles of pronotum rounded (Fig. 304); scutellum gradually raised from mesoscutum which anteriorly has a finely striate stridulatory file (Figs 133-134); all femora similar sized, not keeled (Fig. 304); all tibiae without apical spurs; sternites not telescoped (Fig. 304); dorsal sclerite of kotpresse with separated central plate and laterally extended arms (Fig. 814).

Larva : horizontal configuration of upper frons setae 2+4 (Figs 189, 192); antenna two segmented with globular or flattened sensorium (Figs 189); vertex between Les1, Les2, and epicranial suture rough, with irregular rows of pits (Fig. 189); head capsule without epicranial ridge (Figs 10-11); mandible with overlapping internal tooth (Fig. 190); frontal suture without adjacent tubercles and frons without surface tuberculation (Figs 189, 192); seta Des1 simple and set well behind Aes1-4; all sceleriform setae narrow; all spiracles compound cribriform, and all of similar size (Fig. 266) .

The two described species, from Australia and New Guinea (Gressitt 1965), are very similar. The genus *Aetheomorpha* is weakly defined and it is quite likely that these species should be placed elsewhere. Here I follow Gressitt in allocating them to

Aetheomorpha. The Australian species is illustrated in Figs 304, 356, 504, 595-599, 746-747, 814.

9.6.1 Genus *Aetheomorpha* Lacordaire

The type species is West African and other species are found in Africa, India and south-east Asia to Australia (Clavareau 1913). The description given here is based on Australian material and the description of *A. papuana* (Gressitt 1965). There appear to be two species in the Australian material, with slight differences in colour pattern, aedeagi and spermatheca (Figs 595-599, 746-747).

Description

Adults : size small, ♂2-3mm, ♀3-4mm; colour yellow with black bands or black with yellow blotches; body smooth, shining, rather cylindrical; upper surface almost impunctate; eyes large, convex; inner margin of eyes straight (vertical) except slight notch near base; antennal segments 4-10 serrate (Fig. 356); labrum with at least 6 dorsal setae (Fig. 375); seta at anterior angle of pronotum not on a tooth (Fig. 304); prosternum concave between coxae and posteriorly elevated, fore-coxae projecting and almost touching, and fore-coxal cavities open; prosternal process without antennal grooves, very elongate; pronotum non-tuberculate; scutellum elevated posteriorly, not notched, triangular (Fig. 304); mesoscutum without lateral setal patches; elytral epipleuron expanded at base (Fig. 304); first tergite with transverse rows of dense, short setae (Fig. 567); venter of penis setose and apex pointed (Figs 595-599); spermatheca simple, C-shaped (Figs 746-747).

First instar larva : the larva of *Aetheomorpha* is unknown, but presumably inhabits ant nests, like other Clytrina (Erber 1988).

Host plants

Hosts are not known for the Australasian species and apparently not recorded elsewhere.

9.7 TRIBE **Pachybrachini** Chapuis

In Australia this subtribe is represented by two deliberately introduced species of the neotropical genus *Metallactus*, which have apparently failed to become established (Julien 1987; MacFadyen 1987). There are no Pachybrachini in the south-west Pacific region.

Diagnosis

Adult : antenna longer than half body length (Fig. 306), with basiconic sensilla in circular pits (Fig. 78); pronotum with a broad, truncate posterior lobe and all sides strongly bordered, without teeth (Fig. 306); hind angles of pronotum prominent; procoxal cavities closed (Fig. 105); profemora strongly inflated and ventrally keeled (Fig. 306); middle and hind tibiae with a single spur; middle of transverse rectal sclerite secondarily thickened (Figs 816, 818).

First instar larva (see LeSage 1985) : mandible with large non-overlapping internal tooth and Ms1 papillate (Fig. 226); frontal setae in 2+4 configuration; sensillum Csm1 above Cs1.

9.7.1 Genus *Metallactus* Suffrian

The species of this genus are all native to South America. Jacoby (1892) noted that there was little practical difference between this genus and *Griburius* Haldeman (= *Scolochrus* Suffrian). Larvae are unknown. One of the introduced species, *M. nigrofasciatus*, is illustrated in Fig. 306.

Diagnosis

Adult : size 4-5.5mm; yellow with black markings; eyes weakly convex; canthus broad and shallow; length of elytra 1.5 x length of pronotum (Fig. 306); pygidium almost entirely exposed (Fig. 306).

Easily diagnosed in the Australian fauna from the tribal characteristics.

Host plant : the two species were introduced for the control of the South American weed *Baccharis halimifolia* (MacFadyen 1987).

9.8 TRIBE **Cryptocephalini** Gyllenhal 1813.

This tribe includes the great majority of Australasian Camptosomata.

Diagnosis

Adult : antennae not serrate, segments 4-5 not sensory (Figs 357-367); if posterior margin of pronotum bordered then antennal basiconic sensilla not in circular pits (Figs 91-92) and often procoxal cavities open; hind angles of pronotum prominent (Figs 473-482, 492-499); scutellum not trapezoid with apex widest (Figs 503-519); elytral suture not serrate, but often feebly crenulate at base (Fig. 559); tibiae without spurs; profemora not inflated but may be longer than other femora; transverse rectal sclerites not secondarily thickened.

First instar larva : antennae three segmented (Figs 200, 212); mandibular setae simple (Figs 227-238); tibiae with four ventral setae (Figs 253-263).

The regional fauna includes four of the five subtribes, two of which, Platycolaspina and Ditropidina, are endemic to the region.

9.8.1 SUBTRIBE **Platycolaspina** subtribe nov.

The subtribe Platycolaspina is endemic to Australia and New Zealand. It includes five genera and approximately 35 species, only eight of which have been described.

Diagnosis

Adult : last five or six segments of antennae expanded, without sensory pits (Figs 88-92); eyes evenly and strongly convex (Figs 66-70), generally without a canthus or canthus not acutely angled (except one species Fig. 894); hind margin of pronotum flat or bordered, without conspicuous teeth (Figs 109-110, 161-170); scutellum gradually raised from mesoscutum (Fig. 139); pygidium concealed by elytra (Fig. 307); abdominal tergites weakly sclerotised; apex of aedeagus with dorsal and ventral setae (Figs 600-636, 638-641); spermatheca with elongate collum (Figs 752-763).

First instar larva : mandible without prominent internal tooth (Figs 194, 198, 201, 203, 205), setae simple; upper epicranium smooth or tuberculate (Figs 14-18).

9.8.1.1 Genus *Arnomus* Sharp

This is a small genus of four species, endemic to New Zealand but similar to the Australian endemic, *Semelvillea*. It is the only genus of Camptosomata native to New Zealand. The type species, *A. brouni*, is illustrated in Fig.308.

Diagnosis

Adult : size 2.5-5mm; last segment of maxillary palpi not expanded at apex; all sides of pronotum distinctly and broadly or narrowly bordered; prosternal process transverse to quadrate, not greatly expanded at apex (Figs 477-478); elytral punctation confused; basal border of sternite III reaching lateral margin; sutural locking mechanism complete to apex; claws simple.

First instar larva : internal tooth of mandible weak, not overlapping edge; epicranium smoothly keeled (Fig. 18); Aes2 much larger than Aes1 (Fig. 18); femora and tibiae spiculate; thoracic and abdominal spiracles cribriform.

Very close to *Semelvillea* in Australia but the latter has larger eyes, longer scutellum, narrower prosternum, toothed claws, elytral interlocking mechanism effaced apically, and truncate maxillary palpi.

Host plants : nothing known.

9.8.1.2 Genus *Atenesus* Weise

Weise did not designate a type species. *Atenesus mjoebergi* Weise is designated here on the basis of page priority, ease of identification and relative abundance of material. *Atenesus* was originally placed in the Stylosomini, on the strength of the cylindrical body and rounded, non-emarginate eyes. This is a small genus of about 10 species endemic to Australia. The species are found throughout Australia but are particularly diverse in the drier interior. The habitus of an undescribed species is illustrated in Figs 150 and 162.

Diagnosis

Adult : size small 1.3-3.5mm; pronotum and elytra smooth, not isodiametrically microsculptured (Fig. 162); posterior lobe of pronotum bluntly rounded (Fig. 162);

prosternal process narrow, raised and slightly expanded towards apex (Fig. 112); procoxal cavities open, distance between prosternal process and hypomeron greater than length of hypomeral process (Fig. 112); apex of scutellum truncate (Fig. 129); elytra striate, at least on disc (Fig. 162); abdominal pleurites free; apex of aedeagus produced or bent ventrally (Figs 625-636); spermathecal collum elongate (Fig.753); kotpresse with lateral arms on broad dorsal and ventral sclerites (Fig. 828).

First instar larva : upper epicranium and frons without ridge or tubercles (Figs 14, 32, 204); setae Aes1, Aes3-4, Fs1-3 not papillate and only slightly clavate at apex (Fig. 204); mandibular teeth short and broad (Fig. 205); spiracles small with less than 10 'cells' (Figs 58, 269); femora smooth (Fig. 207).

Host plants : the species have been collected feeding on flowers of *Podolepis*, *Dillwynia*, *Acacia* (phyllodinous) and *Cassia*, all of which are yellow, although the beetles are mostly black. The last three genera belong to the three separate families or subfamilies (Morley and Toelken 1983), which constitute the superfamily Fabales.

9.8.1.3 Genus ***Leasia*** Jacoby

Leasia was described for a species placed in the Megalostomina, Clytrini, and *Agetinella* for a species in the Eumolpinae. Subsequently, *Leasia* was subjected to an anatomical study by Monros (1956) who concluded that it belonged outside the Chrysomeloidea altogether. However its place in the Cryptocephalinae was supported by Crowson (1965). The genus *Agetinella* has remained unstudied until the present work, and is synonymysed with *Leasia* here because of the lack of any good synapomorphies to separate its species from *Leasia*. The structures of the female reproductive system, the male genitalia and the larvae confirm the position of *Leasia* in the Cyptocephalinae. There is no evidence to support the idea that these beetles are particularly associated with ants by adoption of a 'clytrine habit' (Crowson 1967). *Leasia* is endemic to Australia and includes about 10 species, distributed throughout the country (except Tasmania). *Leasia minuta* and undescribed species are illustrated in Figs 163-166.

Diagnosis

Adults : size very small, 1.2-2.5mm; upper surface of head and pronotum densely microreticulate and extremely finely and sparsely punctured (Fig. 67); prosternal process narrow, raised and slightly expanded towards apex (Fig. 111); procoxal cavities open, distance between prosternal process and hypomeron greater than length of hypomeral process (Fig. 111); apex of scutellum rounded (Figs 130, 167-170); elytra regularly striate (Figs 163-166); abdominal pleurites absent; apex of aedeagus triangular (Figs 640-641); spermathecal collum elongate (Fig.752); kotpresse with lateral arms on broad dorsal and ventral sclerites (Fig. 829).

First instar larva : upper epicranium and frons without ridge or tubercles (Figs 15, 30, 200, 202); setae Aes1, Aes4, Fs1-6 papillate and but slightly clavate at apex (Fig. 204); Aes2 much longer than Aes1; setae in 2+2 or 2+2+2 configuration (Figs 200, 202); mandibular teeth narrow, inner tooth overlapping inner margin (Figs 201, 203); spiracles normal sized (Figs 58, 269); femora smooth (Fig. 254). The larva is similar to *Ditropidus* but does not have the mandible type of that genus.

Host plants : the five species of *Leasia* for which data are available are all *Acacia* flower feeders (bipinnate or phyllodinous).

9.8.1.4 Genus ***Platycolaspis*** Jacoby

This endemic Australian genus was originally placed in the Colaspini, Eumolpinae, where it remains in the most recent checklist (Seeno and Wilcox 1982). However, there are specimens determined by Lea as 'allied to *Cryptocephalus pauperculus*' (MVM) so it seems that Lea was aware that it was a cryptocephaline. For subfamily placement, the structures of the female, the male genitalia and the larvae are decisive. There are three species, confined to south-east Australia. The habitus of *Platycolaspis australis* is illustrated (Fig. 161).

Diagnosis

Adult : small, 1.5-2mm; pronotum strongly and densely punctate and microsculptured (Fig. 161); pronotal lateral margins broadly explanate, hind margin straight (Fig. 161);

procoxal cavities open externally, the gap between hypomeron and prosternal process shorter than the hypomeral lobe (Fig. 126); elytral disc striate (Fig. 161); basal border of sternite III curving posteriorly before reaching lateral margin; claws appendiculate; aedeagus with simple apex (Figs 638-639); ejaculatory guide stilleto-like (Fig. 638); spermatheca with long collum (Figs 755-756); kotpresse with laterally extended broad transverse sclerites (Fig. 830).

First instar larva : head capsule without epicranial ridge, tubercles absent except for anterior margin of epicranium (Figs 31, 197); setae Aes1, Aes4, Fs1-6 papillate and but slightly clavate at apex (Fig. 197); Aes2 much longer than Aes1; setae in 2+2+2 configuration (Fig. 197); mandibular teeth narrow, inner tooth overlapping inner margin (Fig. 198); spiracles normal sized; femora spiculate (Fig. 255).

Host plants : the only species with host information is exclusively an *Acacia* flower feeder, but shows no allegiance to any particular subgenus.

9.8.1.5 Genus ***Semelvillea***, gen. nov.

Type species: *Semelvillea acaciae*, sp. nov.

Diagnosis

Adult : size 2.5-6.5mm; last segment of maxillary palpi expanded at apex (Fig. 433); all sides of pronotum distinctly and broadly bordered (Figs 893, 897-898); prosternal process elongate and greatly expanded at apex (Figs 109-110); sutural locking mechanism evanescent before apex (Figs 893, 897-898); elytral punctation confused; basal border of sternite III curving posteriorly before reaching lateral margin (Fig. 569); claws appendiculate.

First instar larva : internal tooth of mandible weak, not overlapping edge (Figs 194, 227); epicranium smoothly keeled or angulate (Figs 16-17); Aes1 and Aes2 similar sized, or Aes2 not twice length of Aes1 (Figs 16-17, 193); femora and tibiae spiculate (Figs 34, 196, 253); thoracic spiracle moniliform, abdominal spiracles cribriform.

The genus is similar to *Arnomus* which has simple maxillary palpi, smaller eyes, shorter scutellum, wider prosternum, simple claws, complete elytral locking mechanism and simple basal border of sternite III, in the adult, and larva with homogenous spiracles and Aes2 much longer than Aes1. From *Platycolaspis* it may be distinguished by the larger size, smooth shining upper surface and closed procoxal cavities and larval frontal tubercles.

Description

Adult : size 2.5-6.5mm; body cylindrical to depressed; colour entirely yellowish- or reddish-brown to red or yellow and black or blue; dorsum glabrous or pubescent.

Head (see Figs 69-70, 894, 896, 899): relatively broad because of convex eyes, projecting from thorax (Figs 893, 897-898); vertical punctation never strigose, rather sparse; eyes relatively small, distance between always greater than eye length, but evenly convex; development of canthus variable, shallow or deep; antennae inserted near lower third of eyes; sides of clypeus variable, sinuate or parallel; antennae with all segments elongate, 5-7 slightly broadest; antennal length 2/3 to 3/4 body length (Figs 893, 897-898); last segment of maxillary palpi truncate, usually expanded to apex (Fig. 433); antennae without circular pits of basiconic sensilla (Figs 91-92).

Prothorax (see Figs 109-110, 307, 475-476, 893, 897-898): pronotum evenly curved at sides and only slightly contracted at apex; all sides of pronotum strongly bordered, lateral margins explanate; disc with or without lateral depressions; all corners with seta on a tooth; prosternal process elongate, strongly narrowed in middle and expanded at apex; mesothorax : scutellum elongate, slightly broader at base and gradually elevated (Fig. 139); mesoscutum without lateral patches of microchaetae, a longitudinal median ridge or a broad stridulatory file (Fig. 140); elytra (see Figs 307, 893, 897-898), 2-3 x length of pronotum; elytra parallel-sided for basal 3/4 then gradually attenuate; apex of elytral sutural locking mechanism evanescent before apex; punctation of elytra confused; epipleuron gradually attenuate to apex (Fig. 307); legs long and slender; all tarsal segments elongate (Figs 895, 900); claws appendiculate.

Abdomen : tergites thin, weakly sclerotised, pleurites absent, spiracles free (Fig. 568); basal border of sternite III recurved before reaching lateral lobe (Fig. 569); males may have sternite VII indented and sternites V and VI connate (Figs 568-569); females with apex of egg-hollow deeply indented and produced on either side (Fig. 153); aedeagus (Figs 600-621) straight, but apex strongly recurved in most species; dorsal and ventral aedeagal setae present, dorsal setae may be very long; ejaculatory guide variable (Figs 603, 604, 617); tegmen variable in shape (Figs 620-621); vaginal palp (hemisternite) narrow, apical border not sclerotised (Fig. 723); spermatheca with long collum, but short compared to other Platycolaspina, and usually falciform (Figs 758-763); kotpresse diverse, but always with posteriorly directed dorsal transverse sclerites, median expansion and transverse ventral sclerite reaching sides of rectum (Figs 821-826).

First instar larva : head capsule with or without epicranial ridge, but at least angulate; upper epicranium smooth or tuberculate; frons with tubercles, at least in upper half; setae Aes1, Aes3 and Fs1-5 papillate; frontal setae in approximately 2+2 arrangement; Des1 not part of Aes1-4 row; mandible with tooth 5 absent or barely expressed; femora and tibiae spiculate; mesothoracic spiracles moniliform, abdominal cribriform.

Scatoshell : of the normal Cryptocephalini type with spiral ridges or with large thin blades (Fig. 1).

Distribution

On the great Dividing Range of eastern Australia, and neighbouring ranges.

Host plants

The adults feed on the leaves of *Acacia*, *Eucalyptus*, *Nothofagus*.

Etymology

The generic name is a latinisation of the personal name S. E. Melville, and is feminine.

9.8.1.6 Key to species of *Semelvillea*

1. Upper surface with scattered erect long hairs; body entirely brownish-yellow or with iridescent purple around elytral suture; size > 4mm .... *hirsuta* sp. nov.

\- Upper surface glabrous; if reddish-yellow < 3.5mm 2

2.(1) Size larger, 4.5-6.5mm; sides of pronotum broadly explanate; antennal seg. 5 much broader than 4 3

\- Size smaller, 2.5-4mm; sides of pronotum usually narrowly explanate; width of antennal seg. 5 similar to 4 4

3.(2) Upper surface entirely iridescent purplish-green; pronotum and elytra very strongly and closely punctured; pronotum smooth .... *punctata* sp. nov.

\- Elytra bluish-black, head , pronotum and scutellum yellowish-red; pronotum and elytra less strongly and closely punctured; pronotum transversally grooved on each side of disc .... *acaciae* sp. nov.

4.(2) Pronotum without transverse groove lateral to disc, densely punctured; upper surface entirely brownish-yellow, except darker suture .... *nothofagi* sp. nov.

\- Pronotum with transverse groove lateral to disc, usually sparsely punctured; if entirely pale, without darker suture 5

5.(4) Inner margin of eye deeply excavate; head and pronotum reddish-yellow, elytra and metasternum black; size larger, 3.5-4mm .... *waraganji* sp. nov.

\- Inner margin of eye weakly indented; without this colour combination; size smaller, 2.5-3.5mm 6

6.(5) Entirely reddish-brown; pronotum strongly and closely punctured .... *bunyae* sp. nov.

\- Pronotum reddish-yellow, elytra black; pronotum finely and sparsely punctured 7

7.(6) Head, metasternum and tibiae reddish-yellow; form more ovate; head and elytra more strongly and closely punctured .... *eungellae* sp. nov.

\- Vertex, frons and metasternum black, tibiae piceous; form elongate; head and elytra weakly and sparsely punctured .... *parva* sp. nov.

9.8.1.6.1 *Semelvillea acaciae*, sp. nov.

Types

Holotype ♂/31.53°S 151.32°E Dilgry River, Barrington Tops S. F., NSW 15-16 Nov 1981 T. Weir/ [ANIC].

Paratypes (47) New South Wales10♂♂7♀♀ same data as holotype [ANIC]; 11♂♂ 10♀♀ /Dilgry River Loop, Barrington Tops S. F., on Acacia melanoxylon and A. barringtonensis, 26.xi.1985 C. Reid/ [ANIC]; 1♀ same data but on A. melanoxylon, 25.xi.1986 [ANIC]; 2♂♂2♀♀ /Vicinity of Jenolan Caves (J. C. Wilburd)/18004 N.S.Wales/ [SAM]; 2♀♀ /Prison Farm Glen Innes, July 1969-Dec. 1970 Coll? Donated/ ANIC Uni. of New England Coll. Donated 1983/ [ANIC]; 1♀ /Barrengarry Mtn NSW on Ac. melanoxylon 7 Oct. 1986 C. Reid/ [ANIC]; 1♀ /90 k NW Wauchope NSW, rainforest margin, 18.xi.1987 G. Williams/ [ANIC].

Diagnosis

The combination of red and black colouration and large size separates this species from its congeners. The canthus is much less developed than in *S. waraganji* .

Description

Body (Fig. 898) convex and more cylindrical than other large species. Colour : head, entire thorax and appendages red, elytra, antennomeres 5-11 and abdomen black, tarsi pitchy. Elytra with dull metallic blue or rarely green reflections. Sides of metasternum and base of vertex occasionally pitchy. Dorsal surface without pubescence. Pygidium completely covered in male, almost completely exposed in female. Size : 4.8-5.2 (male), 5.7-6.3 (female).

Head (Fig. 899): eyes large, convex, with a fairly deep and angulate canthus; interocular space c.1.5 times eye length (male) to twice eye length (female); scrobal ridge perpendicular; frons shining, with irregular fairly dense punctuation and median depression between eyes; vertex microsculptured; antenna 0.75 body length in male, 0.5-0.65 in female; antennomeres 5-7 dilated; apical segment of maxillary palp dilated at apex.

Thorax (Fig. 110): pronotum transverse, twice as wide as long, with broad explanate margins, and transverse depression each side of disc; surface of pronotum shining, diffusely punctate on disc, more dense in depressions and at sides; hypomeron impunctate; scutellum minutely and sparsely punctured, elongate trapezoid with straight margins; metasternum shining, sparse punctures and pubescence becoming denser at sides.

Elytra : with explanate side margin and rounded apex, broadest about 0.7 length from base; without raised interstice near lateral margin.

Legs : elongate, tarsal segments very long (Fig. 900).

Abdomen : ventrites diffusely punctate with wrinkled microsculpture, denser towards apical segment which is also reticulately microsculptured.

Male : apex of tergite 7 rounded; apex of tergite 8 shallowly incised; apex of sternite 7 deeply emarginate, disc with a shallow depression; aedeagus (Figs 614-615) with broad downturned apical lobe, sparse, short pubescence on ventral and dorsal surfaces; tegmen flat and narrow with truncate base.

Female : apex of tergite 7 shallowly excavate; apex of tergite 8 deeply cleft; sternite 7 with a deep egg-hollow which is apically produced as two lobes with a deep concave incision between (Fig. 153); kotpresse complex (Fig. 822); spermatheca (Fig. 759).

Distribution

Locally distributed on the Dividing Range between Glen Innes and Kangaroo Valley, New South Wales.

Biology

Host plants *Acacia melanoxylon* and *A. barringtonensis*. Adults present only in October and November.

9.8.1.6.2 *Semelvillea bunyae*, sp. nov.

Type

Holotype ♀ /Bunya Mts NP, QLD 11-12 Dec. 1979, M. A. Schneider and G. Daniels mv. lamp/ [UQIC]

The species is based on a single female specimen with damaged antennae, but with a combination of attributes which easily separates it from all other species.

Diagnosis

Separated from all other species by the combination of : entirely yellowish-brown colour, except claws and possibly apical antennal segments; lateral pronotal depressions present; pronotum strongly and closely punctured; scrobal grooves straight; sternite 7 of female with blunt apical projection.

Description (female only).

Appearance : short, squat and convex; entirely yellowish-brown, claws pitchy; dorsal surface without pubescence; length 3mm, width across shoulders 1.5mm.

Head : eyes convex, inner margin very shallowly emarginate; interocular space twice eye length; scrobal ridge perpendicular; frons and clypeus shining with large moderately close punctures on disc becoming sparse and fine towards sides and vertex; antenna with segments 5-11 missing; last segment of maxillary palp not expanded at apex, parallel-sided.

Pronotum very transverse (width twice length), closely and very strongly punctured, with narrow lateral borders and transverse impressions either side of disc; hypomeron impunctate (as *acaciae*); scutellum as acaciae; metasternum shining, strongly and closely punctured at sides, pubescence short and recumbent.

Elytra truncate, explanate border narrow, strongly and closely punctured and substriate, with raised convex interstice from shoulder almost to apex.

Legs normal.

Abdomen : basal ventrites finely and sparsely punctured, becoming closer towards apex.

Female : sternite 7 with deep egg-hollow which is apically produced as a broad blunt lobe with barely excavate margin; kotpresse (Fig. 826); spermatheca (Fig. 758).

Distribution

Known only from Bunya Mountains National Park.

Biology

Host unknown. This is the only specimen of *Semelvillea* to have been taken at light.

9.8.1.6.3 *Semelvillea eungellae*, sp. nov.

Types

Holotype ♂/ QLD : Eungella NP, 80 km NW Mackay x-16-1979/ H. E. Evans Biol. note no. 2688/ Voucher specimen 80-7/ [ANIC]

Paratypes (3) 1♂2♀♀ same data as holotype [ANIC]

Diagnosis

A small bicoloured species with transverse pronotal grooves, which is only likely to be confused with parva, and bunyae if the latter has a bicoloured male. From parva it may be distinguished by the entirely reddish-yellow head, tibiae and metasternum and stronger punctuation of the head and pronotum. From a putative bicoloured male of bunyae it would be distinguished by the much sparser and weaker punctuation of the pronotum.

Description

Appearance : convex, cylindrical species with rounded apex; pygidium completely covered by elytra in both sexes; head, entire thorax and appendages reddish-yellow, except elytra and antennomeres 5-11 black, and scutellum and tarsal segments 3-5 pitchy-black; elytra without metallic reflection; dorsal surface without pubescence. Size : male 2.5mm long and 1.25mm across shoulders; female 3mm long and 1.5mm across shoulders.

Head : eyes convex, internal angle weakly emarginate; scrobal ridge straight; interocular space 1.75 (male)-2 (female) times eye length; punctures of head larg, moderately close on frontal disc which is depressed, finer and sparser on vertex; antennal segments 6-11 equally expanded, 5 slightly less so; antennae 0.75 (male) or 0.5 (female) body length; maxillary palp not expanded to apex, parallel sided.

Thorax : pronotum very transverse, width twice length; deep transverse depression each side of disc; margins narrow; surface shining, strongly but sparsely punctured; hypomeron impunctate; scutellum as*acaciae* metasternum strongly and closely punctured at sides, almost impunctate on disc, pubescence recumbent.

Elytra strongly and closely punctured, substriate; broadest 0.75 from base; explanate margin narrow; with raised interstice from shoulder almost to apex.

Legs normal.

Abdominal ventrites closely punctured and transversely wrinkled, shining.

Male : apex of tergite 8 shallowly excised; apex of sternite 7 bisinuate; aedeagus (Figs 614-615) with very short scattered ventral pubescence, dorsal pubescence long, in two lateral patches; tegmen narrow, slightly keeled with bilobed base.

Female : apex of tergite 7 simple, tergite 8 deeply excavate; sternite 7 with deep egg-hollow extending as truncate apical lobe; kotpresse (Fig. 825); spermatheca (Fig. 761).

Distribution

Known only from type locality, Eungella National Park.

Biology

The short type series was collected as prey of *Cerceris* sp (H. E. Evans' biological note). Host is unknown.

9.8.1.6.4 *Semelvillea hirsuta*, sp. nov.

Types

Holotype ♂/Acheron Way, Warburton-Marysville 12.i.1966. E. Vic. B. Cantrell/ [UQIC]

Paratype ♂/Mt. Donna Buang 4,080 ft. Vic. via Healesville 10.i.1966 T. Weir/ [UQIC]

Diagnosis

The only species with long erect dorsal setae, but also distinguished by large, dense punctures, lack of lateral pronotal grooves and large size.

Description (male only)

Appearance : body elongate, cylindrical; colour entirely brownish-yellow, except antennomeres 5-11 increasingly pitchy-black, extreme apex of femora and apices of tarsal segments 1-5 pitchy and in the holotype there is a broad metallic blue stripe along suture, occupying half elytral width and extending to 0.75 elytral length. All surfaces clothed in long erect yellowish setae. Size : length 5.5mm.

Head : eyes very convex, with shallowly angulate emargination on inner margin; frons strongly and closely punctured; interocular distance 1.75-2 times eye length; scrobal ridge angulate; antennae 0.75 body length, gracile, segments 5-11 approximately equally expanded; last segment maxillary palp expanded to apex.

Thorax : pronotum transverse, width 1.7 times length; strongly and fairly closely punctured, without obvious lateral grooves; explanate margins very broad; hypomeron impunctate; scutellum almost elongate rectangular, punctate and pubescent; metasternum shallowly and sparsely punctured except densely in apical corners.

Elytra : very strongly and closely punctured, some punctures coalescing transversely; explanate margin narrow; apex rounded; without raised lateral interstice.

Legs elongate, especially tarsi.

Abdomen : ventrites finely and fairly sparsely punctured.

Male : apex tergite 8 very slightly emarginate; apex sternite 7 fairly deeply and narrowly excised; aedeagus (Figs 605-608) with broad downturned apical lobe, with dense ventral and dorsal setae, longest near base of lobe; tegmen without keel, broadly V-shaped with rounded base; ejaculatory guide (Fig. 607).

Distribution

Known only from two localities in the vicinity of Mount Donna Buang, Victoria.

Biology

Host plant unknown.

9.8.1.6.5 *Semelvillea nothofagi*, sp. nov.

Types

Holotype ♂/Cobark Park, Barrington Tops S. F. NSW on Nothofagus moorei 25.xi.1986 C. Reid/ [ANIC]

Paratypes (16) 3♂♂same data as holotype; 1♂7♀♀/31.53°S 151.32°E Dilgry R. Loop, Barrington Tops S. F. NSW, on Nothofagus moorei, 26.xi.1985 C. Reid/ [ANIC]; 1♂4♀♀ same data as above except 25.xi.1986 [ANIC].

Diagnosis

Small and somewhat depressed, dorsum entirely brownish-yellow except dark brown suture, no lateral pronotal grooves, no dorsal pubescence, hypomeron punctate.

Description

Appearance : small, depressed, head prognathous, without dorsal pubescence, apex of female pygidium exposed. Colour sexually dimorphic : male entirely brownish-yellow, except elytral suture, abdomen, tarsal segments 3-5 and antennomeres 5 (apex only) to 11 dark brown; female as male except abdominal ventrites brownish-yellow. Size : male 2.7-3.0mm long, 1.0-1.25mm across shoulders; female 3.0-3.4mm long, 1.25-1.6mm across shoulders.

Head : eyes very convex, shallowly emarginate on inner margin; interocular space 1.75 (male) to 2 (female) times eye length; frons and vertex closely and moderately strongly punctured, sparser on vertex; scrobal ridge angulate; antenna 0.75 (male) to 0.6 (female) body length, segments 5-7 longer and more expanded than others; last segment of maxillary palp expanded to apex.

Thorax (Fig. 109): pronotum transverse, width 1.7 times length, without deep transverse lateral depressions, with broad explanate margins, closely and strongly punctured; hypomeron with scattered large punctures; scutellumas acaciae; metasternum with scattered finepunctures on disc and dense stronger punctures at sides, transversely microreticulate.

Elytra : closely and strongly punctured, substriate, with raised interstice from shoulder almost to apex; rounded at apex; narrow lateral explanation.

Legs normal.

Abdominal ventrites rather closely and strongly punctured, entirely transversely microreticulate.

Male : tergite 8 simple; apex sternite 7 bisinuate, with shallow median hollow; apical lobe of aedeagus (Figs 616-617)with lateral spur, short ventral setae and 10 very long dorsal setae on each side; tegmen broad, slightly keeled and apex with V-incision; ejaculatory guide (Fig. 617).

Female : tergite 7 simple; apex of tergite 8 shallowly excised; sternite 7 with deep egg-hollow not produced as a lobe; kotpresse (Fig. 823); spermatheca (Fig. 763).

Distribution

Known only from the type locality, Barrington Tops, New South Wales, where it is common.

Biology

Host plant *Nothofagus moorei.* Adults collected only in November.

9.8.1.6.6 *Semelvillea parva*, sp. nov.

Types

Holotype ♂/Dorrigo N.S.Wales W. Heron/ [SAM]

Paratypes (2) : ♀, same data as holotype, plus / M[onolepta]. minuscula Lea? / [ANIC]; ♀/10k W. Samford, N. Brisbane, QLD, on Ac. melanoxylon, rainforest gully, 17-21.xi.1986 C. Reid/ [ANIC]

Diagnosis

A small bicoloured species with transverse pronotal grooves, black vertex, metasternum and abdomen and sparse, fine pronotal punctuation.

Description

Appearance : relatively elongate, cylindrical species with rounded elytral apices; no dorsal pubescence. Colour : elytra, scutellum, metathorax, upper half of face and antennomeres 5-11 black; external faces of tibiae, tarsi, dorsal surface of antennomeres 1-4, and abdomen pitchy (also maxillary palp and apical half of femora in female); lower face, prothorax, and mesosternum, ventral surface of legs and antennal segments 1-4 yellow; no metallic reflection. Size : male 2.6mm long and 1.2mm across shoulders; female 2.7mm long and 1.3mm across shoulders.

Head : eyes strongly convex, with shallow internal emargination; interocular space 1.5 (male) to 2 (female) times eye length; frons and vertex finely and sparsely punctured with shallow median impression between eyes; antennomeres 5-11 equally expanded, antennae 0.75 (male) to 0.7 (female) times body length; maxillary palp not expanded to apex, parallel sided or slightly narrowed.

Thorax. Pronotum transverse, width 1.7 times length, with very sparse fine punctures and deep transverse impressions either side of disc, lateral margins narrow; hypomeron impunctate; scutellumshaped as acaciae but punctures invisible; metasternum sparsely punctured and transversely microsculptured on disc.

Elytra with 10 irregular striae between epipleuron and suture, and many interstitial punctures; punctures becoming finer towards apex, where they are absent in the female; apex of elytra rounded; side margins broadly explanate; slightly raised interstice from shoulder to apical third.

Legs unremarkable.

Abdomen with ventrites finely and fairly closely punctured, dense at sides and towards apex.

Male : sternites 5 and 6 connate; apex tergite 8 rounded; apex sternite 7 shallowly excavate; aedeagus (Figs 618-620) short and broad with a few short apical setae; tegmen flat and broad, rounded at base.

Female : apex tergite 7 broadly and deeply excised; apex tergite 8 deeply and narrowly cleft; sternite 7 with deep egg-hollow produced apically as a broad lobe with emarginate apex; kotpresse (Fig. 821); spermatheca (Fig. 760).

Distribution

Known only from two widely separated sites at Dorrigo, New South Wales and Samford, Queensland.

Biology

Host plant *Acacia melanoxylon*.

9.8.1.6.7 *Semelvillea punctata*, sp. nov.

Type

Holotype ♂/Blackall Rgs, Q. Oct. 1920 F. E. Wilson/ prost. subtriangularly prod. in middle/F. E. Wilson Collection/ [MVM]

Diagnosis

Distinguished from all other species by large, depressed form, lack of dorsal pubescence, dorsal metallic reflections, lack of pronotal grooves, and extremely deep punctuation.

Description (male only)

Appearance (Fig. 897) : an elongate, depressed species with prognathous head, strongly resembling certain Eumolpinae in form; elytra completely covering abdomen; without dorsal pubescence. Colour : dorsal surface pitchy-brown, with metallic blue or brassy reflections; scutellum, lateral margins of pronotum and antennomeres 3-4 brownish-yellow; entire venter and basal half of femora reddish-yellow; antennomeres 1, 2, 5-11, palpi, apical half femora, tibiae, and tarsi black. Size : 5mm.

Head (Fig. 896) : eyes large and convex, broad and deep angulate canthus on inner margin; interocular space equal to eye length; frons and vertex irregularly rugosely punctured; antennae 0.75 body length; antennomeres 5-7 more expanded than other segments; last segment of maxillary palp slightly expanded to apex.

Thorax. Pronotum : transverse, width 1.7 times length, without transverse impressions; side margins very broadly explanate; fairly sparsely but very strongly punctured. Hypomeron impunctate. Scutellum elongate rectangular, sparsely punctate. Metasternum finely but closely punctured over whole surface.

Elytra very strongly and closely punctured; explanate margins narrow; apices rounded; traces of raised interstice near lateral margin.

Legs elongate, especially tarsi (Fig. 895).

Abdomen with sparsely and finely punctured ventrites.

Male : tergite 7 rounded; apex tergite 8 very slightly indented; apex sternite 7 with shallow depression and bisinuate margin; aedeagus (Figs 600-604) with ventrally produced triangular apical lobe and long dense lateral pubescence; tegmen slightly keeled, V-shaped with rounded base; ejaculatory guide (Figs 603-604).

Distribution

Known only from the Blackall Range, north Queensland.

Biology

Nothing known.

9.8.1.6.8 *Semelvillea waraganji*, sp. nov.

Types

Holotype ♂/Picadilly Circus, powerline clearing, ACT 16 Dec.1984 C. Reid on Euc. pauciflora/ [ANIC]

Paratypes (10) 3♀♀ same data as holotype [ANIC]; 1♀/Hampton New South Wales 27.xii.1968 C. E. Chadwick/ on leaves ?Angophora sp/ Department of Agriculture, Sydney, N. S. W. Australia/ C. I. E. Coll. A14048/Cryptocephaline Genus sp. indet. det M. L. Cox 1982/ [BCRI]; 1♀/36.12°S 148.43°E Dainers Gap, NSW, 6 Feb. 1974 P. Morrow / 1585metres Euc. pauciflora, stellulata and perriniana forest/ [ANIC]; 1♀/Cape Otway VIC 29 Nov. 1966 A. Neboiss/ [MVM]; 1♀/Dicky Coopers Ck, Kosciusko NP, NSW, on Euc. pauciflora, fire regrowth, 29.i.1985 C. Reid/ [ANIC]; 1♀/13k SE Braidwood, NSW, on Euc. stellulata by road, 12.xi.1985 C. Reid/ [ANIC]; 1♀/Canberra ACT Black Mtn, 12 Dec. 1987 D. B. McCorquodale, C. antipodes prey/ [ANIC]; 1♀/Mount Ginini ACT Euc. pauciflora, 1700m 7.i.1989 C. Reid/ [ANIC].

Diagnosis

A bicoloured species similar in pattern to parva, but much larger, and more elongate than any other species (resembles *Monolepta* in Galerucinae). The shape, larger canthus, and non-metallic elytra separate *waraganji* from *acaciae.*

Appearance (Fig. 893) : elongate, cylindrical, no dorsal pubescence, pygidium completely covered in both sexes. Colour : head, prothorax, mesothorax (except scutellum), femora, basal 0.6-0.8 of tibiae, and antennomeres 1-3, reddish-yellow;

elytra, abdomen, and antennomeres 5-11 black; apical 0.4-0.2 tibiae, tarsi, palpi and hind coxae pitchy-red; scutellum pitchy-red to black. Lateral elytral margins of Cape Otway specimen yellow. Size : male 3.2mm long, 1.25mm across shoulders; female 3.7-4.0mm long, 1.45-1.6mm across shoulders.

Head (Fig. 894) : eyes large, very convex, with a deep rightangled canthus; interocular space equal to (male) or 1.5 times (female) eye length; scrobal ridge perpendicular; frons moderately strongly and closely punctured, with an elongate depression between eyes, punctures becoming sparser and finer on vertex. Antennae very long, body length (male) to 0.75 times body length (female); segments 5-11 almost equally dilated. Maxillary palpi parallel sided (male) or slightly contracted to apex (female).

Thorax. Pronotum transverse, width twice length; narrow side margins; deep transverse impression either side of disc; puctures diffuse, of variable size; hypomeron impunctate; scutellum elongate rectangular, impunctate. Metasternum sparsely and finely punctured on disc, closely at sides.

Elytra : densely and closely punctured, substriate; interstice from shoulder to apex barely raised; rounded at apex; explanate margin narrow; almost parallel sided.

Legs normal.

Abdominal ventrites finely punctured and transversely strigose at base, punctures increasingly dense to apex.

Male : apex tergite 8 slightly emarginate; sternite 7 with deep hollow and deeply and broadly emarginate at apex; aedeagus (Figs 609-610) with triangular downturned apical lobe, short ventral setae on lobe and four very long setae each side of dorsal apex; tegmen broad, slightly keeled, rounded apex.

Female : tergite 7 simple; apex tergite 8 slightly emarginate; sternite with deep egg-hollow, not extended as an apical lobe; kotpresse (Fig. 824); spermatheca (Fig. 762).

Distribution

Scattered localities on mountain ranges between Hampton, New South Wales and Cape Otway, Victoria. The most widely distributed species of *Semelvillea*, but never common.

Biology

Host plants *Eucalyptus stellulata* and *E. pauciflora*. Adults collected from November to February. One specimen collected as prey of *Cerceris antipodes*.

9.8.2 SUBTRIBE **Coenobiina** subtribe nov.

This subtribe includes three genera and at least 100 species, in Africa, India, south-east Asia and the western Pacific.

Diagnosis

Adults : very small sized, 1-4 mm; antennal segments without apical sensory pits (Figs 82-84), and last six segments sensory (expanded) (Fig. 83); head deeply inserted into prothorax (Fig. 64); eyes large and close, often holoptic in male, with deep, approximately equilaterally triangular, canthus, the upper margin of the canthus horizontal (Figs 64, 335); front margin of pronotum usually thickened and produced, like a collar (Fig. 64); prosternal process broad, sides parallel and ridged (Fig. 106); scutellum elongate or quadrate, not fusiform, abruptly raised from mesoscutum but with a basal step (Figs 128, 506-507); sternites V and VI free; aedeagus with few, long dorsal setae (Figs 642-645); ejaculatory duct massive (strongly sclerotised) and short (Figs 642-644); spermatheca reduced to a globular pump with short thick duct (Figs 764-766).

First instar larva : frons and upper epicranium smooth, without tubercles (Fig. 208); frontal setae in 2+4 configuration; all frontal and upper epicranial setae broad and papillate; mandibles with overlapping apical internal tooth (Fig. 209); femora and tibiae spiculate (Fig. 256); distance Dts1-Dts2 much greater than Dts2-Dts3.

There is one genus in the Australasian-western Pacific region.

9.8.2.1 Genus *Aprionota* Maulik

The type species of *Aprionota* is Samoan. I have made *Aprionota* the senior synonym of *Pycnophthalma* because it comes first in page order and is an equally widely used name. *Cephalocryptus* was described for two species which are typical of *Aprionota*. The new definition of *Aprionota* given here raises the number of described species to at least 35 and there are probably many more, both described and undescribed.

For example many species described under *Ditropidus*, *Elaphodes* and *Coenobius* from New Guinea (Gressitt 1965), and under *Coenobius*, *Bucharis* and *Adiscus* from south-east Asia (Kimoto and Gressitt 1981) may belong in *Aprionota*. Descriptions of species of *Coenobius* and *Adiscus* from China are too poor for recognition of their genera (Gressitt and Kimoto 1961). I have seen undescribed species of *Aprionota* from Fiji, Solomon Islands, Tonga, New Guinea, Vanuatu, and northern Australia.

There are five described Australian species.

Description

Adult : size 1.2-3.5mm, cylindrical in shape; head always deeply sunk into prothorax (Fig. 64); eyes large, occupying 2/3-3/4 side of head (Fig. 64); groove or ridge present between bases of antennae; antennae approximately 1/2 body length; pronotum often obliquely grooved at sides of disc; pronotal posterior lobe bluntly triangular, apex may be bifid (Fig. 106); posterior margin of pronotum with or without teeth; hind margin of prosternal process straight or slightly concave; scutellum elongate, rounded at tip (Fig. 128); mesosternum transverse; elytra striate; epipleura often strongly lobed at base; claws appendiculate; sternite III longer than succeeding sternites.

First instar larva : as described for subtribe.

Distribution : pending a revision of the whole genus it is not possible to give precise distribution limits. Members of this genus certainly occur in Fiji, Tonga, Samoa, Vanuatu, Micronesia, Solomon Islands, New Guinea, and north and east Australia. It may also occur in south-east Asia including China, if references to *Coenobius* indicate this genus (Kimoto and Gressitt 1981; Gressitt and Kimoto 1961).

Host plants : in Australia *Aprionota inconstans* (Lea) is exclusively an *Acacia* flower feeder (phyllodinous spp. only). Elsewhere, recorded hosts of *Aprionota* species include *Macaranga*, *Glochidion*, *Theobroma* (Gressitt 1955; Bryant and Gressitt 1957). African material of *Isnus* (label data in BMNH) was collected from flowers and it is likely that most or all members of this subtribe are flower feeders. They do not digest pollen grains.

9.8.3 SUBTRIBE **Ditropidina** subtribe nov.

The subtribe is endemic to the Australasian region, with three genera and at least 280 species in Australia, New Guinea (including islands west) and New Caledonia.

Diagnosis

Adult : antennae with basiconic sensilla in circular pits (Figs 85-87); pronotum with a narrow triangular posterior lobe (Figs 107-108); hind margin of pronotum with a row of teeth (Figs 107-108); prosternal process broad, sides parallel and ridged (Figs 107-108); scutellum abruptly raised from mesoscutum, fusiform or oval (absent in *Adiscus*, not treated here) and anteriorly stepped (Figs 138, 508-510); mesoscutum on either side of scutellum with a narrow strip of microchaetae (Figs 138, 508-510); sternites V and VI fused; aedeagus with few long dorsal setae (Figs 155, 647-661); ejaculatory duct not strongly sclerotised; spermatheca normal, usually falciform (Figs 768-780); kotpresse variable (635-641).

First instar larva : epicranial keel absent (Figs 12-13); upper epicranium not pitted (Figs 12-13); epipharynx with median triangular sclerotisation; mandible with large tooth half way along inner margin (Figs 228-232); sensillum Csm1 dorsal to seta Cs1 (Figs 212, 215, 218, 220); frontoclypeal suture internally thickened; mesothoracic spiracles at least twice as large as abdominal spiracles; femora and tibiae smooth (Figs 257-260); distance Dts1-Dts2 much less than Dts2-Dts3.

There are three genera, *Ditropidella*, *Ditropidus* and *Scaphodius*.

9.8.3.1 Genus *Ditropidella* gen. nov.

Type species : *Coenobius binotatus* Lea.

This endemic Australian genus is erected for approximately 15 species which have distinctive adult and larval facies. The four described species were previously placed in *Ditropidus* and *Coenobius* and some species are superficially similar to *Aprionota*.

Diagnosis

Adult (other characters as for Ditropidina): size small, 1-2mm, globular shape; canthus deep, about 90° and eyes large and close (Fig. 339), even holoptic; frons usually produced medially (Fig. 339); gena long, impunctate; clypeal region between and below antennae with triangular demarkation (Fig. 339); lower margin of clypeus narrowly concave; antenna inserted near base of eye, of normal ditropidine type (Fig. 364); mandible apparently without setae (Fig. 420); submentum complete (Fig. 456); pronotum very transverse, anterior border raised and constricted at sides (collared) and posterior lobe strongly raised (Fig. 488) and bifid (Fig. 489); posterior angles of pronotum produced; pronotal disc obliquely grooved at sides; elytra with strongly punctate striae and prominent humeri; tibiae excavate on apex of external face for more than 1/4 of length; aedeagus with apex strongly reflexed and long dorsal setae (Fig. 660); spermatheca variable (Figs 773-778); ventral transverse sclerite of kotpresse with lateral arms, dorsal sclerite small (Fig. 839).

First instar larva : Aes1 distant from frontal suture (Figs 218, 220); Aes2 papillate (Figs 218, 220); internal mandibular tooth weak and basal process obtusely rounded (Figs 219, 221); fore tibia with at least one spatulate seta (Figs 257-258).

Distribution : widespread throughout the southern half of Australia.

Host plants : the species feed on either *Eucalytpus* or *Acacia* (only *D. binotata*)).

Etymology : from the name *Ditropidus* and the diminutive suffix -ella. Feminine.

9.8.3.2 Genus *Ditropidus* Erichson

A large genus of more than 250 species endemic to Australia, New Guinea and south-east Indonesia (Dory, Mysol). The habitus of two species is illustrated (Figs 309-310).

Diagnosis

Adult : lacking the diagnostic combinations of attributes in *Ditropidella* and *Scaphodius*; eyes smaller, with shallower canthus than in *Ditropidella*; clypeal area not triangularly delimited (Figs 65, 336-338, 340); posterior lobe of pronotum rarely raised (Fig. 484); if eyes small like *Scaphodius*, without a canthus, then male with simple head (Fig. 336), claws simple.

First instar larva : Aes1 and Aes2 equidistant from frontal suture (Figs 212, 215); without spatulate tibial setae (Figs 259-260).

Host plants : adults feed on a wide range of plants including *Acacia*, *Angophora*, *Bossiaea*, *Cassia*, *Chenopodium*, *Dillwynia*, *Epaltes*, *Eucalyptus*, *Gastrolobium*, *Grevillea*, *Hakea*, *Melaleuca*, *Melilotus*, *Muhlenbeckia*, and *Pultenea*. The records of feeding on Proteaceae are the only records for this plant family in the Camptosomata but these plants are part of a range of genera fed upon by a single polyphagous species.

9.8.3.3 Genus ****Scaphodius*** Chapuis

This is a small group of about 15 species, confined to New Caledonia. The larva is unknown.

Diagnosis

Adult : eyes small, without a canthus, convex (Figs 341-342); male with elongate mandibles, at least as long as eyes, and clypeal border produced in middle or at sides; antennae longer than head width, apical segments elongate; front angles of pronotum not strongly constricted, hind angles posteriorly produced; elytra puncture striate; claws appendiculate; median lobe of aedeagus produced (Fig. 661); dorsal transverse sclerites extending beyond sides of rectum (Fig. 835).

Host plants : unknown.

9.8.4 SUBTRIBE **Cryptocephalina** Gyllenhal 1813

This subtribe is cosmopolitan and includes most species of Cryptocephalini, in approximately eight genera. In Australasia there are three endemic genera and one introduced or immigrant from America. Habitus drawings of various Cryptocephalina are illustrated (Figs 311-330).

Diagnosis

Adult (see Figs 311-330): hind margin of pronotum generally broadly but weakly produced, rarely rounded, usually with a row of teeth, never bordered (Figs 115-117, 120, 123); prosternal process without parallel ridges along the side margins, dilated to apex (Figs 115-117, 492-499); scutellum clearly visible, large, elongate rectangular to triangular to transverse rectangular, not stepped (Figs 511-519); sternites V and VI free; dorsal aedeagal setae absent (Figs 662-700); ejaculatory duct not strongly sclerotised; spermatheca normal, usually falciform (Figs 781-805); kotpresse variable (Figs 842-851).

First instar larva : frontal setae in 2+2 or 2+2+2 configuration (Figs 37-40); mandible with overlapping inner tooth (Figs 233-238); at least upper frons tuberculate; tibiae and femora simple, not spiculate, without spatulate setae (Figs 261-263).

9.8.4.1 Genus *Aporocera* Saunders

Aporocera includes the bulk of the Australian Cryptocephalina. About six species are found further afield in New Guinea, Borneo and Burma. The extensive generic synonymy under *Aporocera* is justified in Chapter **8**. Several species of *Aporocera* are illustrated in Figs 319-330.

Diagnosis

Adult (see Figs 319-330) : most species shining and metallic or brightly coloured; eyes frequently bulging laterally and large; pronotum rarely densely punctured and microsculptured, if so scutellum quadrate, impunctate and only shallowly notched; scutellum never keeled or pubescent; scutellum almost always truncate tipped; mesoscutum with longitudinal median keel and lateral oval microchaetal patches (Fig.519); kotpresse reduced (Figs 848, 850, 851).

First instar larva (see Figs 19-21, 36-39) : apparently not separable from *Cadmus* : with or without the following features: epicranial keel, upper epicranial pitting; Des1 in Aes1-4 row; moniliform spiracles; papillate prothoracic setae; and also sharing with *Cadmus* the following : sensillum Aesm1 in front of level with Aes1 and further from epicranial suture; upper frontal setae in 2+2 configuration; distance Fs2-Fs2 equal to or less than Fs3-Fs3.

Two subgenera are recognised.

9.8.4.1.1 Subgenus *Aporocera* s. str.

Diagnosis (adult only, see Figs 319-330): without the combination of attributes found in *Diandichus*; upper surface not densely microreticulate and scutellum not long and narrow, or if so pronotal disc with oblique grooves and clypeus transverse with non-parallel sides; pronotal lateral margins rarely feebly crenulate.

First instar larva : some species similar to *Diandichus*.

Host plants : adults feed on a range of genera including *Acacia*, *Angophora*, *Callistemon*, *Eucalyptus*, *Helichrysum*, *Hibbertia*, *Leptospermum* and *Melaleuca*.

9.8.4.1.2 Subgenus *Diandichus* Chapuis

Diagnosis

Adult : at least apex of abdomen and often whole body, bright yellow; upper surface densely microsculptured and may be tuberculate; eyes bulging laterally, with deep and narrow canthus; clypeus quadrate with parallel sides; lateral margin of pronotum broadly explanate and feebly crenulate; pronotal disc without lateral oblique grooves; base of pronotum evenly rounded or feebly produced, with elongate teeth (Fig. 127); prosternal process elongate, width usually less than half procoxal width; scutellum narrow, very elongate (Fig. 127); female apical abdominal hollow large and deep (Fig. 152); aedeagus simple (Figs 679-680); spermatheca simple (Fig. 797).

First instar larva (see Figs 37-38): upper epicranium smooth, without tubercles; apex of galea with large flattened seta-like sensilla; distance Dts1-2 less than Dts2-3 (Fig. 261).

Distribution : endemic to Australia and found throughout the southern half, except Tasmania.

Host plants : the four species with host information have only been found feeding on *Acacia* flowers, for which they are ideally coloured.

9.8.4.2 Genus *Cadmus* Erichson

The genus *Cadmus* includes about 65 species (40 described), all endemic to Australia, especially the east and south-east. I have relunctantly provided two new names for subgenera of *Cadmus*, *Aorocarpon* and *Cadmoides*, because the groups of species they represent need to be named if *Brachycaulus* and *Lachnabothra* are to be given subgeneric or higher status. Several species are illustrated (Figs 314-318).

Diagnosis

Adult (see Figs 314-318) : all species dull red, yellow, brown or black, without blue or green; eyes not laterally convex and swollen (except *Aorocarpon*); pronotum densely punctured and usually pubescent; lateral pronotal margins often crenulate (Fig. 314); prosternum flat, except anterior border reflexed or longitudinally ridged (Brachycaulus), not gradually raised towards anterior from middle (Figs 314-318); scutellum quadrate or triangular with truncate apex, basally notched and almost always punctate; mesoscutum with median longitudinal ridge and lateral oval patches of spiculae (Fig. 518); aedeagus and spermatheca variable; kotpresse reduced (Fig. 849).

First instar larva (see Figs 222-223) : apparently not separable from *Aporocera* : with or without the following features: epicranial keel, upper epicranial pitting; Des1 in Aes1-4 row; moniliform spiracles; papillate prothoracic setae.

9.8.4.2.1 Subgenus *Cadmus* s. str.

Diagnosis

Adult (see Figs 315-317) : surface of head and pronotum deeply and rugosely punctured, with dull, narrow interspaces; lateral margins and sides of anterior margin of pronotum strongly and fairly evenly crenulate; scutellum quadrate and convex, or truncate-triangular and longitudinally keeled; elytra not tuberculate, but may be canaliculate; second tarsal segment of mid and hind legs elongate or quadrate.

Host plants : all species feed on *Eucalyptus*.

9.8.4.2.2 Subgenus *Aorocarpon* subg. nov.

This name is proposed for the combination of two loosely associated species-groups. The type species is *Brachycaulus posticalis* Lea.

Diagnosis

Adult : eyes often strongly laterally convex; antennae not obviously sexually dimorphic; dorsal surface tuberculate or at least uneven (elytral tuberculation similar in pattern to *Lachnabothra*); front angles of pronotum projecting beyond prosternum (*apicalis*-group) or not projecting; lateral margins of pronotum simple or uneven but not crenulate; mesepimeron pubescent or densely strigose; scutellum longitudinally ridged or convex, punctate or strigose and truncate-triangular; tarsal segments elongate; aedeagus not modified, setae lateral (Fig. 673); spermatheca (Fig. 794).

Distribution : the species appear to be confined to the eastern seaboard.

Host plants : this group of species is most heterogeneous morphologically and also by host plant. Hosts include bipinnate *Acacia* (*C. posticalis*) *Eucalyptus*, and *Amyema*.

Etymology : from the Greek, aoro and karpon, meaning pendulous fruit. Masculine.

9.8.4.2.3 Subgenus *Brachycaulus* Fairmaire

This is a small group of about 10 species with characteristic very rugose sculpture, which appears to be the Australian analogue of the Chlamisini. For this reason the Chlamisini have often been placed at the tail of the Cryptocephalini in classifications (Chapuis 1874; Clavareau 1913), an association supported by the joint possession of 'antennal grooves' on the prosternum (Kasap and Crowson 1976), but the latter are clearly independently derived if even analogous. The presumed larva of *Brachycaulus* described by Kasap and Crowson (1976) is actually a ditropidine, and the larvae of *Brachycaulus* are typical of the Australian Cryptocephalina.

Diagnosis

Adult (see Fig. 314) : upper surface entirely deeply and rugosely punctured and coloured dull yellow to dark brown; ventral surface almost flat, elytra completely covering abdomen; antennae short, less than 1.5 times head width; punctation not rugosostriate behind eyes; pronotal disc with a pair of smoothly rounded large tubercles which almost coalesce, in both sexes; side margin of pronotum strongly and regularly crenulate; front margin of pronotum crenulate; anterior angles of pronotum protruding from prosternal anterior margin; prosternum not reduced to a ridge between coxal cavity and head and at least slightly grooved either side of middle; prosternal process with two central ridges or raised central rectangular area on anterior two-thirds; elytra with prominent interstrial ridges and tubercles; mesoscutellum lateral lobes without setal patches; tibiae strongly keeled externally; apical setae of aedeagus reduced in size or absent (Figs 670, 674); spermathecal retinaculum not falcate, of even diameter with blunt tip (Figs 792-793).

Distribution : the species are found throughout southern and eastern Australia, including Tasmania, with greatest diversity in the south-east.

Host plants : the adults feed exclusively on *Eucalyptus*. A single record of association with *Xanthorrhoea* (Hawkeswood 1985) is of casual specimen(s) of *B. klugi* which is a fairly common species on *Eucalyptus*.

9.8.4.2.4 Subgenus **Cadmoides** subg. nov.

This is a small group of distinct species which appear to be intermediate between *Lachnbothra* and *Cadmus* s. str. The type species is *Cadmus pacificus* Suffrian.

Diagnosis

Adult : size 3.5-7.5mm; black to dull brown, with or without red bands; densely clothed in pubescence and fine punctation, interspaces densely reticulate; antennae longer than body in male and segments parallel-sided, shorter and wider in female; pronotal pubescence in rosettes, as in *Lachnabothra*, apex of prosternal process convex; prosternal process not densely pubescent, surface visible; anterior angles of pronotum not produced beyond prosternum; mesepimeron pubescent; scutellum quadrate and at least laterally punctate and pubescent; elytral striae present but punctures confused or doubled, interspaces convex; aedeagus simple, with very few apical setae (Fig. 671).

Distribution : the eastern seaboard from Tasmania to North Queensland.

Host plants : all species feed on *Eucalytpus*.

Etymology : from the stem name Cadm- and the suffix oides, meaning similar to *Cadmus*. Masculine.

9.8.4.2.5 Subgenus **Lachnabothra** Saunders

A distinct group of about 20 species widespread over southern and eastern Australia. The habitus of *Lachnabothra braccata* is illustrated (Fig. 318).

Diagnosis

Adult (see Fig 318) : size 3-7mm; black or dull brown; pronotum with pubescence arranged in rosettes; elytra with at least lateral and apical irregular tubercles (Figs 909-910); males and females mostly strongly sexually dimorphic, male much smaller, with antennae longer than body and segments parallel-sided (Figs 901-902), bi-tuberculate pronotal disc (Figs 906-907), and last ventrite hollowed (one species exceptional in having a male with short female antennae and a female with bi-tuberculate pronotum (sex-linked gene recombination?)); prosternal process transverse, with concave sides and dense pubescence; lateral margins of pronotum thin and feebly crenulate in some species; aedeagus with a pair of apical thinly sclerotised windows, often highly modified (Figs 916-919). I have also illustrated the female antennae (Fig. 904), face (Fig. 906), metasternum (Fig. 912); male protarsus (Fig 913), male hind leg (Fig. 915), vaginal palp and spermatheca (Figs 921-922).

Other characters listed by Baly (1871) and Lea (1904) are only applicable to groups of species, for example swollen male hind femora (Fig. 915).

9.8.4.3 Genus *Diachus* Leconte

The genus is represented in the western Pacific region by a single tramp species that has recently arrived in Australia (Reid 1988). *Diachus* includes approximately 12 species, native to Central and southern North America and the West Indies. The diagnosis given below is for the immigrant species, *D. auratus*. The larvae are unknown but the scatoshells seem to be typical of Cryptocephalina (Swezey 1914).

Diagnosis

Adult : small size, 1.7-2.5mm, and smooth cylindrical shape; eyes with broad, shallow canthus (Fig. 73); pronotum with basal row of small tubercles and without a basal row of teeth (Fig. 123); scutellum triangular and flat, without lateral microchaetal patches (Fig. 143); claws appendiculate (Fig. 148). See also Reid (1988) for further illustrations.

First instar larva (unknown, the following are diagnostic features for known Nearctic Cryptocephalina) : frontal setae in 2+2+2 configuration (Fig. 40); sensillum Aesm2 in front of Aes2 or between Aes1 and Aes2.

Distribution : this species is native to the southern United States and Central America, but has spread across the Pacific this century, reaching Hawaii, Tahiti, Vanuatu, New Caledonia and eastern Australia (Reid 1988). The Australian specimen was collected at Kabra, Queensland, 26.x.1986 [QDPI].

Host plants : *Leucaena* and *Delonix* (Reid 1988) and *Salix* (Wilcox 1954).

9.8.4.4 Genus *Melatia* gen. nov.

Type species : *Cadmus glochidionis* Gressitt

This new genus is described for a group of about 30 distinctive species which have masqueraded under *Cadmus* and *Cryptocephalus*. The larva is unknown.

Diagnosis

Adult : antennae without circular sensillate depressions; eyes laterally convex, relatively small and temples long, therefore distance from top of eye to top of head more than half greatest length of eye (Fig. 347); canthus deep and triangular; mouthparts (Figs 395, 423, 445); prosternal process transverse and truncate to slightly convex (Fig. 496); scutellum triangular, apex sometimes rounded but never truncate, usually flush with elytra (Fig. 517); mesoscutum without lateral patches of microchaetae and with at most a weak longitudinal keel on midline; external edge of tibia usually grooved; lateral lobe at base of abdomen angular (Fig. 575); ventral transverse sclerite of kotpresse absent, dorsal sclerite reduced to two narrow patches (as in Fig. 850).

This genus is only likely to be confused with *Cadmus* species. The latter have a lobate or shallow canthus, usually larger eyes, truncate scutellum, tibiae not grooved and lateral patches of microchaetae present on mesoscutum. *Melatia* may be distinguished from *Melixanthus* and *Cryptocephalus* by the different eye shape and size, lack of antennal sensillar pits and shape of prosternal process.

Description

Adult (many species are well illustrated in Gressitt 1965): size 2-5.5mm; colour, surface sculpture and tuberculation variable : most species reddish-brown to black and clothed in recumbent pubescence, but some with blue elytra and yellow spots (see Gressitt 1965); the tuberculate species may have a pair of pronotal disc tubercles and elytral tubercles of similar distribution to *Brachycaulus* or *Lachnabothra*; head relatively small, sunk in prothorax; eyes laterally convex, relatively small and temples long, therefore distance from top of eye to top of head more than half greatest length of eye; canthus deep and triangular; antennae never more than 2/3 body length, usually c. 1/2; length of each of six apical segments 1.2-2 x width, always slightly wider than five basal (Fig. 367); antennae without circular sensillate depressions; sides of front margin of pronotum often strongly projecting so that anterior view similar to *Chlamisus*; lateral margins of pronotum may be uneven or irregularly crenulate; basal margin of pronotum with or without row of teeth; prosternal process transverse and apex truncate to slightly convex; scutellum variable, from large, triangular and medially keeled to small and flat with rounded apex, but never apically truncate and usually flush with elytra; surface of scutellum glabrous or pubescent, smooth or strigose or punctate; mesoscutum without lateral patches of microchaetae and without a longitudinal keel on midline; external edge of tibia usually grooved; lateral lobe at base of abdomen angular; claws simple or appendiculate (*glochidionis* and others); ventral transverse sclerite of kotpresse absent, dorsal sclerite reduced to two narrow patches (as Fig. 850).

Distribution : most species are in New Guinea, including one shared with North Queensland (*glochidionis*), but others are found in the Moluccas and the Solomon Islands, including Rennell (undescribed).

Host plants : Gressitt (1965) gives hosts for many of the species including *Glochidion* for the Australian species *M. glochidionis*.

Etymology : from the personal name Melati. Feminine.

9.9 Summary and scope of future research

On page 6 I gave a list of objectives which were in retrospect rather optimistic, although this is common to PhD theses.

The Australian Cryptocephalinae comprise one genus of Chlamisini, one genus of Clytrini, one genus of Pachybrachini (introduced) and 11 genera of Cryptocephalini (one introduced). I am unable to provide a well-resolved phylogeny for all the Australian Cryptocephalinae but a putative phylogeny is presented (Figs 954, 955, 949, 956, 957). In the course of determining the monophyly and relationships of the various groups in Australia almost the entire world fauna was examined at generic level in Cryptocephalini and Pachybrachini and at subtribal level in Clytrini. Because the phylogeny is still tentative and because I have taken a cladistic approach, the classification based on these phylogenies is conservative, with much synonymy and few new names. The most important nomenclatural changes are subtribal; I hope that the new classification will allow greater confidence in determination of both adult and larval stages to groups, allowing morphological, biological and evolutionary predictions. The loss of information in making so much synonymy is slight and in any case species-groups which show some behavioural or other distinction may be named as species-groups in the genera, pending further studies.

The determination of species-groups is the next problem in the Australian Cryptocephalinae but this problem is confined to the genera *Ditropidus* and *Aporocera* which each include more than 200 species. This study suggests some morphological attributes which may aid in the determination of species-groups. Finally adequate keys and descriptionsfor species recognition need to be prepared for all Australian Cryptocephalinae.

The interesting biogeographical and coevolutionary implications of the phylogeny presented here have not been explored. I have left these for a rainy day.

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Figures 741-805. Spermatheca of : 741, *Spilopyra sumptuosa*; 742, *Megascelis* sp.; 743, *Syneta japonica*; 744, *Lamprosoma elegans*; 745, *Lychnophaes purpurea*; 746, *Aetheomorpha* sp. A; 747, *A.* sp. B; 748, *Smaragdina graeca*; 749, *Pachybrachis hieroglyphicus*; 750, *Mylassa socia*; 751, *Stylosomus tamaricis*; 752, *Leasia minuta*; 753, *Atenesus* sp. (Yellowdine); 754, *Leasia australis*; 755, *Platycolaspis australis*; 756, *P.*

pubescens; 757, *Arnomus brouni*; 758, *Semelvillea bunyae*; 759, *S. acaciae*; 760, *S. parva*; 761, *S. eungella*; 762, *S. waraganji*; 763, *S. nothofagi*; 764, *Coenobius triangulum*; 765, *Aprionota* sp. (Tonga); 766, *A. inconstans*; 767, *Adiscus grandis*; 768, *Scaphodius forcipata*; 769, *Ditropidus saundersi*; 770, *Ditropidus* sp. 865; 771, *D.* sp. nr *antennarius*; 772, *Ditropidella* sp. 5; 773, *Ditropidus cervinus*; 774, *D.* sp. WA (Serpentine Falls); 775, *D. submetallicus*; 776, *D. aeneolus*; 777, *Ditropidella* sp. 738; 778, *Ditropidus comans*; 779, D. sp. 469; 780, *D. geminus*; 781, *Diachus auratus*; 782, *Lexiphanes coenobita*; 783, *Cryptocephalus incertus*; 784, *Cryptocephalus* [*Bassareus*] *brunnipes*, including transverse section of appendix and outline of receptacular muscle; 785, *Melixanthus erythromelas*; 786, *Melatia glochidionis*; 787, *M. metallicus*; 788, *M. solomonensis;* 789, *Cadmus australis*; 790, *Cadmus* (*Cadmoides*) *pacificus*; 791, *C. luctuosus;* 792, *C.* (*Brachycaulus*) *ferrugineus*; 793, *C.* (*B.*) *mammillatus*; 794, *C.* (*Aorocarpon*) *posticalis*; 795, *Aporocera chlamydiformis*; 796, *A. pauperculus*; 797, *A.* (*Diandichus*) *analis*; 798, *A. haematodes*; 799, *A. gravatus*; 800, *A. libertinus*; 801, *A. flaviventris*; 802, *A. aurantiacus;* 803, *A. australis*; 804, *A. jacksoni*; 805, *A. pulchella*. BC = bursa copulatrix; P = pump; R = receptaculum, SD = spermathecal duct; SG = spermathecal gland. 444

Figures 806-851. Rectum (dorsal left, ventral right, unless otherwise specified) of : 806, *Spilopyra sumptuosa* (ventral, dorsal identical); 807, *Syneta japonica*; 808, *Lamprosoma elegans*; 809, *Oomorphus concolor* (dorsal only); 810, *Chlamisus aterrimus*; 811, *C. mimosae* (ventral only); 812, *Clytra laeviuscula*; 813, *Smaragdina cyanea*; 814, *Aetheomorpha* sp. B; 815, *Acolastus tuberculatus*, including lateral view; 816, *Pachybrachis hieroglyphicus*; 817, *Mylassa socia*;

818, *Griburius larvatus*; 819, *Metallactus* sp. (dorsal only); 820, *Stylosomus tamaricis*; 821, *Semelvillea parva*, including lateral view; 822, *S. acaciae*; 823, *S. nothofagi*; 824, *S. waraganji*; 825, *S. eungellae*; 826, *S. bunyae*; 827, *Arnomus brouni*; 828, *Atenesus* sp. 5 [illegible]; 829, *Leasia australis*; 830, *Platycolaspis australis*; 831, *Coenobius triangulum*; 832, *Aprionota tutuilana*; 833, *A. inconstans*; 834, *Adiscus grandis*; 835, *Scaphodius forcipata*; 836, *Ditropidus saundersi*; 837, *D. geminus*; 838, *D.* sp. nr *antennarius*; 839, *Ditropidella* sp. 5; 840, *D. suffriani*; 841, *Scaphodius striaticollis*; 842, *Diachus auratus*; 843, *Stegnocephala hebetata*; 844, *Cryptocephalus incertus*; 845, *C. sericeus*; 846, *Melixanthus intermedius*; 847, *M. erythromelas*; 848, *Aporocera* (*Diandichus*) *analis*; 849, *Cadmus australis*; 850, *Aporocera viridis*; 851, *A. consors.* Cp = chitinpolster; CR = chitinring; DF = dorsal furrow; LS = lateral sclerite; Se-= sensilla; TS = transverse sclerite. 447

Figures 852-854. Alimentary canal of : 852, *Edusella* nr *lineata*; 853, *Cadmus lucifugus*. Proventricular spines of : 854, *Aprionota tutuilana.* CR = chitinring; Fg = foregut; I = ileum; Mg = midgut; MT = Malpighian tubules; Pr = proventriculus; R = rectum; RC = regenerating crypts. 453

Figures 855-856. Male genitalia of : 855, *Edusella* nr *lineata*; 856, *Cadmus* (*Lachnabothra*) sp. A. AG = assessory gland; LM = longitudinal muscle; P = muscular pump; T = testes; TM = transverse muscle; VD = vas deferens. 453

Figures 857-864. *Chlamisus aterrimus* : 857, dorsum; 858, lateral; 859, anterior; 860, prosternal process; 861, tergite VII; 862, º (top) and o antenna; 863, hind tarsus; 864, claws. 454

AGTW = *Leasia [Agetinella]* sp. 2

AMBR = *Ambrotodes signatipennis*

APAN = *Aporocera analis*

APIC = *Cadmus* (*Aorocarpon*) *apicalis* species-group

APIN = *Aprionota [Coenobius] inconstans*

APOR = *Aporocera* spp.

APRI = *Aprionota* spp.

APTO = *Aprionota* sp. Tonga

ARNO = *Arnomus* spp.

ARSE = *Arnomus* and *Semelvillea* spp.

ATEN = *Atenesus* sp.

AUST = Australian Cryptocephalina (*Aporocera* and *Cadmus*)

BABI = *Babia quadriguttata*

BASS = *Bassareus brunnipes*

BRAC = *Cadmus* (*Brachycaulus*) spp.

BRMA = *Cadmus* (*Brachycaulus*) *mammillatus*

BRFE = *Cadmus* (*Brachycaulus*) *ferrugineus*

BRPO = *Cadmus* (*Brachycaulus*) *posticalis*

BUCH = *Ditropidus [Bucharis] suffriani*

BUSU.= *Ditropidus [Bucharis] suffriani*

CAAS = *Cadmus australis*

CAAU = *Aporocera [Cadmus] aurantiacus*

CADM = *Cadmus* s.str. spp.

CAGL = *Melatia [Cadmus] glochidionis*

CALI = *Cadmus litigiosus*

CAPA = *Cadmus* (*Cadmoides*) *pacificus*

CASO = *Melatia [Cadmus] solomonensis*

CHAT = *Chlamisus aterrimus*

CHLA = Chlamisini

CHMI = *Chlamisus mimosae*

CHPU = *Aporocera [Chariderma] pulchella*

CHVI = *Aporocera [Chloroplisma] viridis*

CLYT = *Clytra laeviuscula* or Clytrini depending on context

COEN = *Coenobius triangulum* or Coenobiina depending on context

CRBI = *Aporocera [Cryptocephalus] bihamatus*

CRCO = *Cryptocephalus coryli*

CRHA = *Aporocera [Cryptocephalus] haematodes*

CRIN = *Cryptocephalus incertus*

CRMO = *Cryptocephalus moraei*

CRSE = *Cryptocephalus sericeus*

CRVE = *Cryptocephalus venustus*

CRYA = Cryptocephalinae sp. A [Pachybrachini]

CRYP = *Cryptocephalus* spp.

CYCH = *Aporocera [Cyphodera] chlamydiformis*

CYPH = *Aporocera [Cyphodera] chlamydiformis*

DIAN = *Aporocera* (*Diandichus*) *analis*

DICS = *Ditropidus comans*

DIFI = *Ditropidella* sp. 5

DIFO = *Ditropidus* sp. 465

DIJA = *Ditropidella* spp.

DIOR = *Adiscus [Dioryctus] grandis*

DISE = *Ditropidella* sp. 728

DITA = *Ditropidus antennarius*

DITR = *Ditropidus* spp. or Ditropidina depending on context

DIWA = *Ditropidus* sp. WA

EDUS = *Edusella* sp. nr *lineata*

ELAE = *Ditropidus [Elaphodes] aeneolus*

ELAP = *Ditropidus [Elaphodes]* spp.

ELCE = *Ditropidus [Elaphodes] cervinus*

ELPI = *Ditropidus [Elaphodes] pilula*

EUDI = *Ditropidus [Euditropidus] variabilis*

EUFL = *Aporocera [Euphyma] flaviventris*

EUKI = *Pachnephorus* sp.

EUMO = Eumolpinae

EUVA = *Ditropidus [Euditropidus] variabilis*

FLJA = *Aporocera [Euphyma] flaviventris* and *A. [Cryptocephalus] jacksoni*

GRIB = *Griburius larvatus*

IDCO = *Aporocera [Idiocephala] consors*

ISCH = *Ischiopachys* sp.

ISNU = *Isnus discoidalis*

LABI = *Labidostomis propinqua*

LABR = *Cadmus* (*Lachnabothra*) *braccata*

LACH = *Cadmus* (*Lachnabothra*) spp.

LAHO = *Cadmus* (*Lachnabothra*) *braccata*

LAMP = Lamprosomatinae

LEAS = *Leasia* spp.

LEXI = *Lexiphanes coenobita*

LODI = *Aporocera* sp. 1049

LOGR = *Aporocera [Loxopleurus] gravatus*

LOLI = *Aporocera [Loxopleurus] libertinus*

LOPA = *Aporocera [Loxopleurus] pauperculus*

LORU = *Aprionota [Loxopleurus] ruficollis*

MEGA = *Megascelis* sp.

MEGO = *Megalostomis pyropyga*

MELI = *Melixanthus intermedius*

META = *Metallactus* sp.

MIVI = *Aporocera [Mitocera] viridipennis*

MYLA = *Mylassa socia*

NRPO = *Ditropidus* sp. 865

OCAU = *Aporocera [Ochrosopsis] australis*

OOMO = *Oomorphus concolor*

PACH = *Pachybrachis hieroglyphicus* or Pachybrachini depending on context

PACI = *Cadmus* (*Cadmoides*) *pacificus*

PALU = *Cadmus [Paracadmus] luctuosus*

PLAT = *Platycolaspis australis*

POGE = *Ditropidus [Polyachus] geminus*

POLY = *Ditropidus [Polyachus] geminus*

POST = *Cadmus* (*Brachycaulus*) *posticalis*

PRAS = *Ditropidus [Prasonotus] submetallicus*

PRIO = *Cadmus [Prionopleura]* spp.

PRRU = *Cadmus [Prionopleura] rugicollis*

PYCN = *Aprionota [Pycnophthalma] tutuilana*

PRSU = *Ditropidus [Prasonotus] submetallicus*

RHJO = *Aporocera [Rhombosternus] jocosus*

SCAL = *Aporocera [Schizosternus] albogularis*

SCAP = *Scaphodius striaticollis*

SCHI = *Aporocera [Schizosternus] albogularis*

SCST = *Scaphodius striaticollis*

SEAC = *Semelvillea acacia*

SEME = *Semelvillea* spp.

SENO = *Semelvillea nothofagi*

SMAR = *Smaragdina affine*

STEG = *Stegnocephala hebetata*

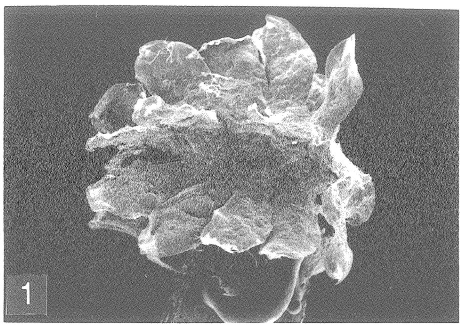
STPL = *Stylosomus* and Platycolaspina

STYL = *Stylosomus tamaricis*

SYNE = *Syneta japonica*

TAPP = *Ditropidus [Tappesia] saundersi*

TASA = *Ditropidus [Tappesia] saundersi*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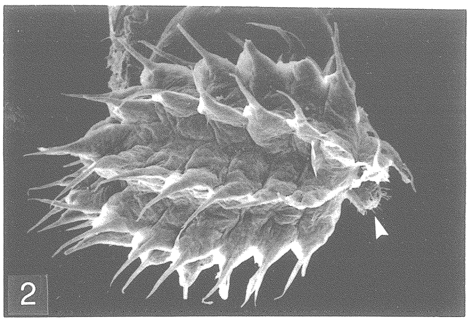
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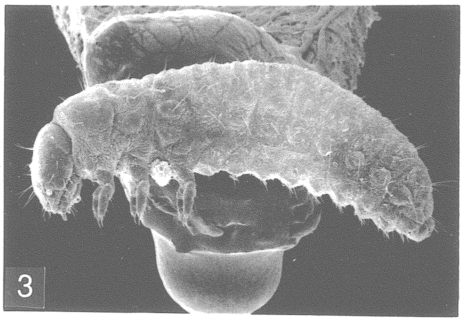
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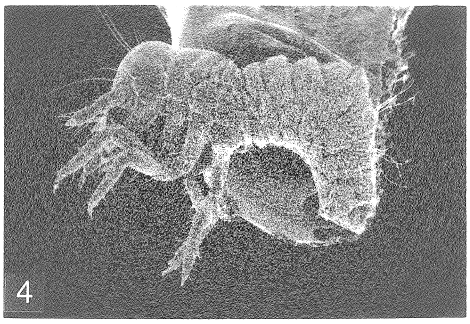
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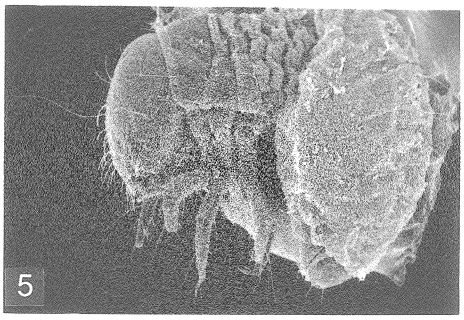
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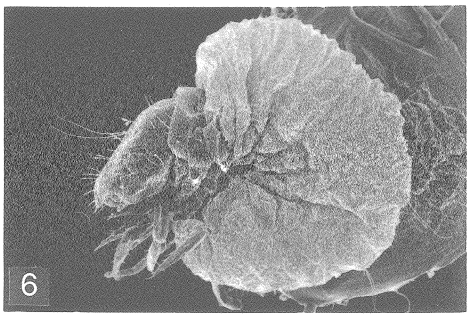
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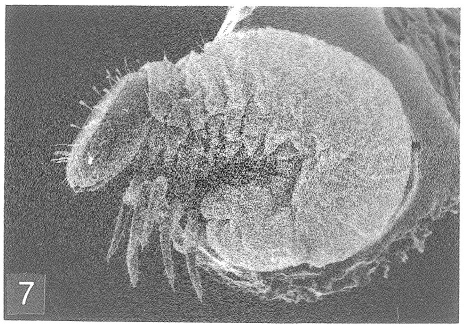
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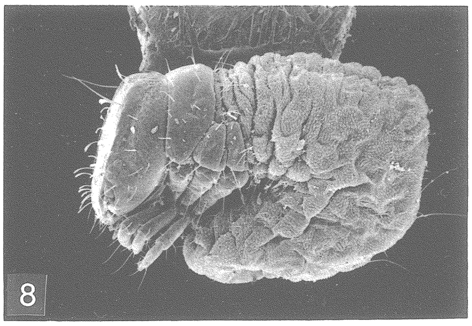
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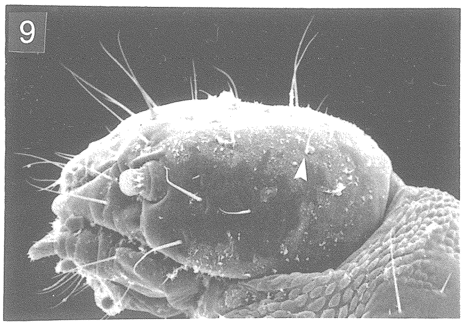
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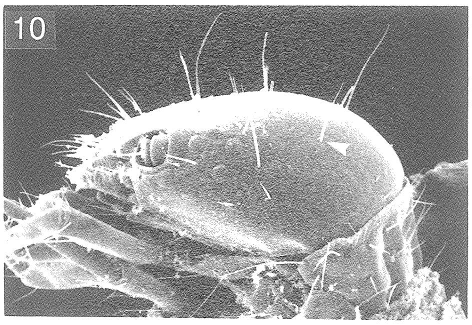
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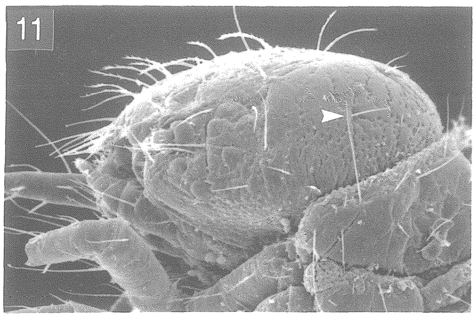
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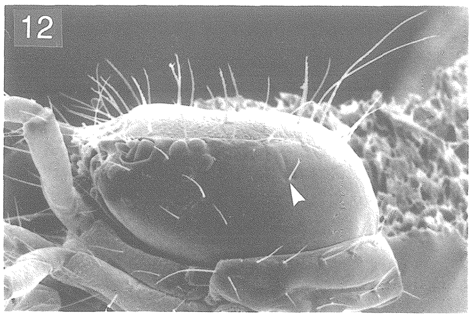
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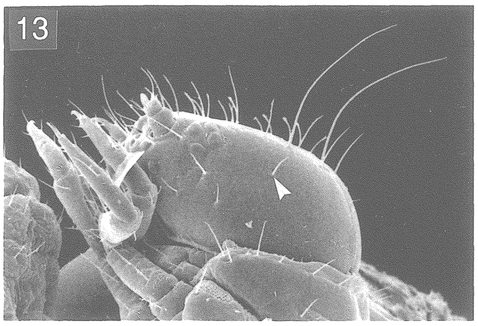
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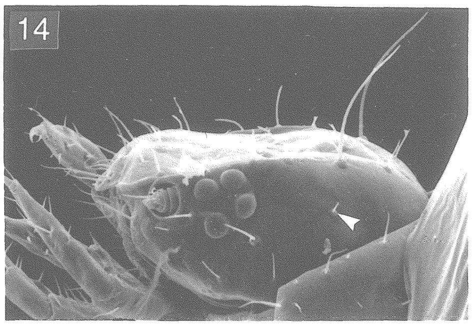
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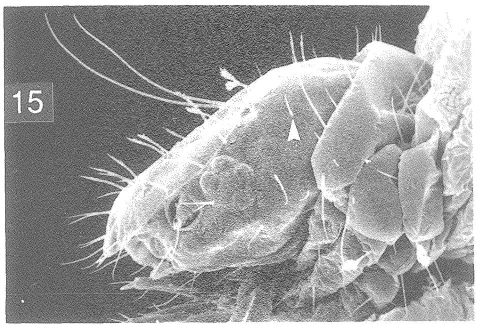
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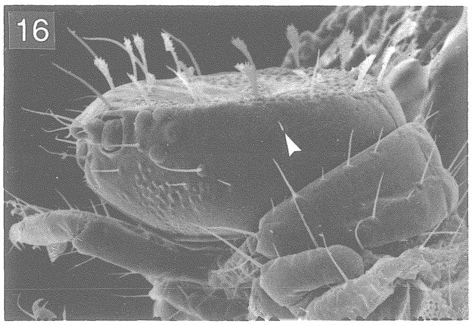
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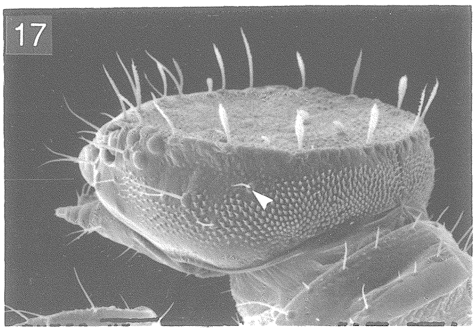
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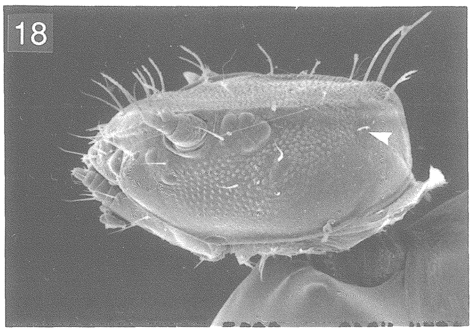
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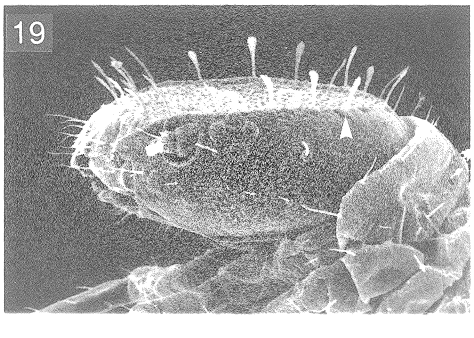
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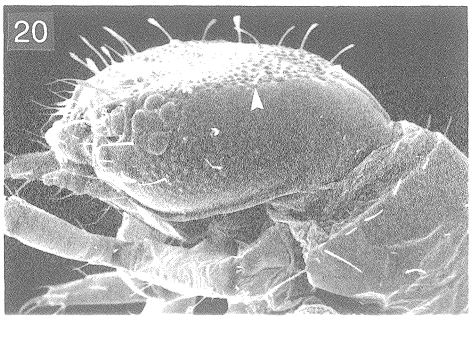
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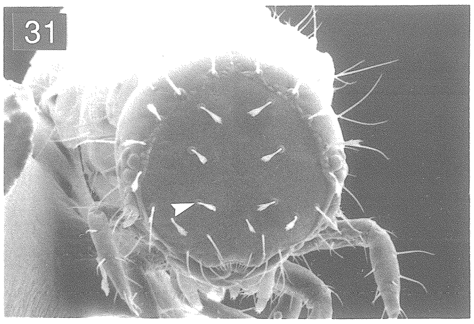
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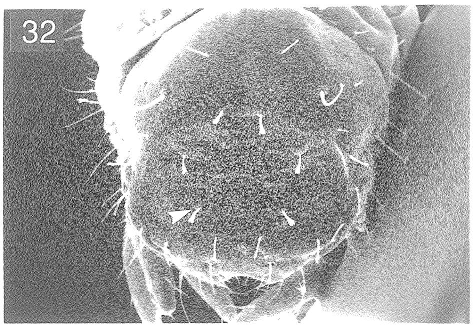
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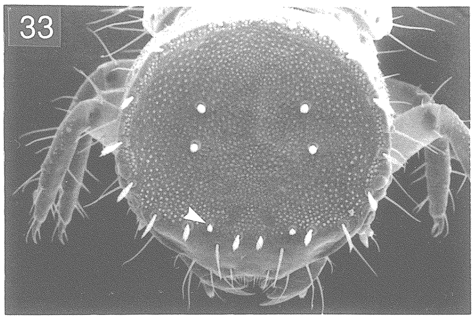
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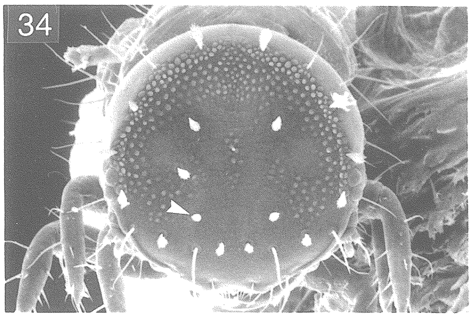
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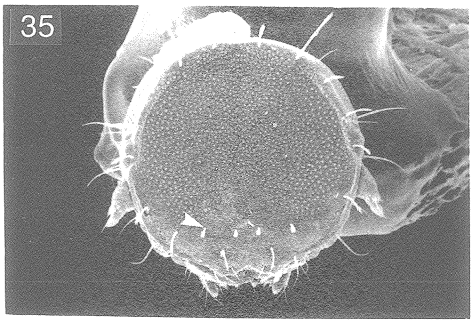
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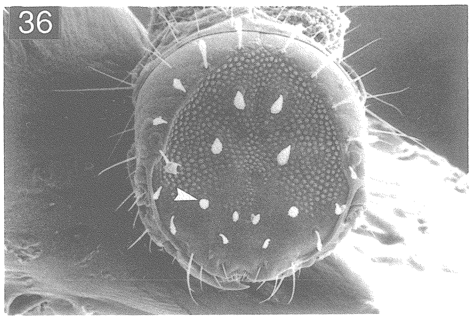
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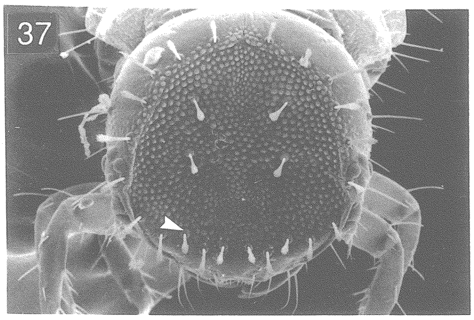
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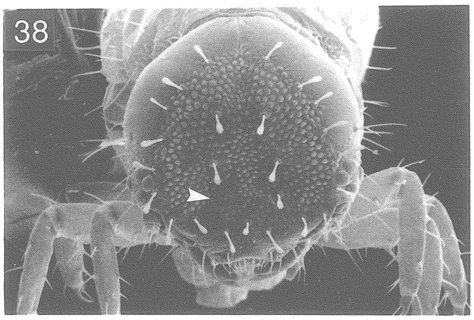
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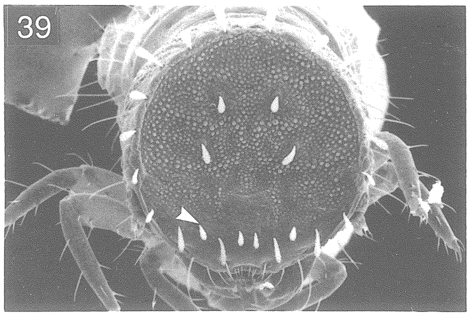
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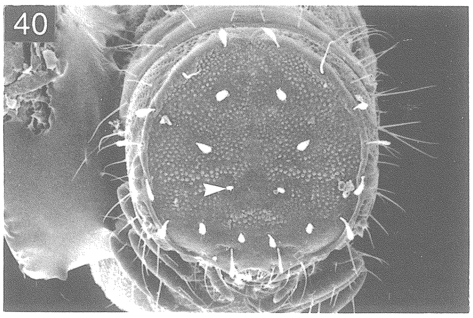
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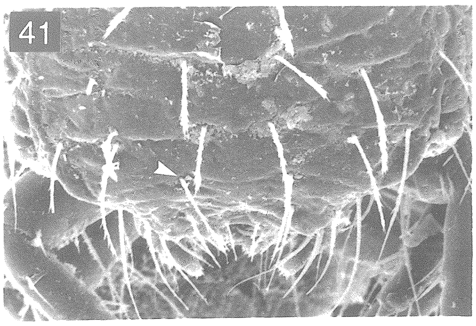

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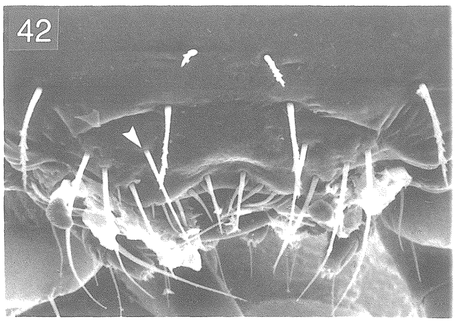

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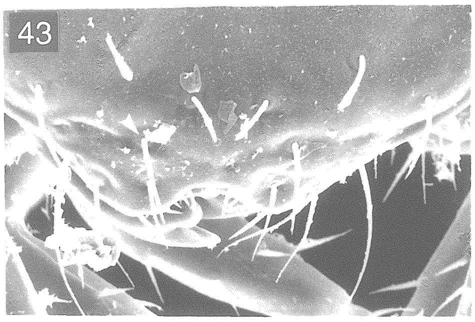

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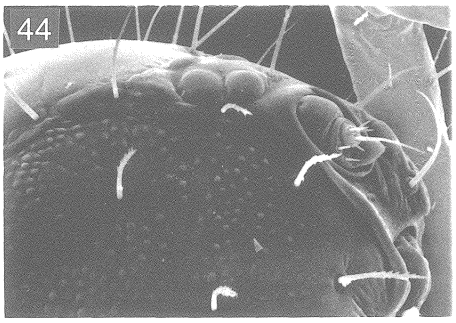

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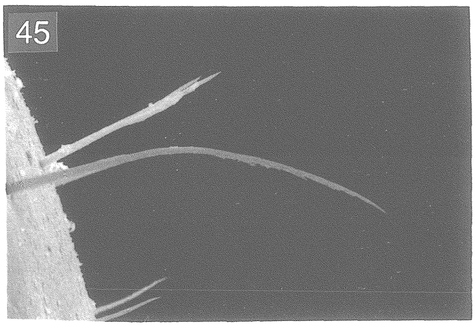

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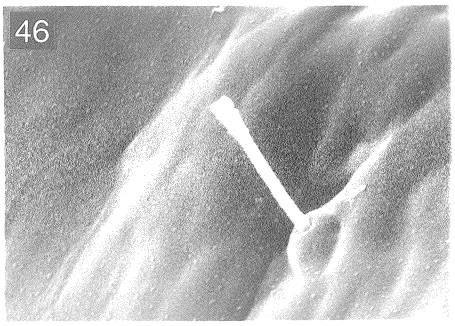

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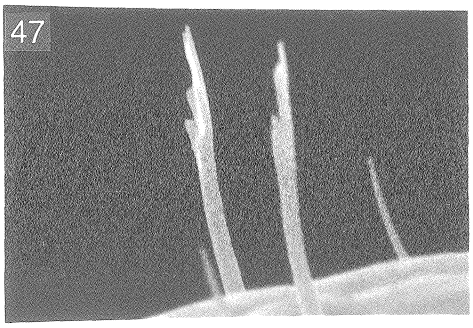

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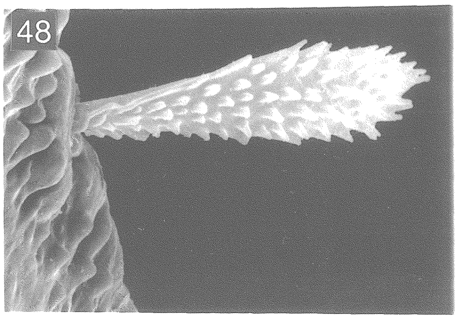

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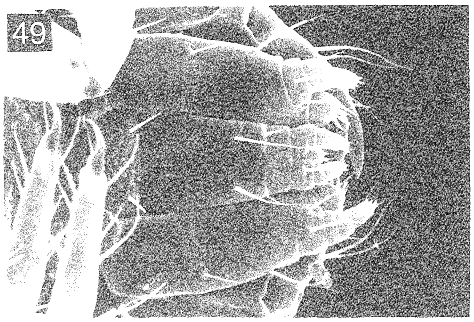

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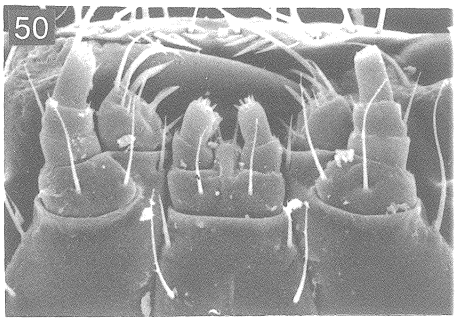

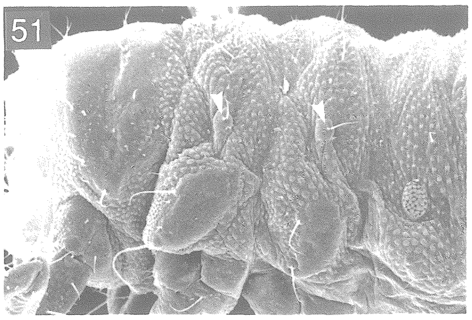
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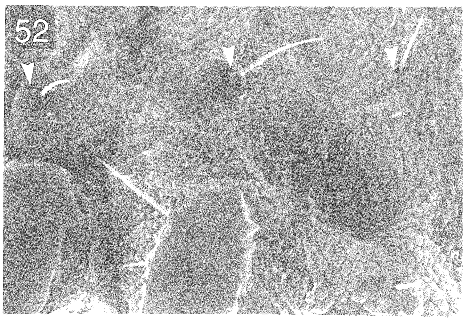
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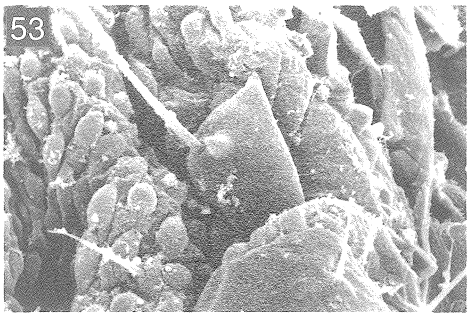
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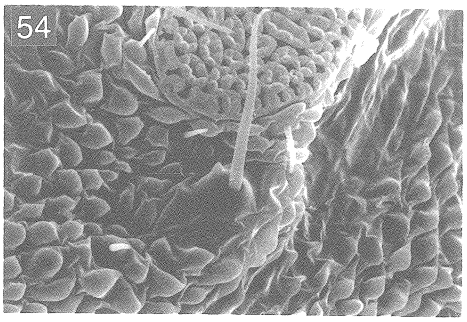
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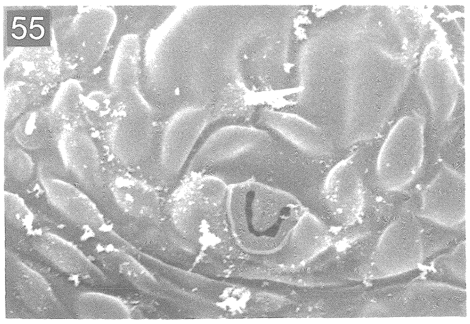
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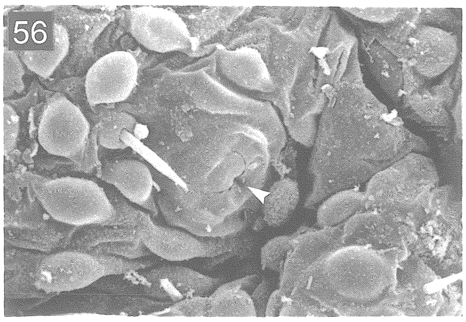
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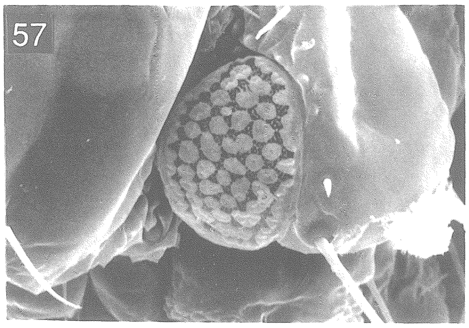
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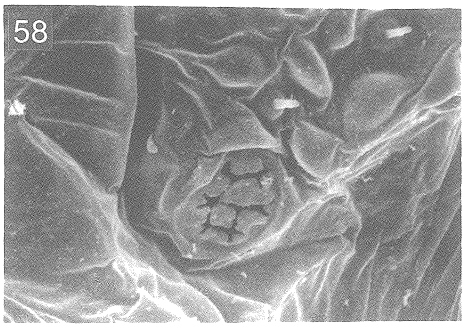
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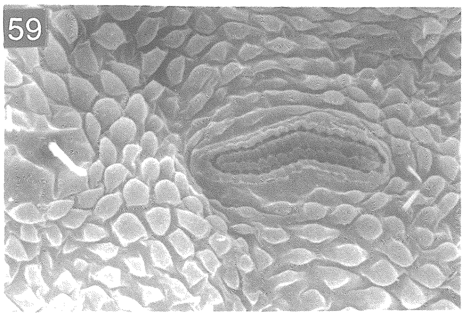
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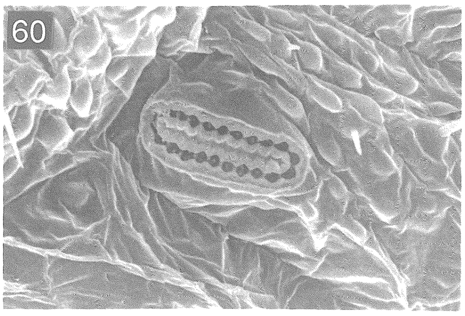
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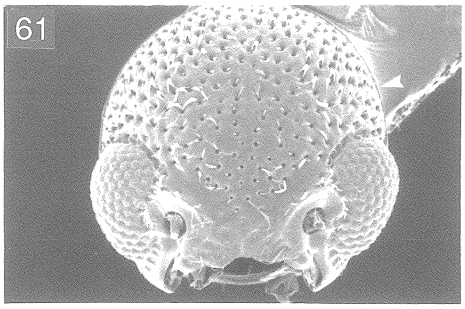
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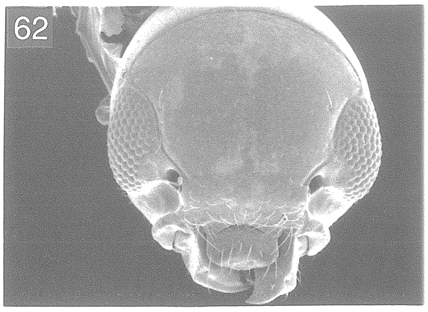
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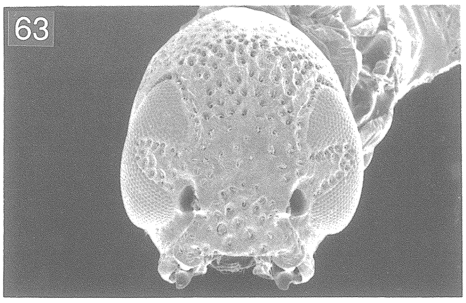
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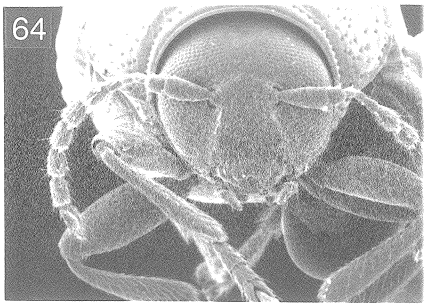
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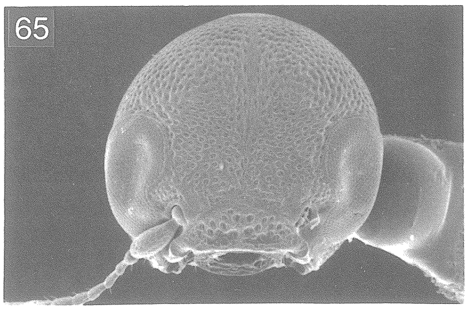
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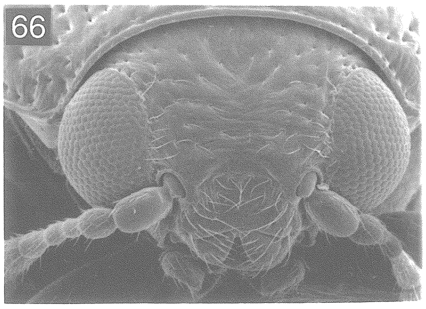
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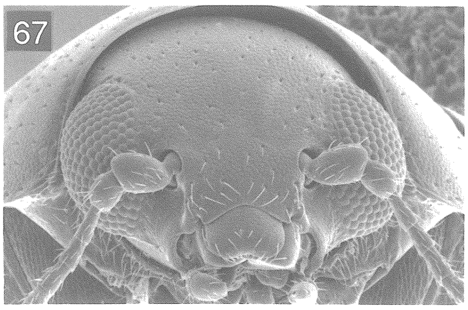
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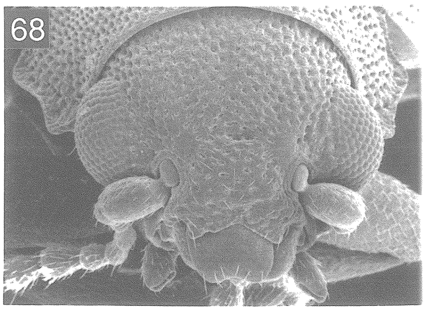
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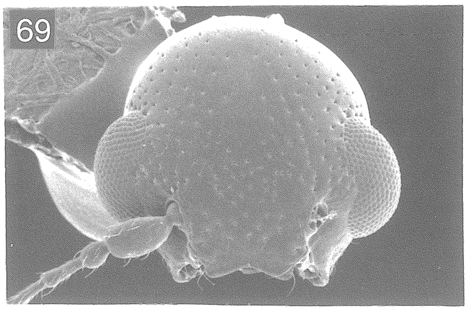
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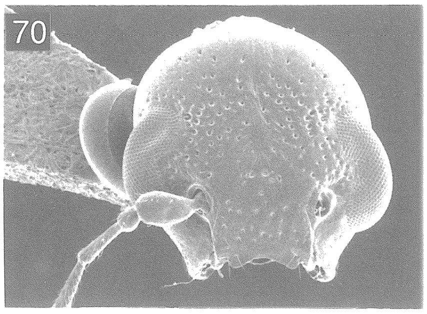
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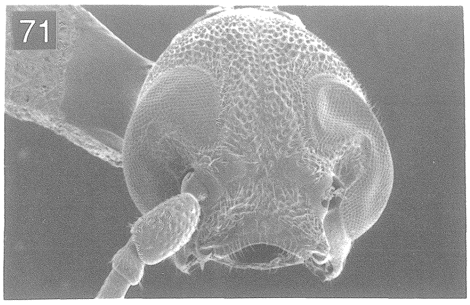
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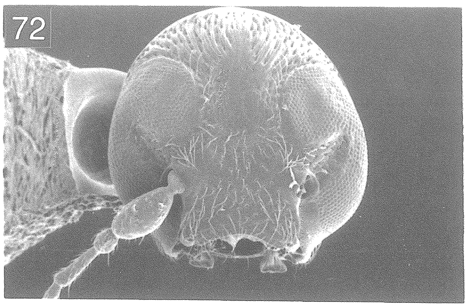
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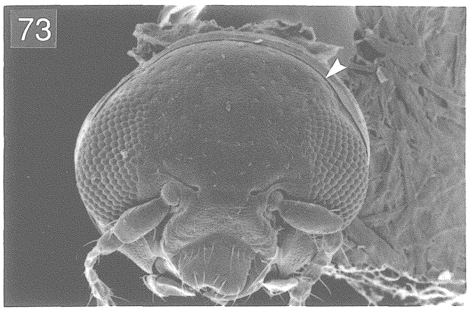
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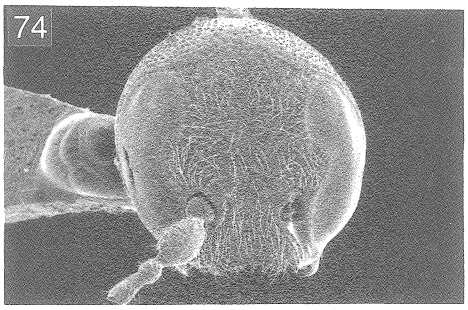
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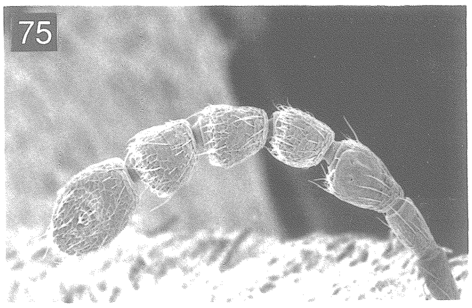
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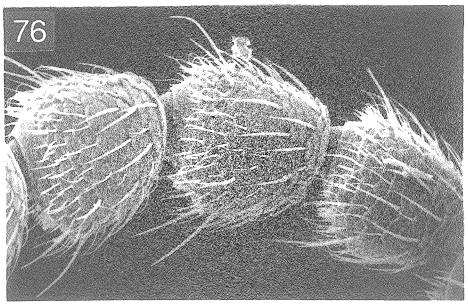
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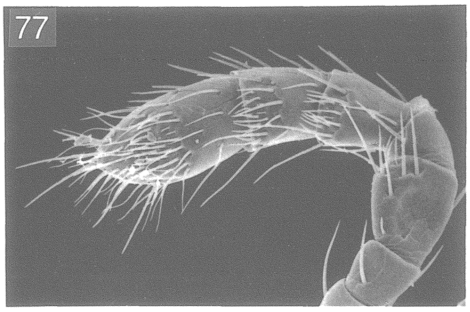
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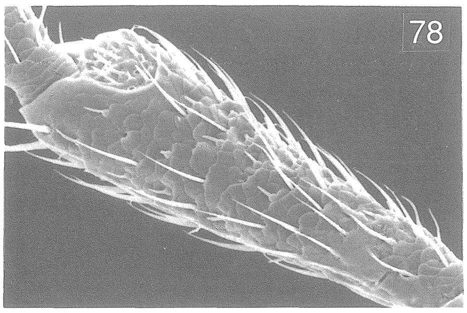
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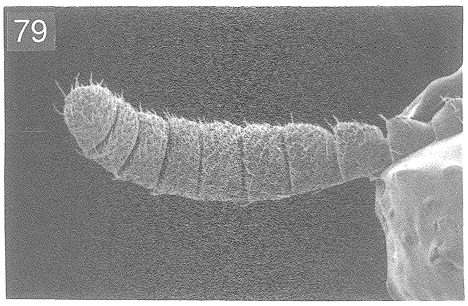
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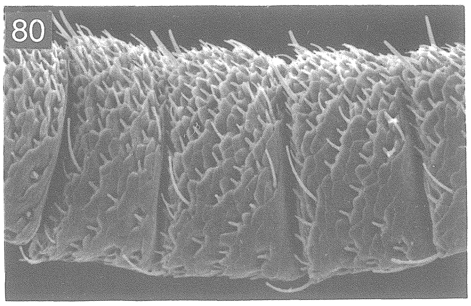
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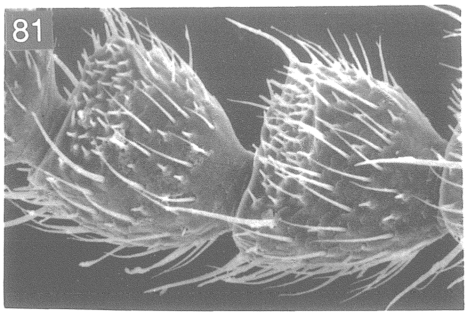
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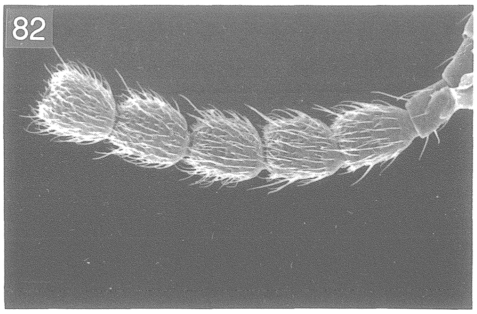
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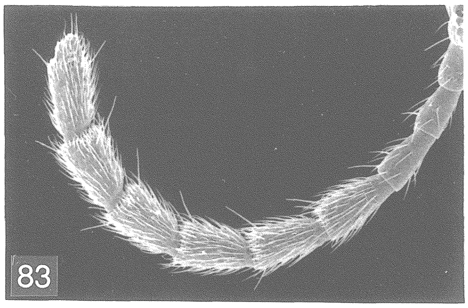
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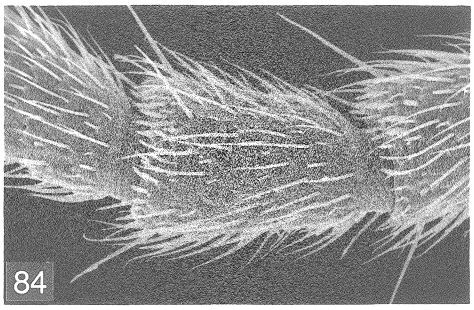
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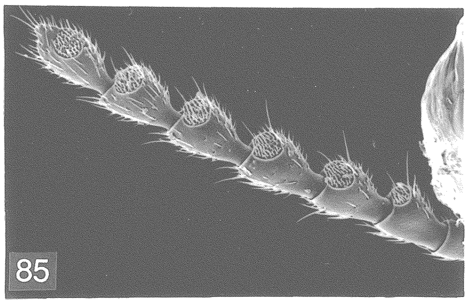
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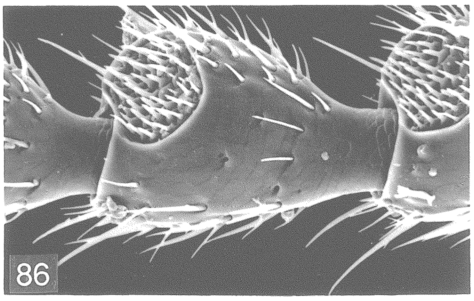
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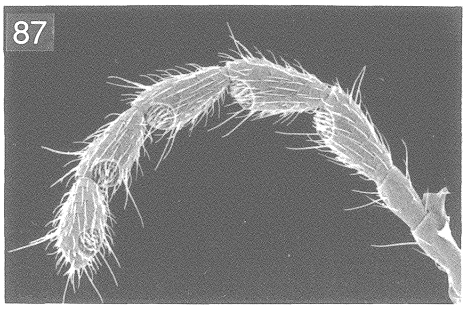
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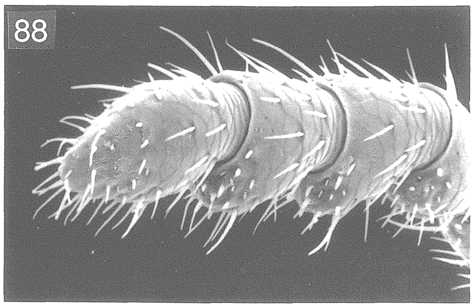
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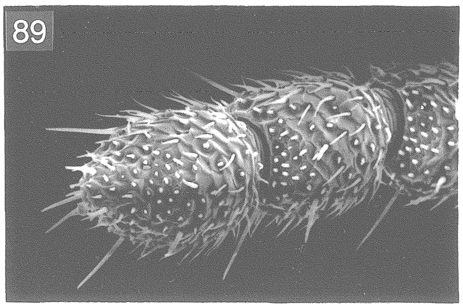
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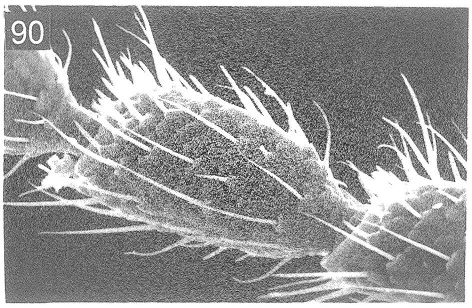
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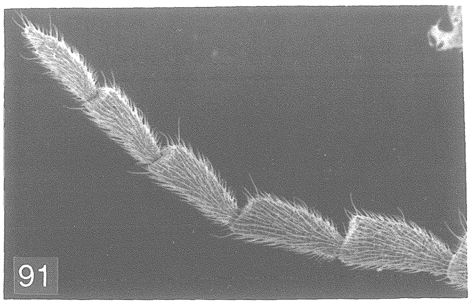
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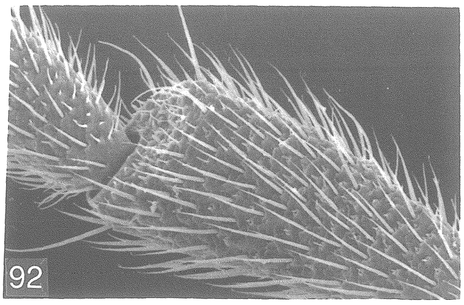
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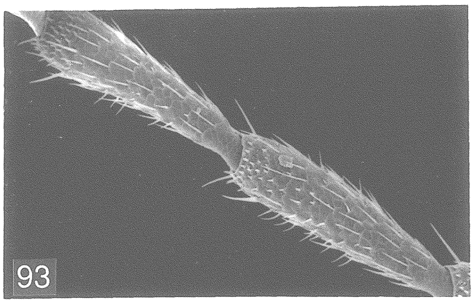
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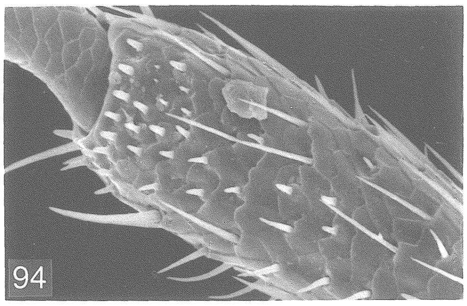
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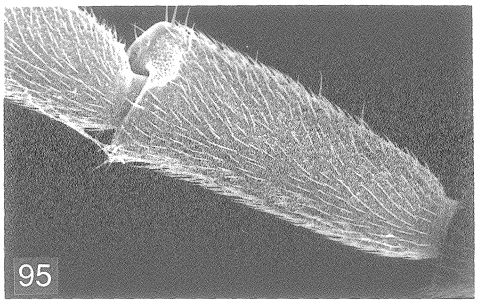
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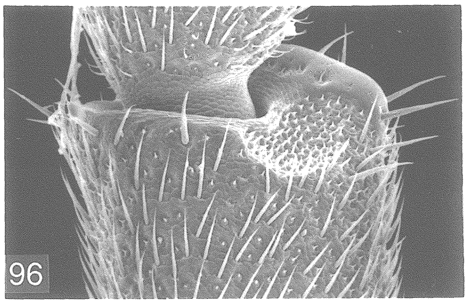
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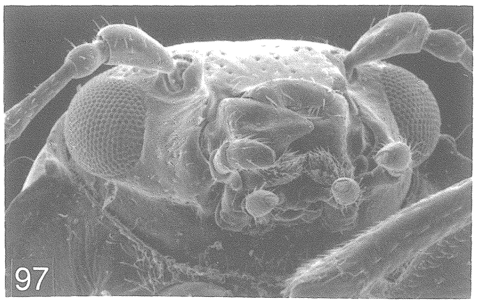
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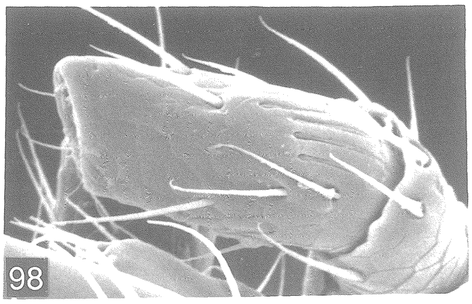
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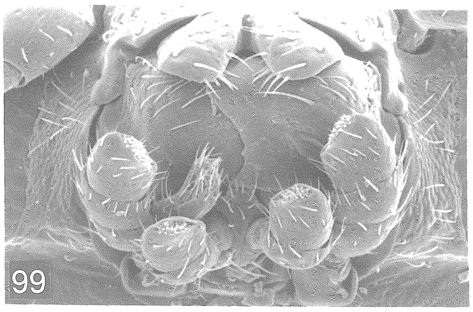
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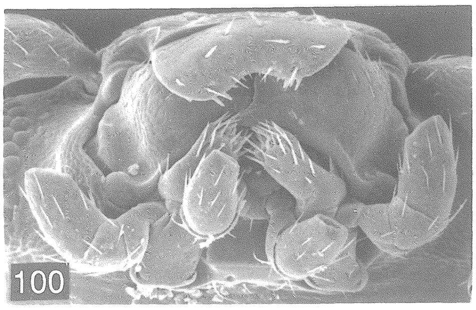
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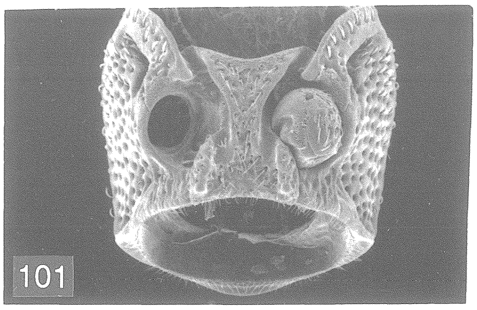

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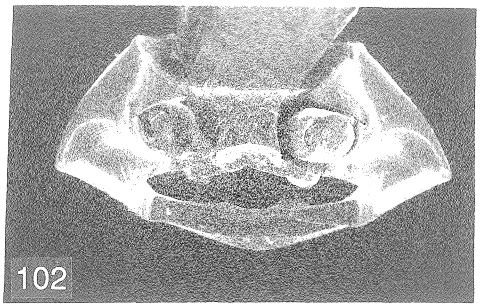

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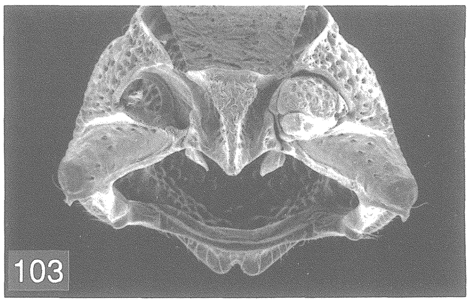

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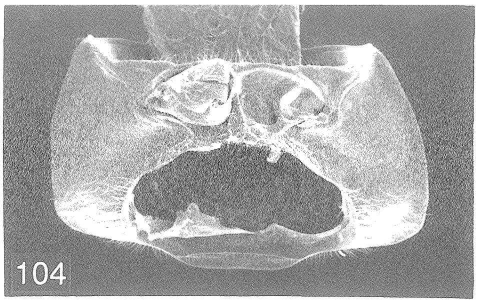

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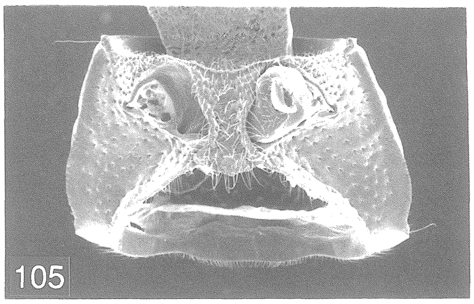

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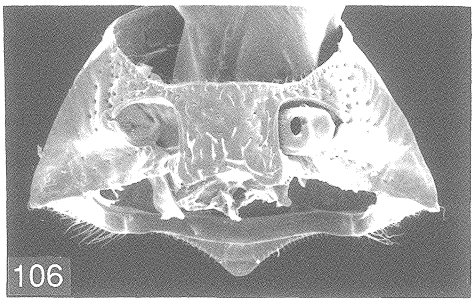

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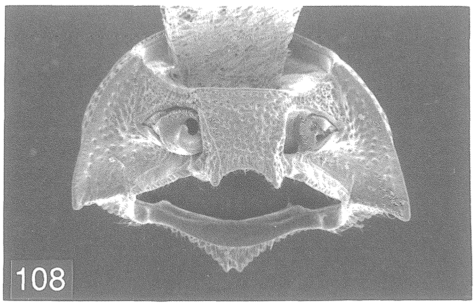

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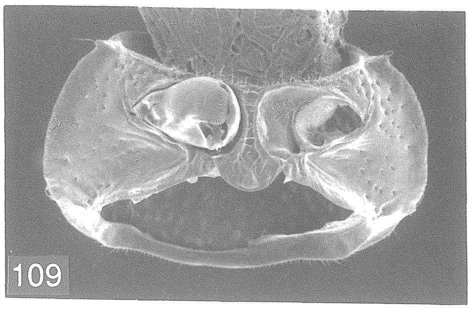

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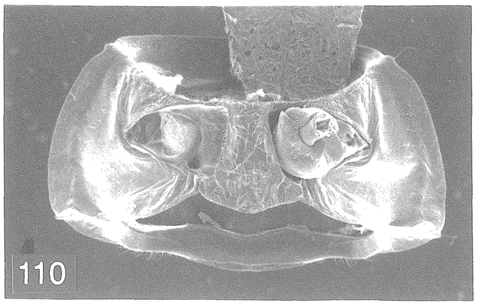

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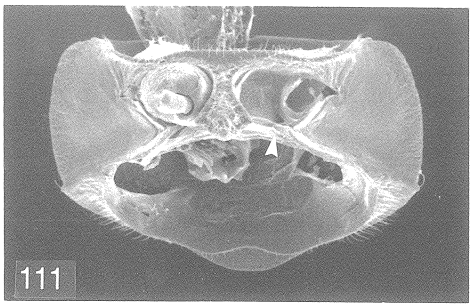
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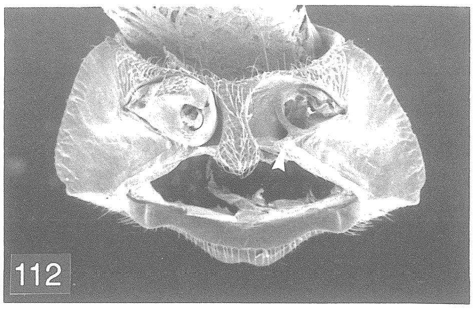
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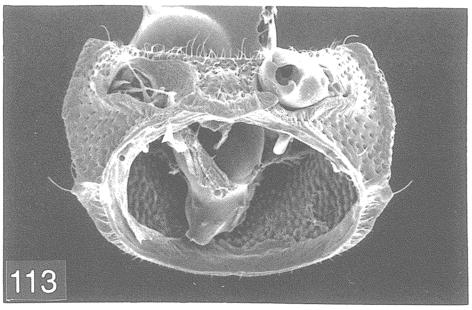
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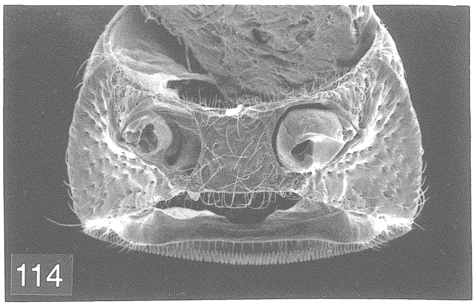
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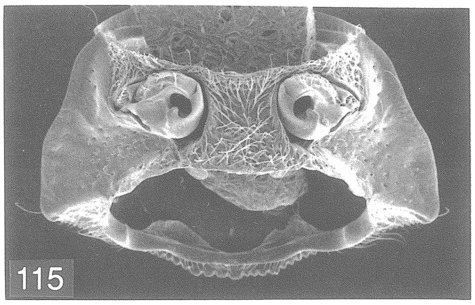
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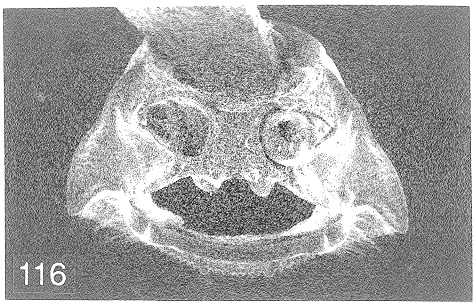
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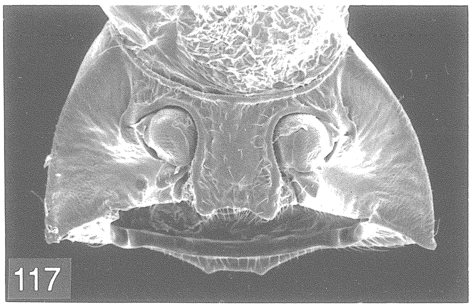
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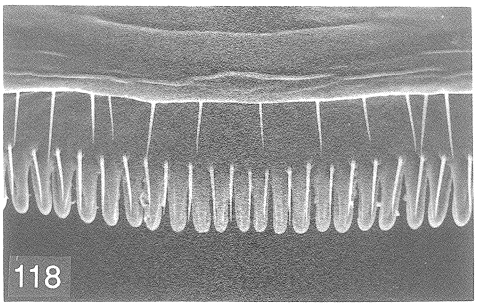
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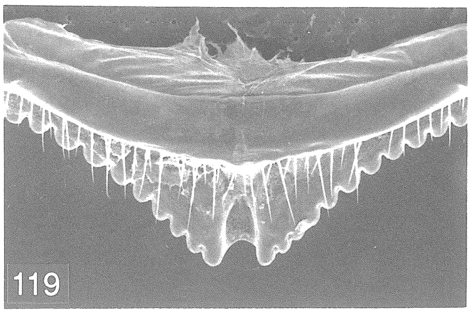
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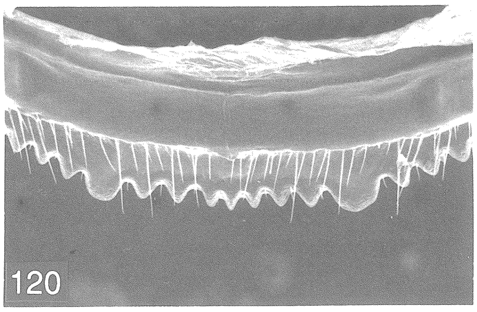
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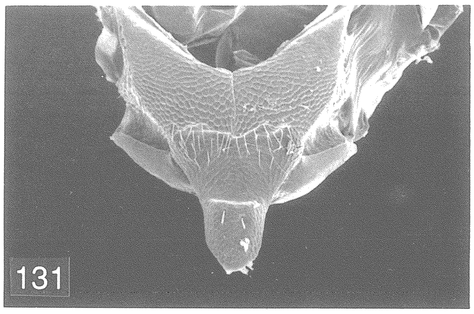
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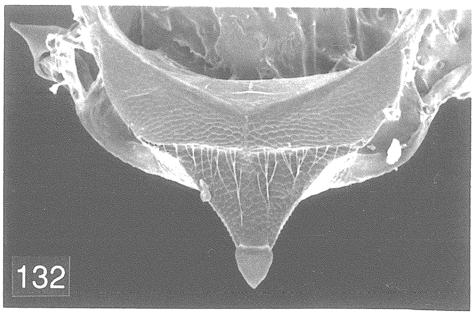
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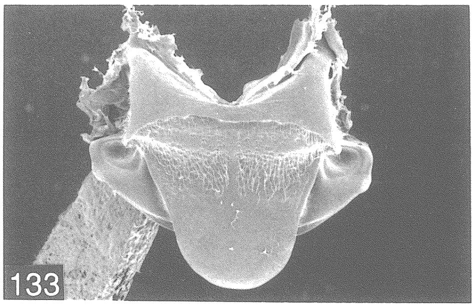
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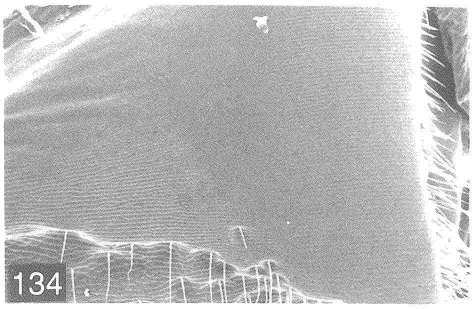
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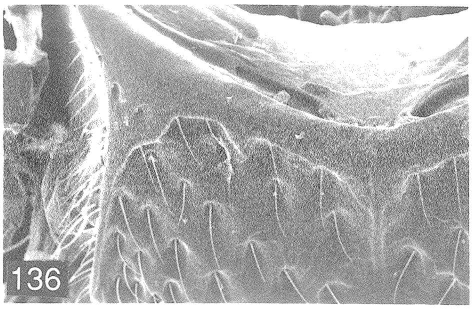
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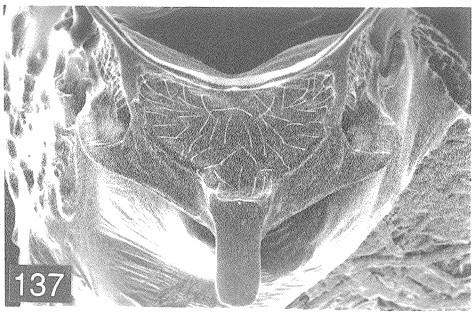
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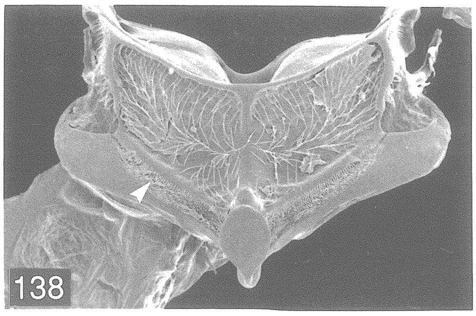
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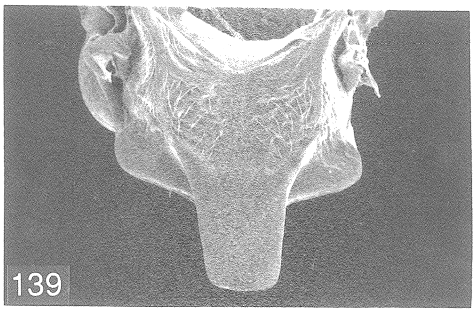
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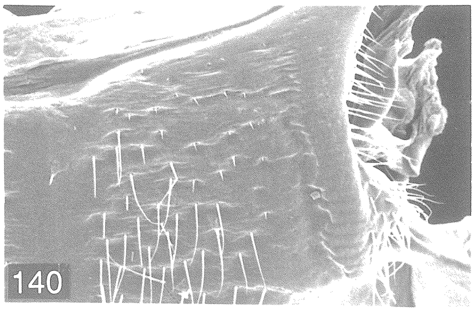
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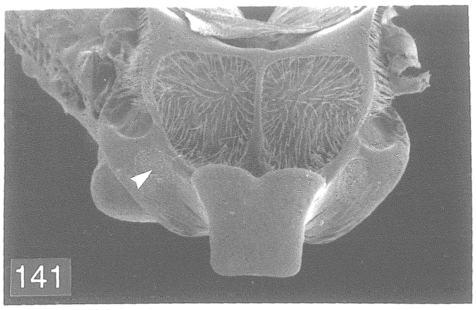
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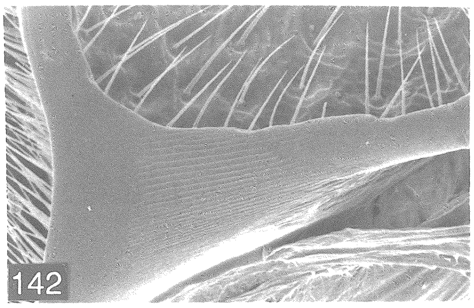
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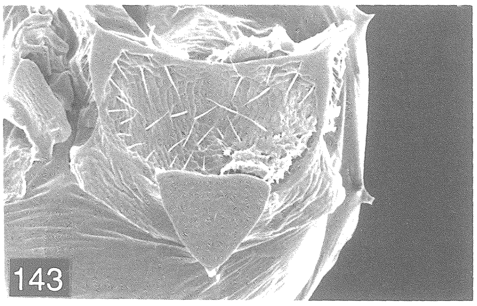
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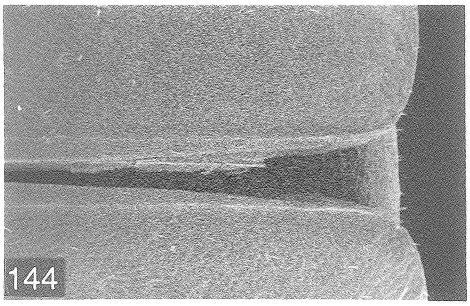
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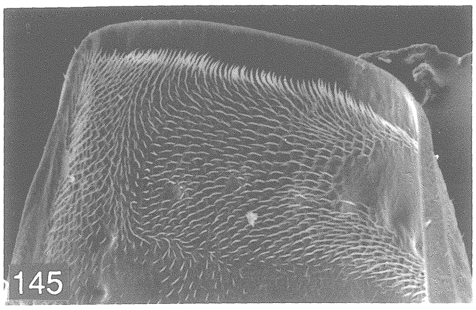
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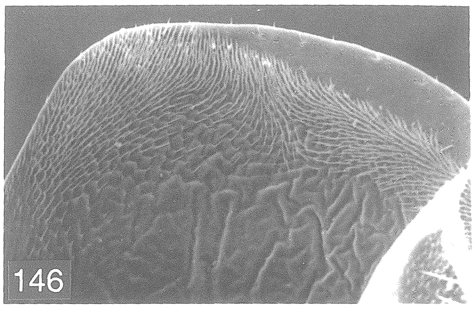
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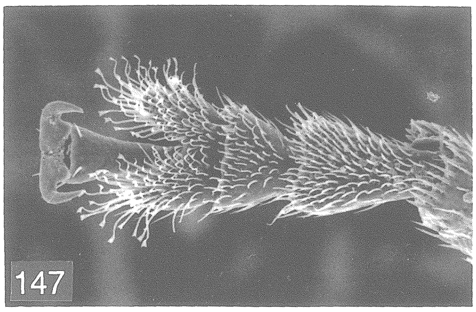
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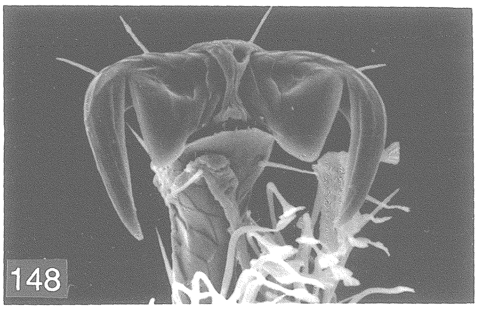
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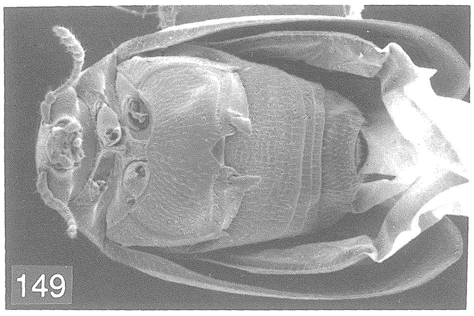
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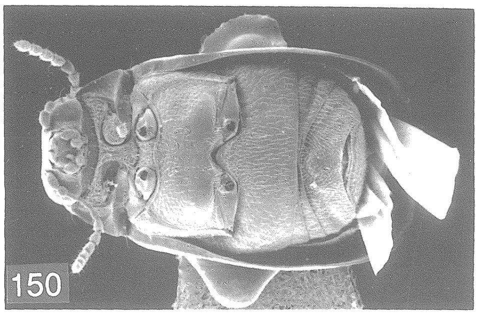
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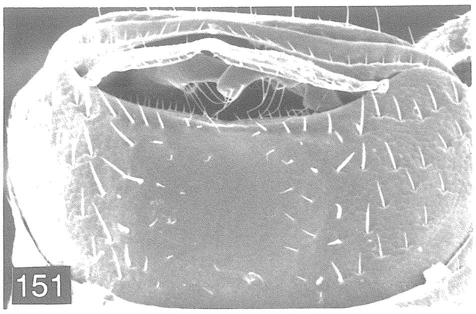
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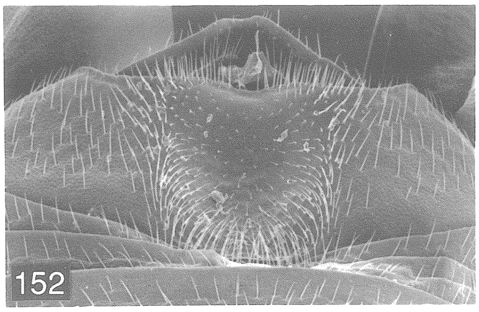
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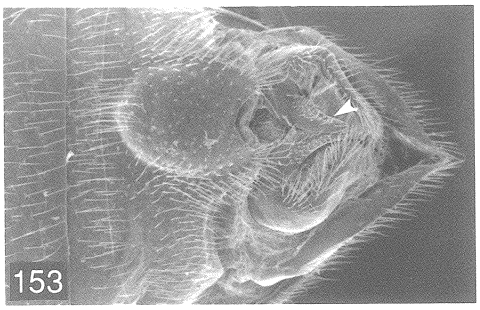
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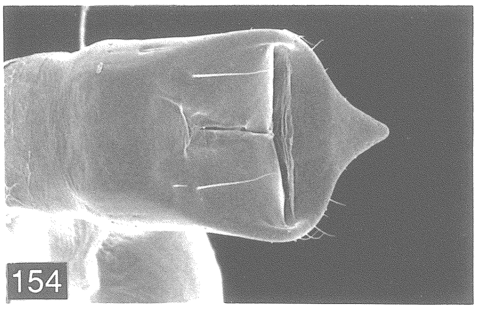
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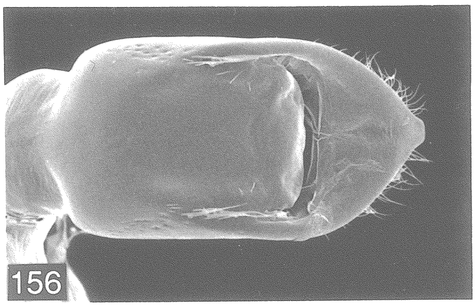
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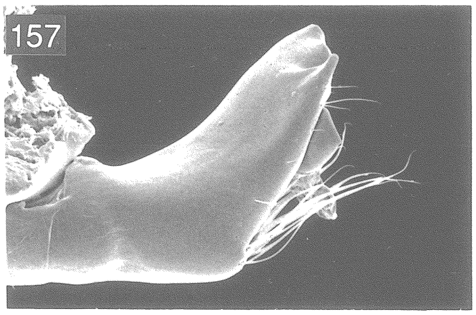
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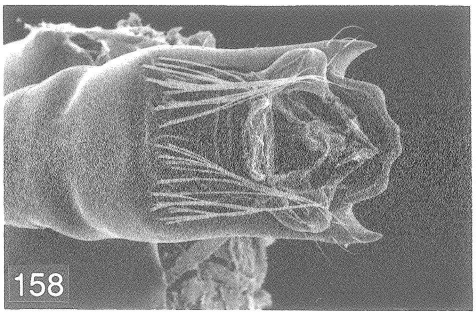
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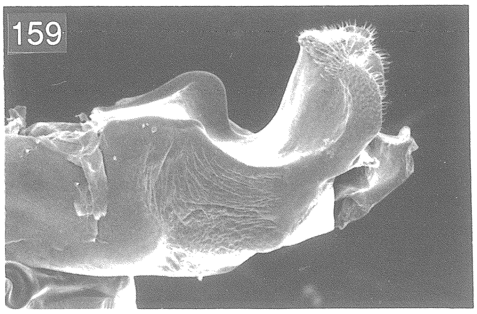
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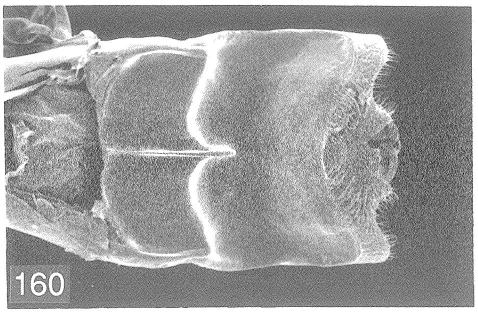
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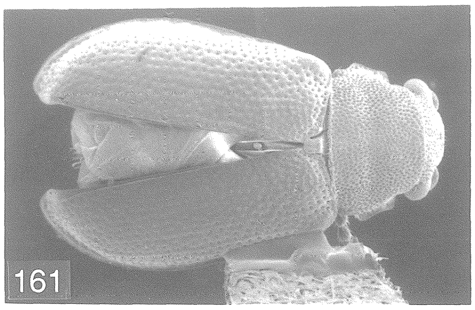
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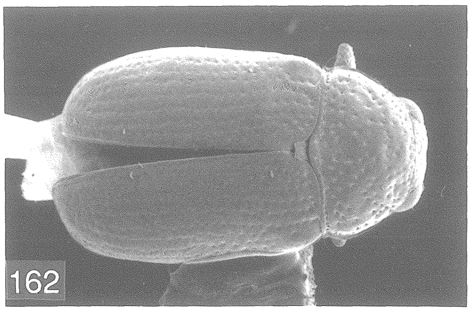
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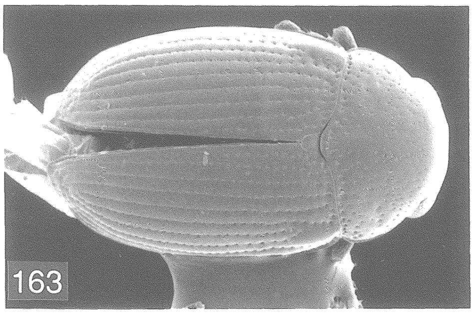
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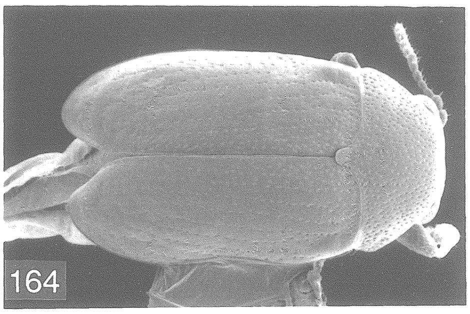
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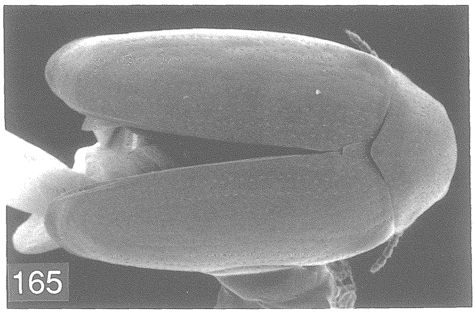
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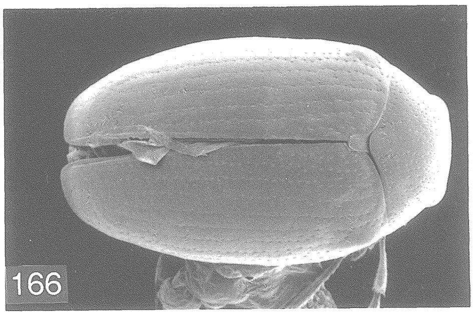
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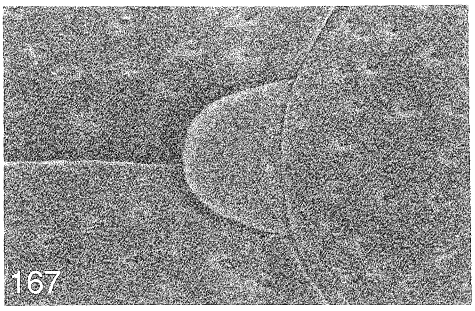
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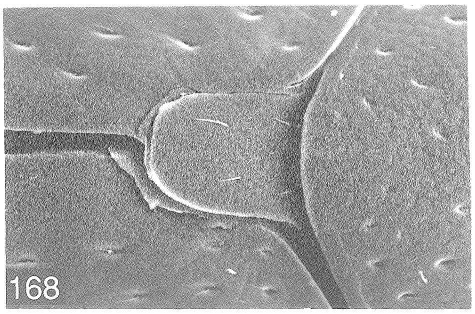
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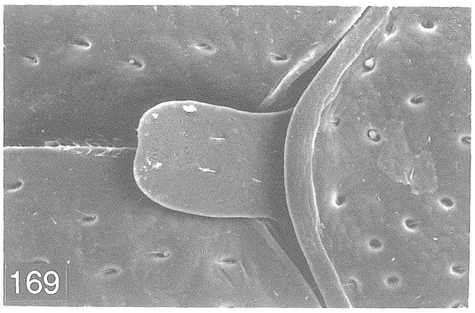
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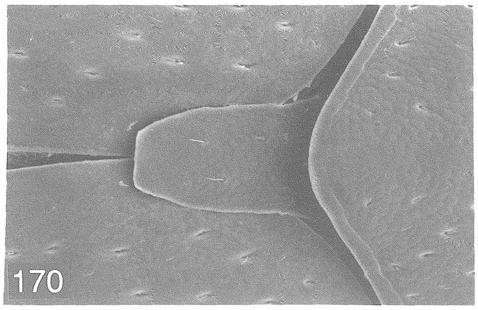
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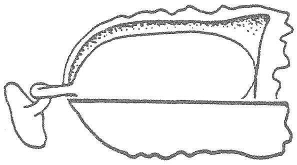

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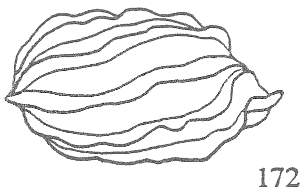

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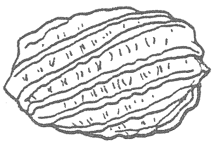

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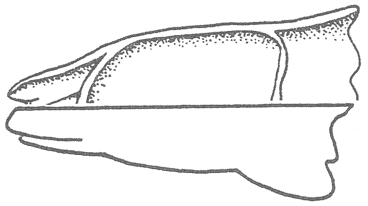

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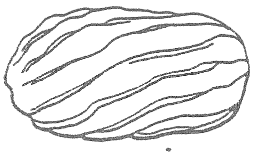

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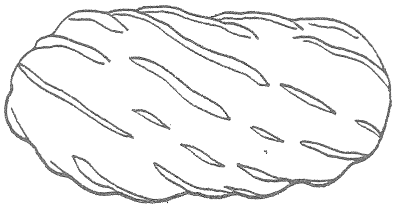

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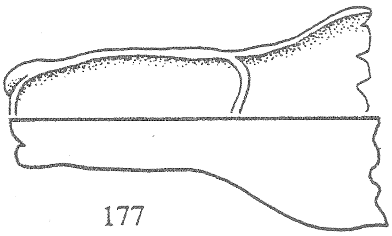

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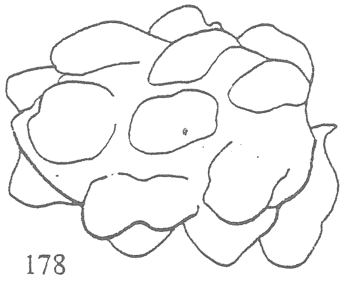

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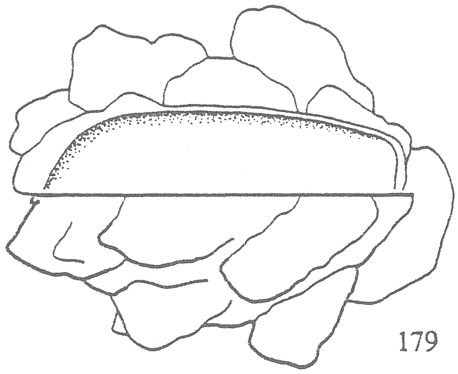

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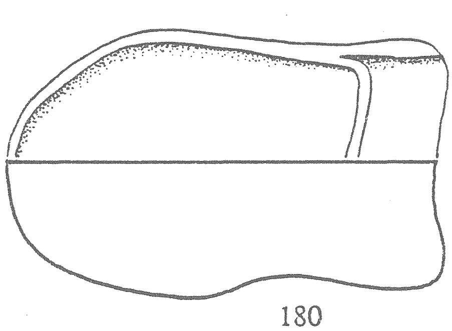

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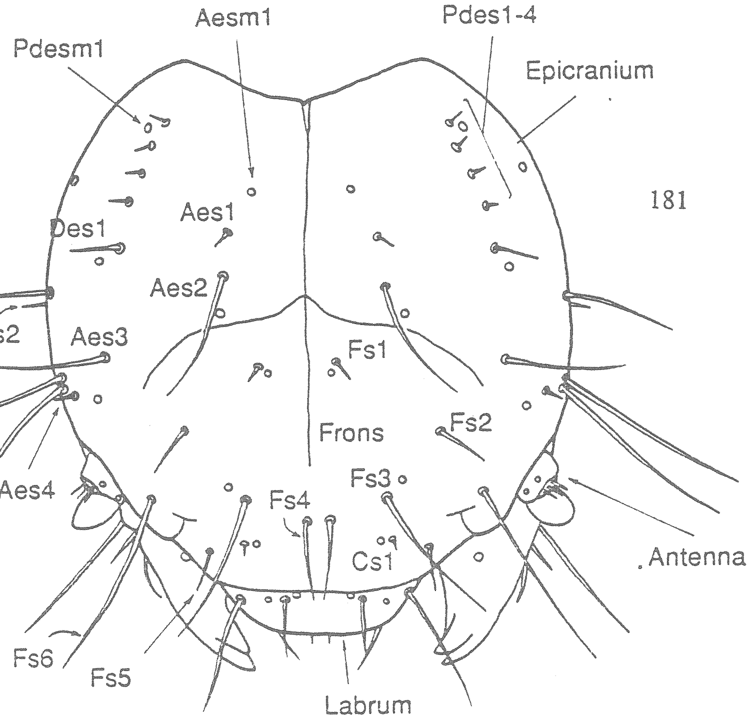

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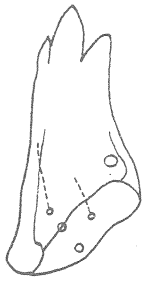

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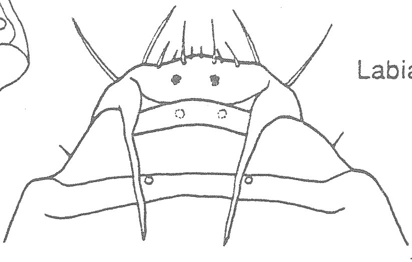

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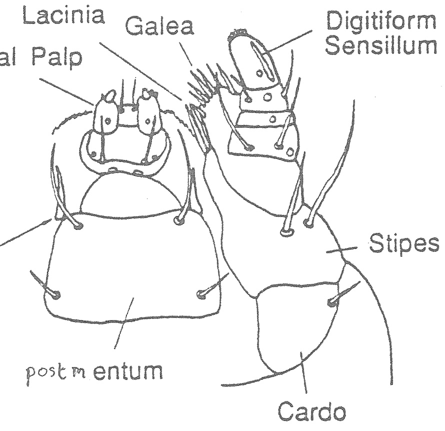

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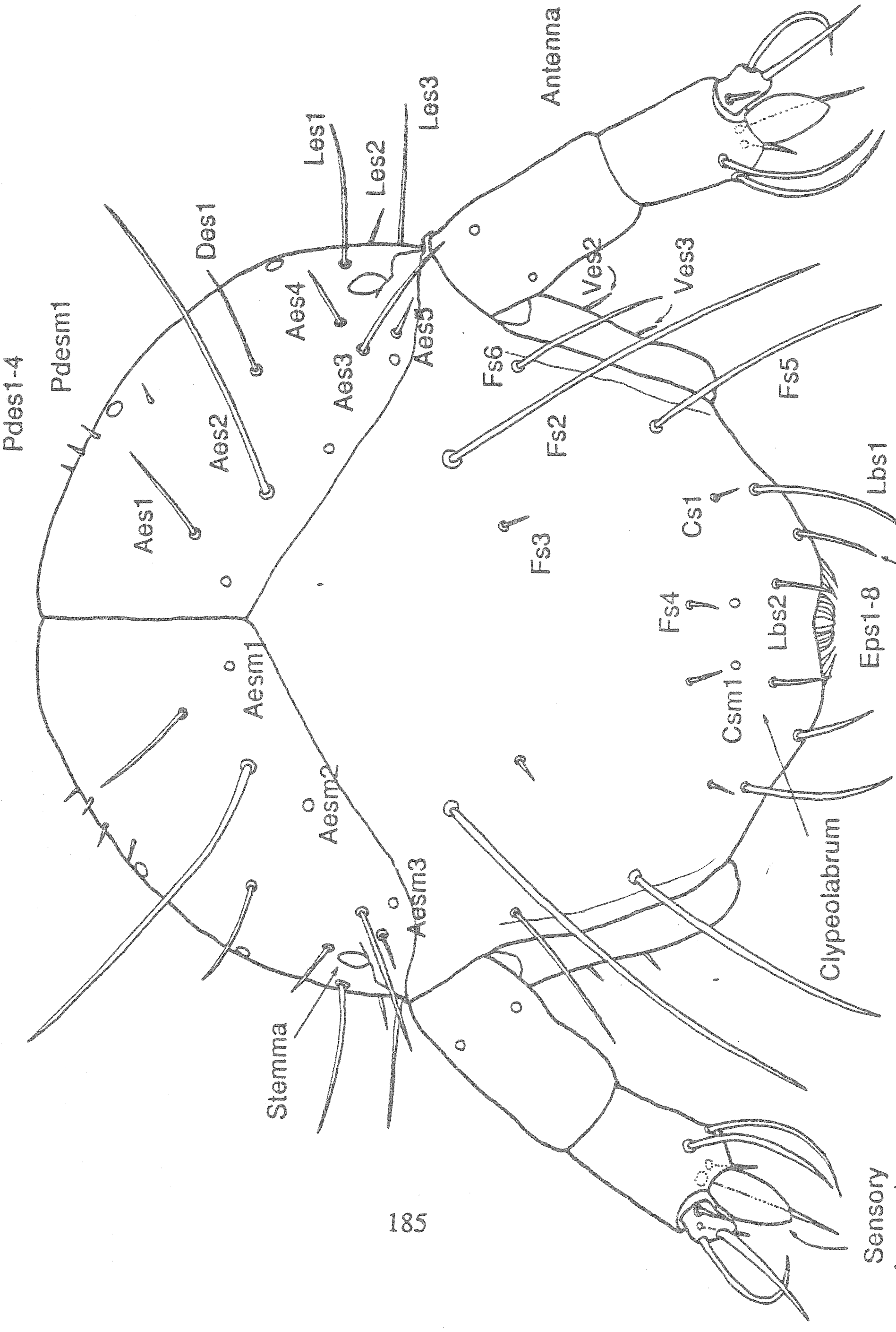
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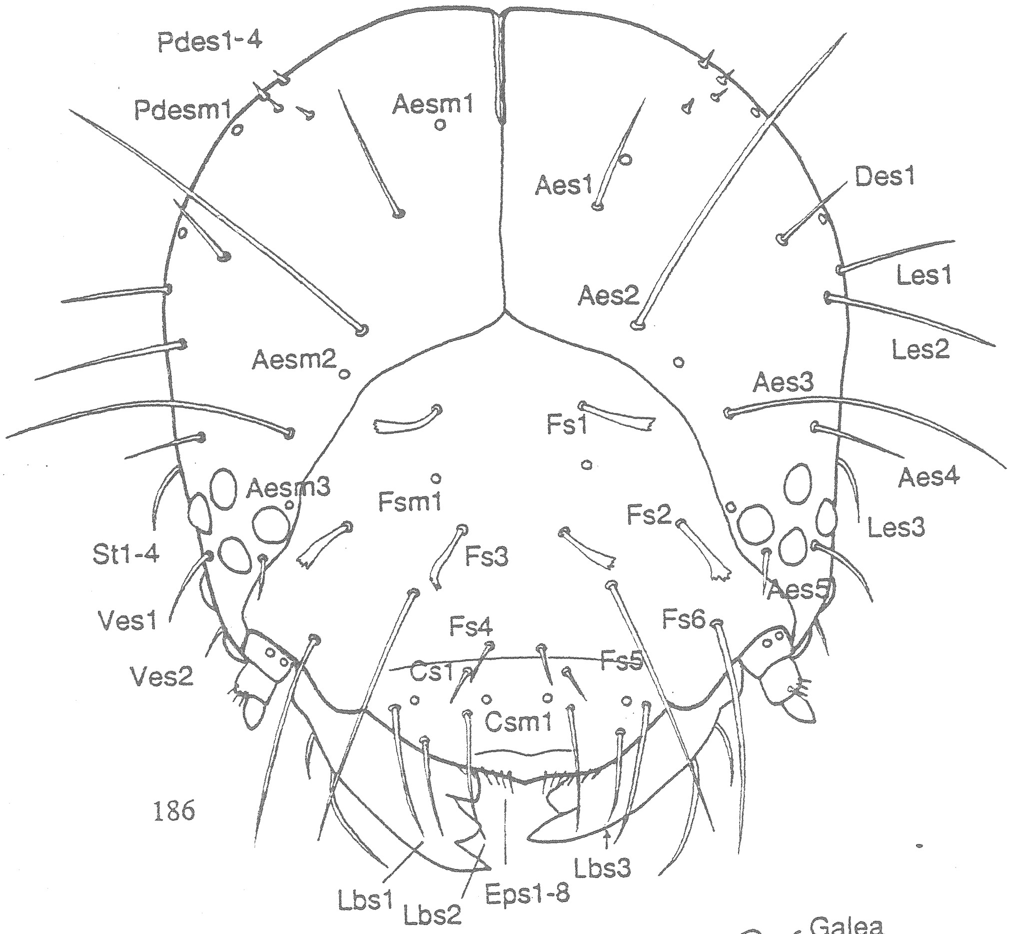
Les1
Les2
Des1
Pdesm1
Pdes1-4
Aes4
Aes5
Aes3
Aes2
Aes1
Ves2
Ves3
Fs6
Fs2
Fs5
Fs3
Lbs1
Cs1
Lbs3
Fs4
Lbs2
Eps1-8
Csm1
Aesm1
Aesm2
Aesm3
Clypeolabrum
Stemma
Sensory
Appendage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Pdesm1
Aesm1
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Des1
Les1
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Les2
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Aes3
Fs1
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Aesm3
Fsm1
Fs2
Les3
St1-4
Fs3
Aes5
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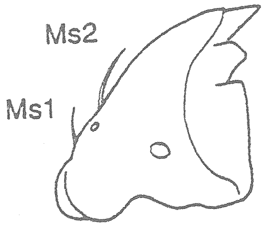
Ms2
Ms1

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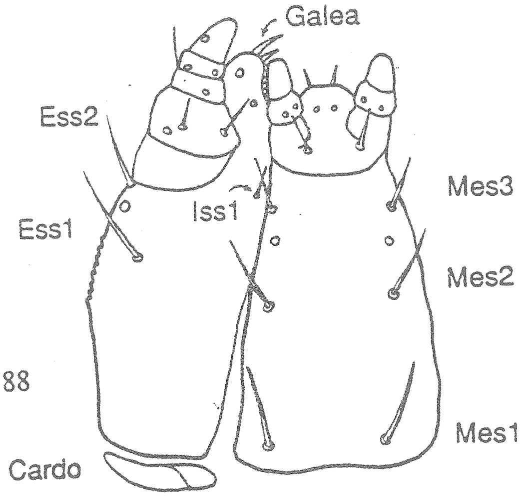
Galea
Ess2
Mes3
Iss1
Ess1
Mes2
Mes1
Cardo

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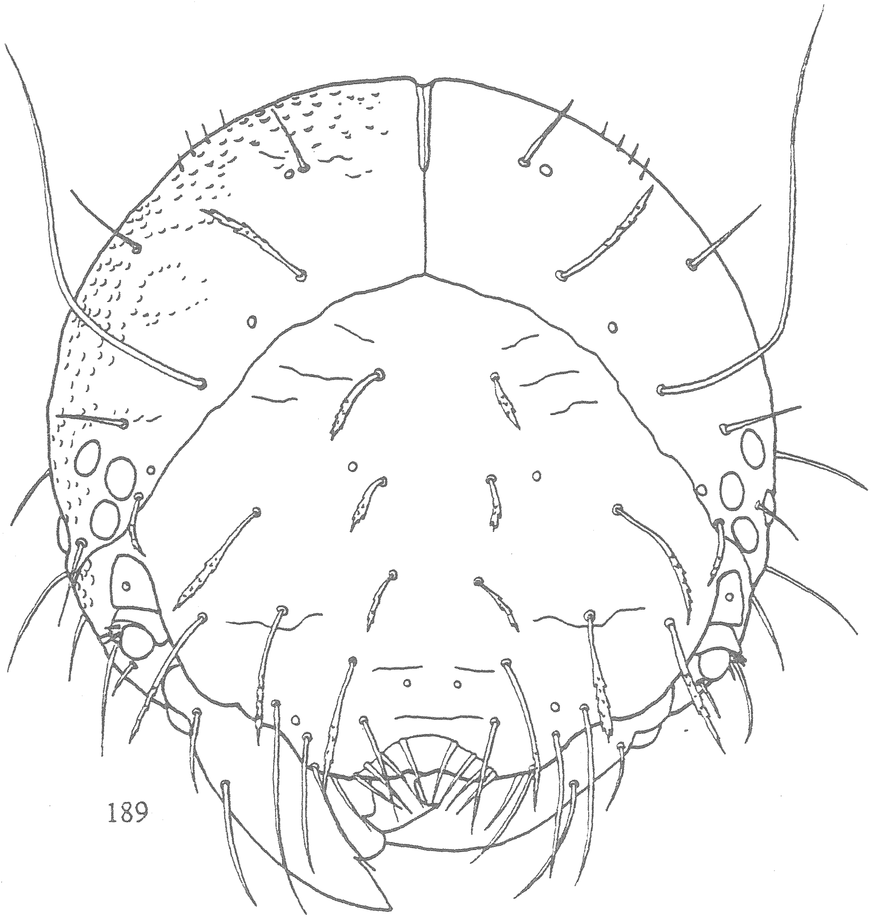

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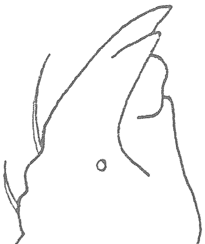

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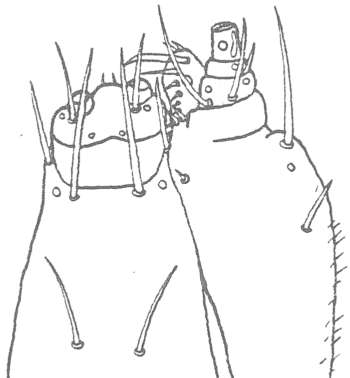

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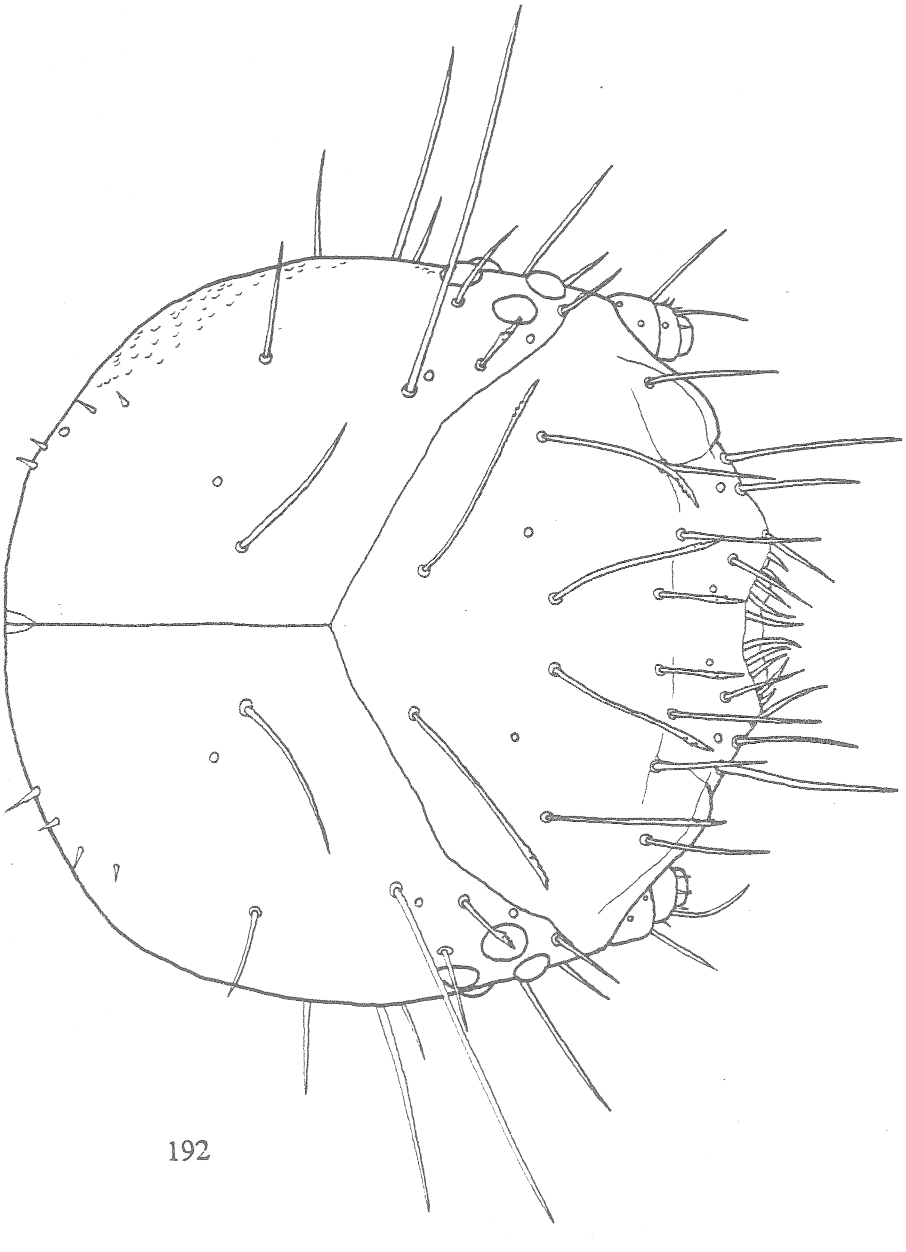

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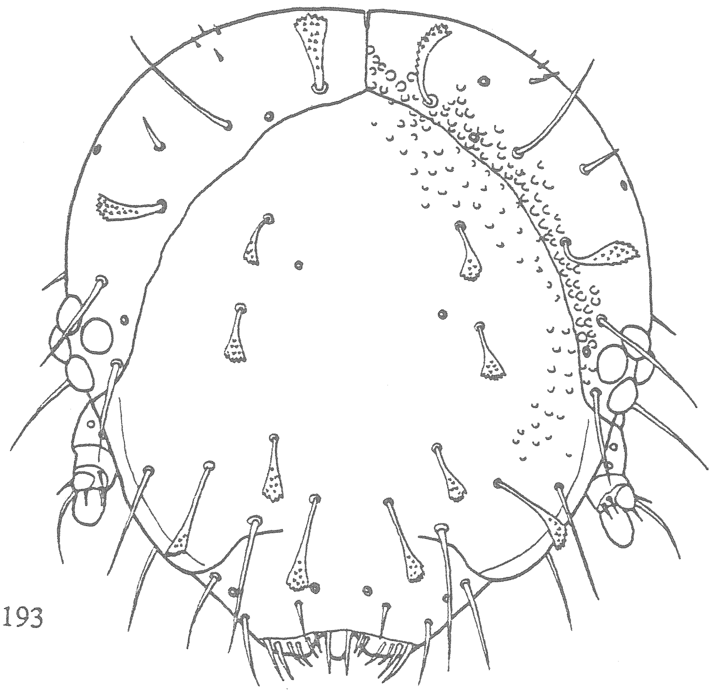
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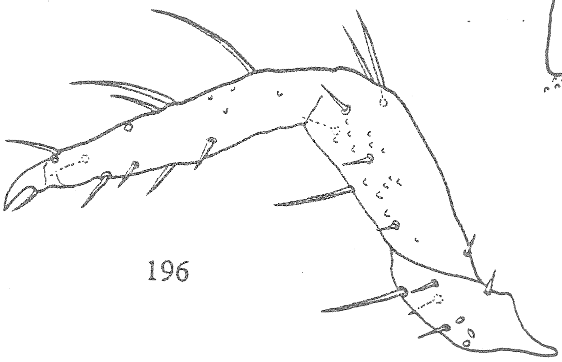
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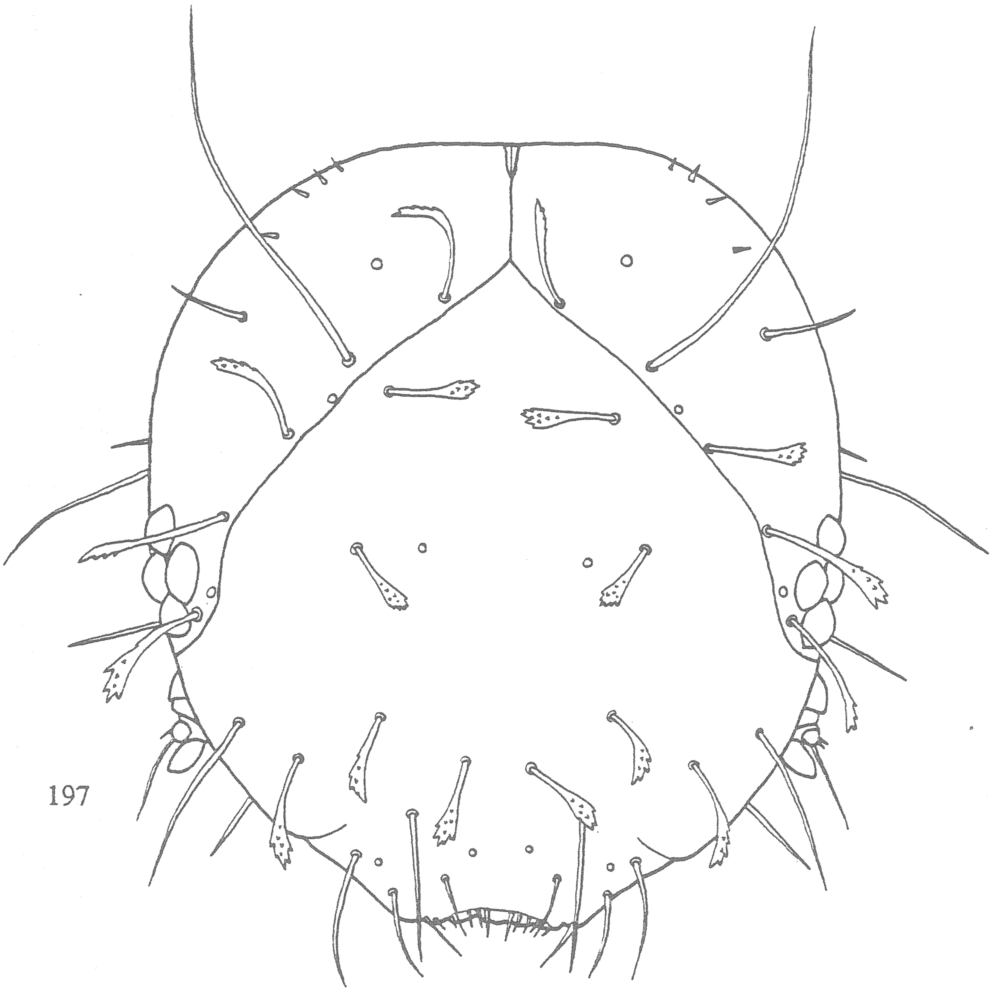
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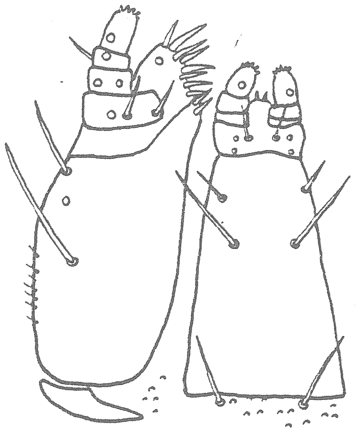
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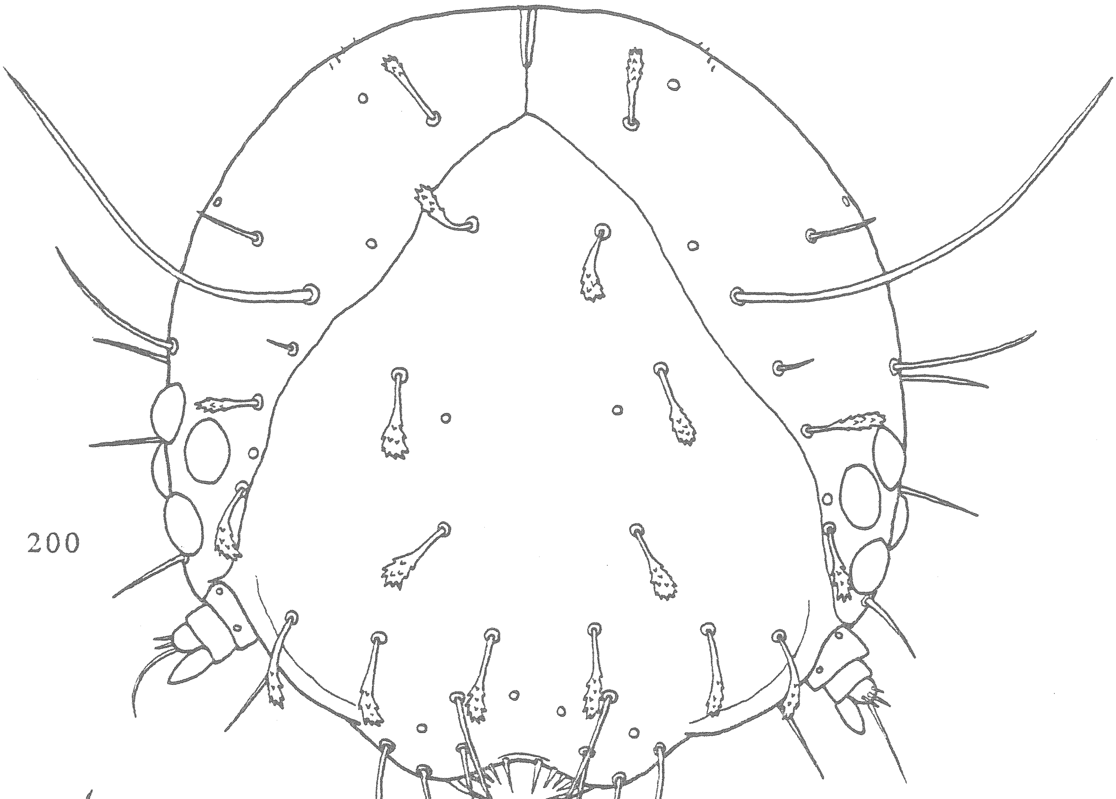

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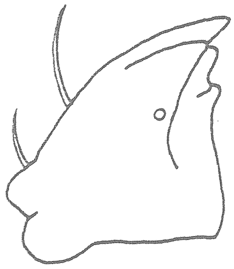

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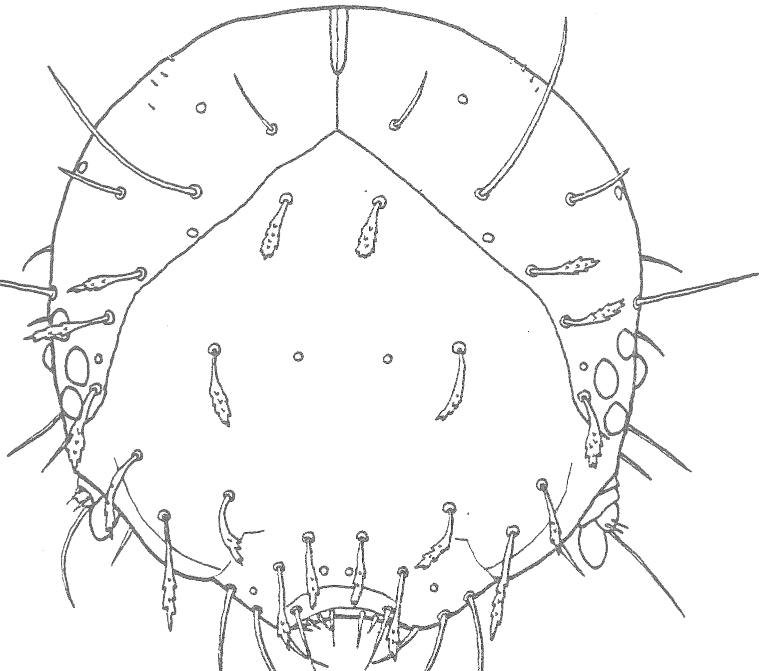

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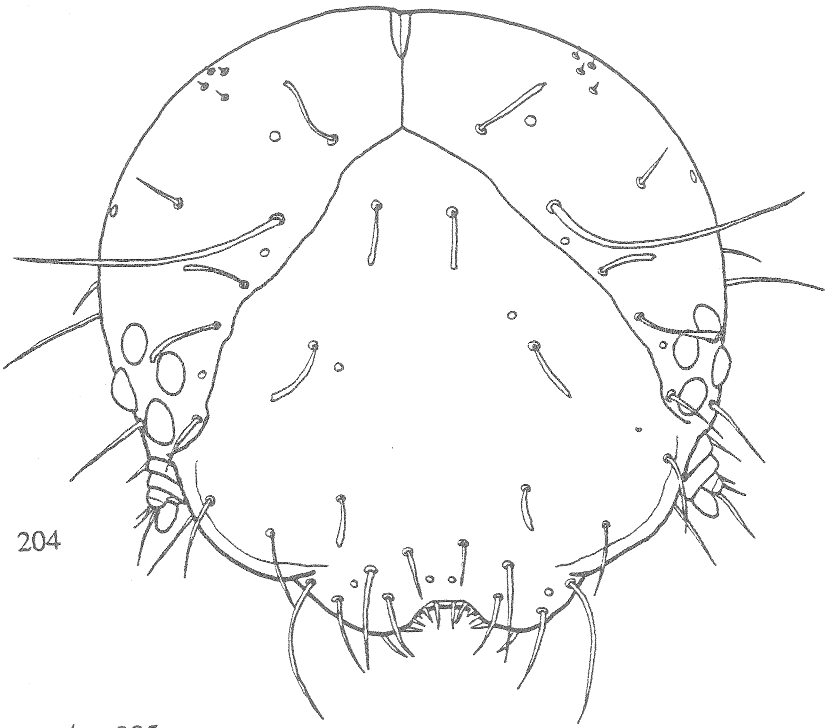

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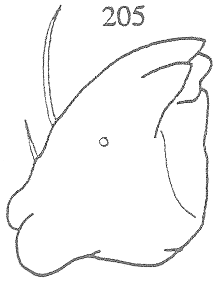

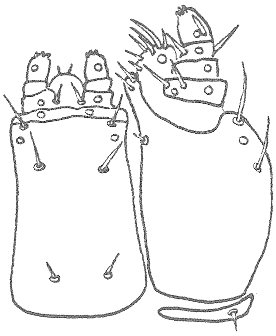

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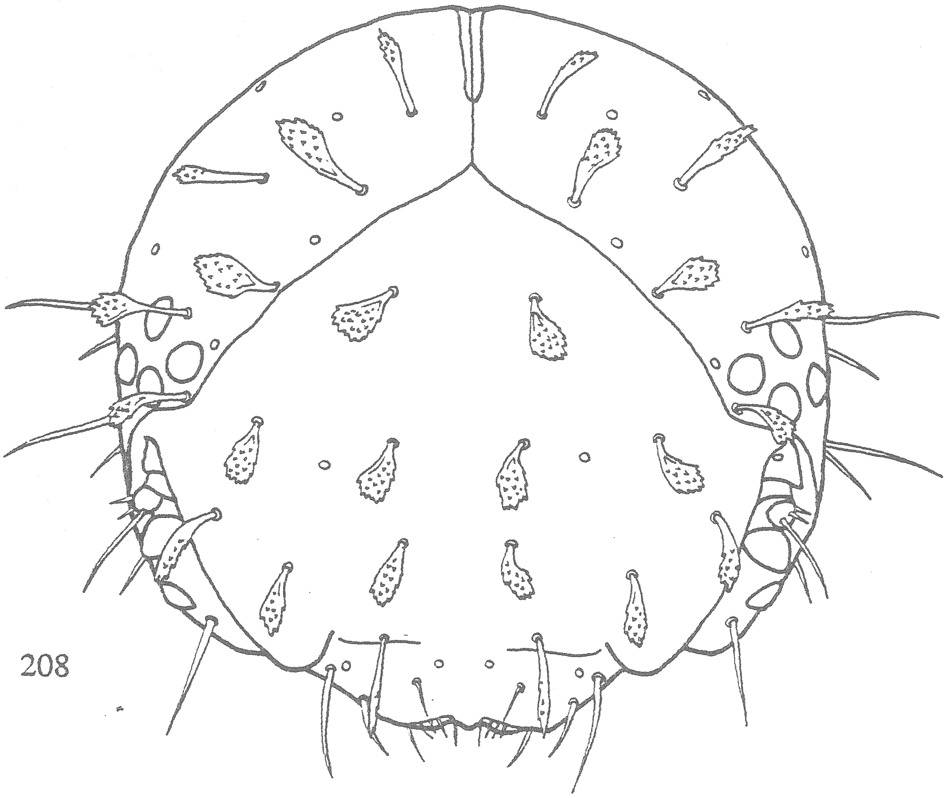

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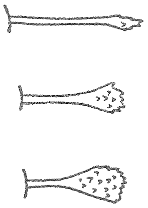

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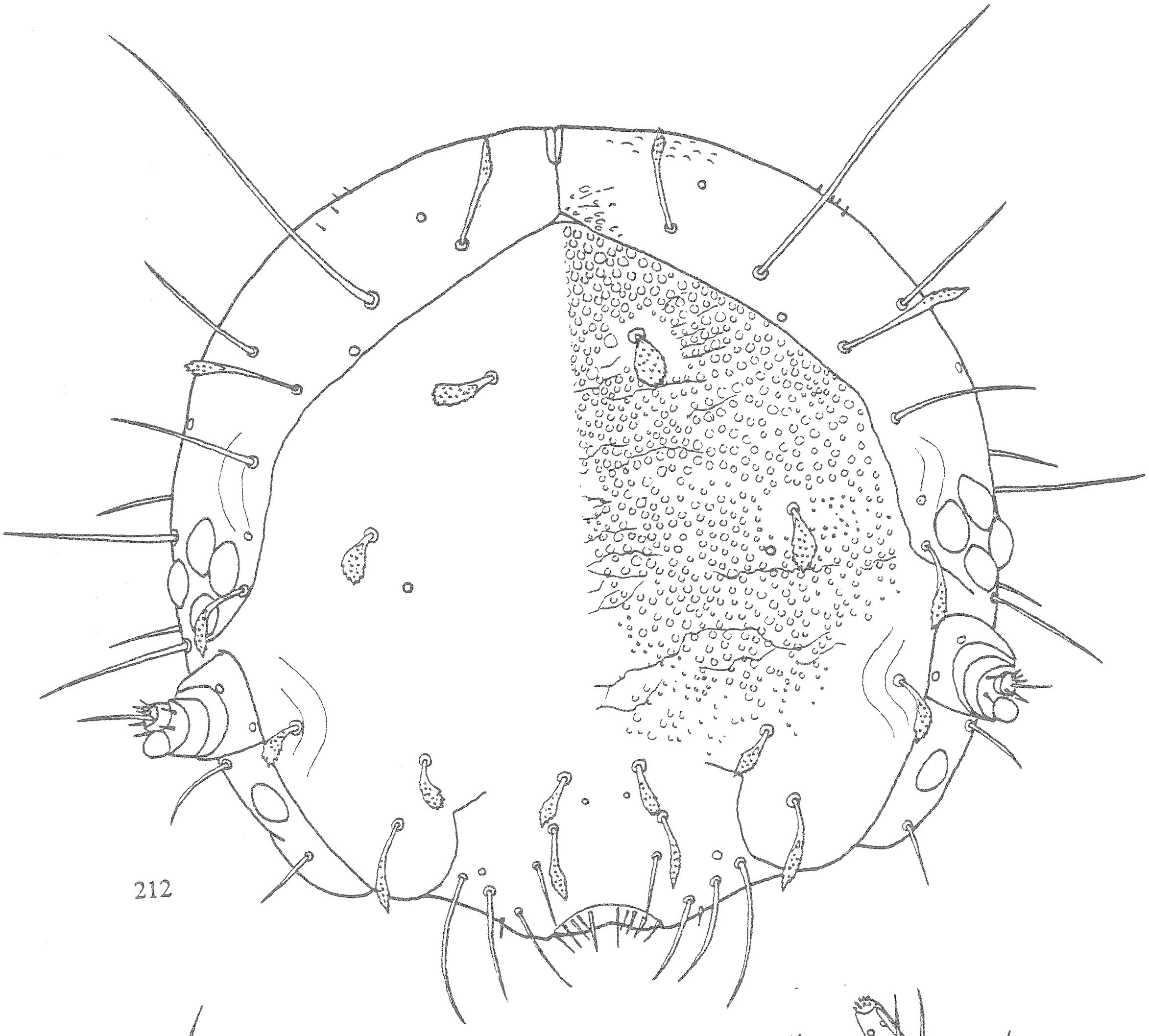

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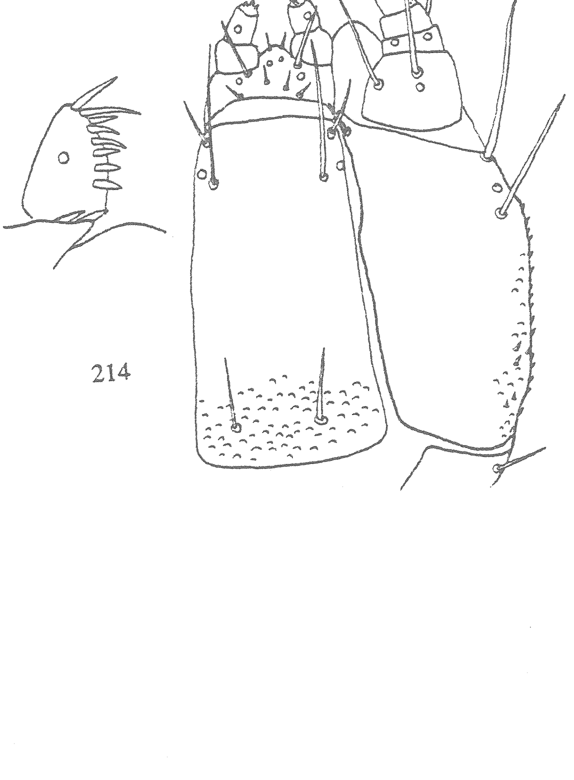

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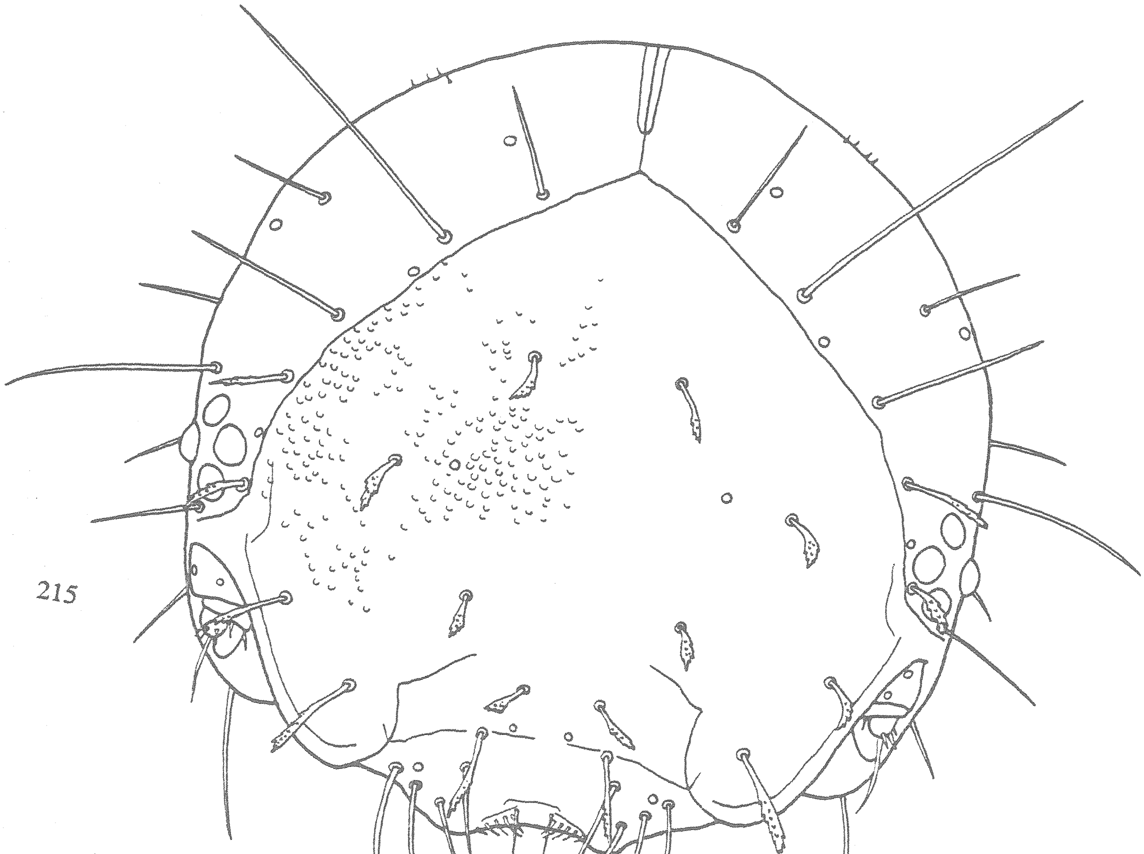

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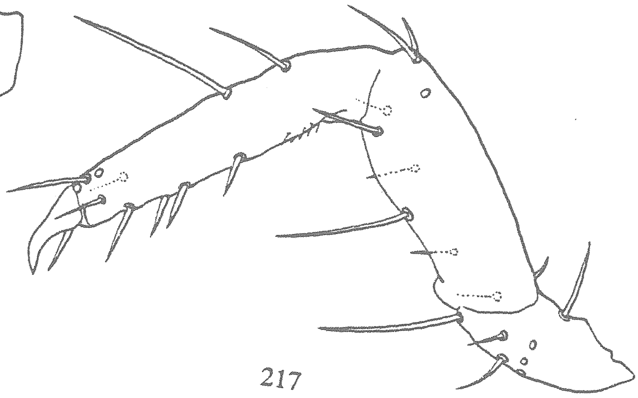

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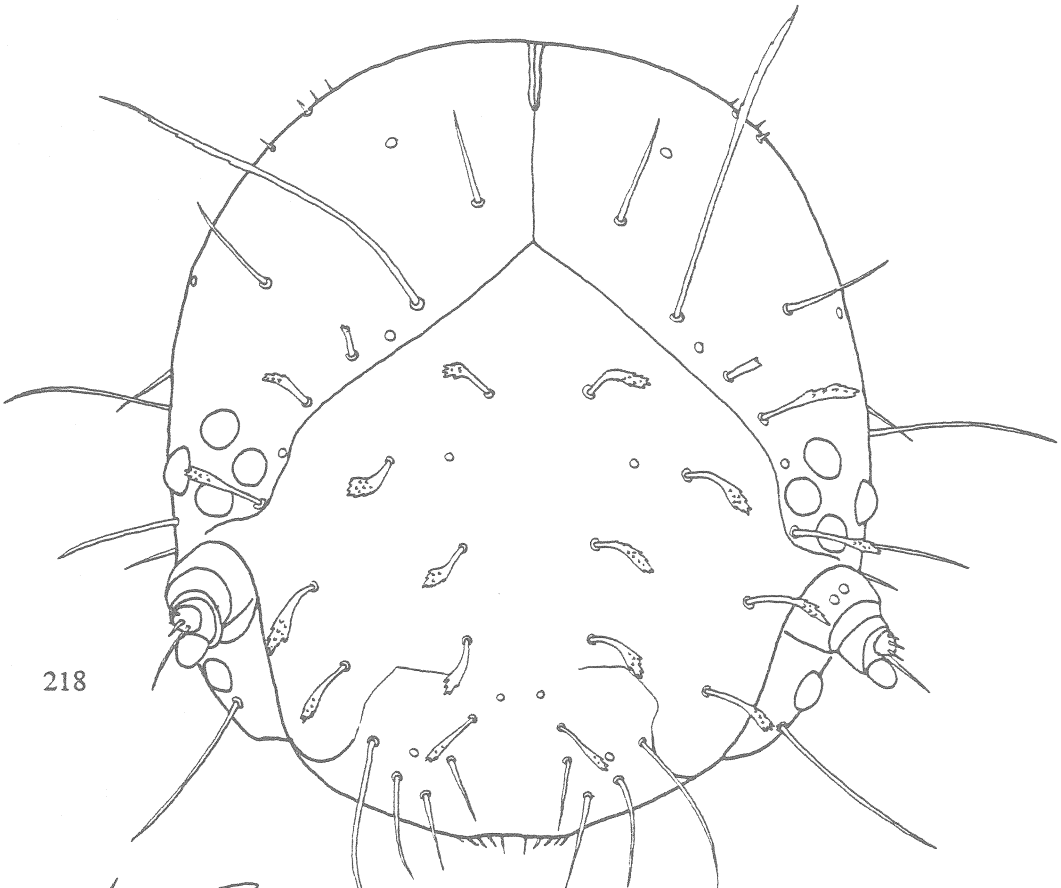

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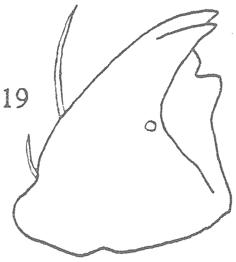

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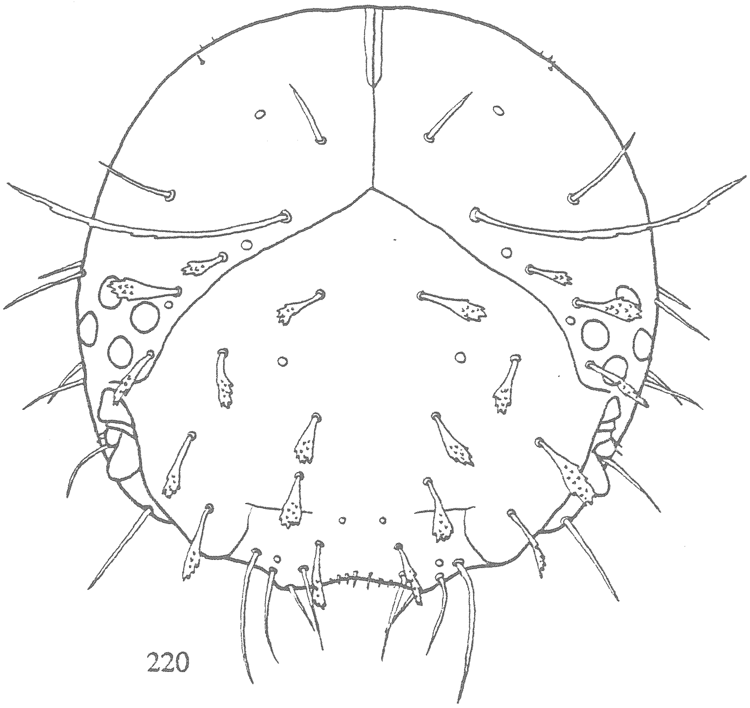

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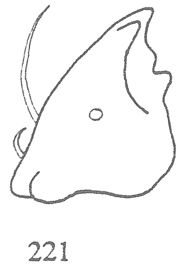

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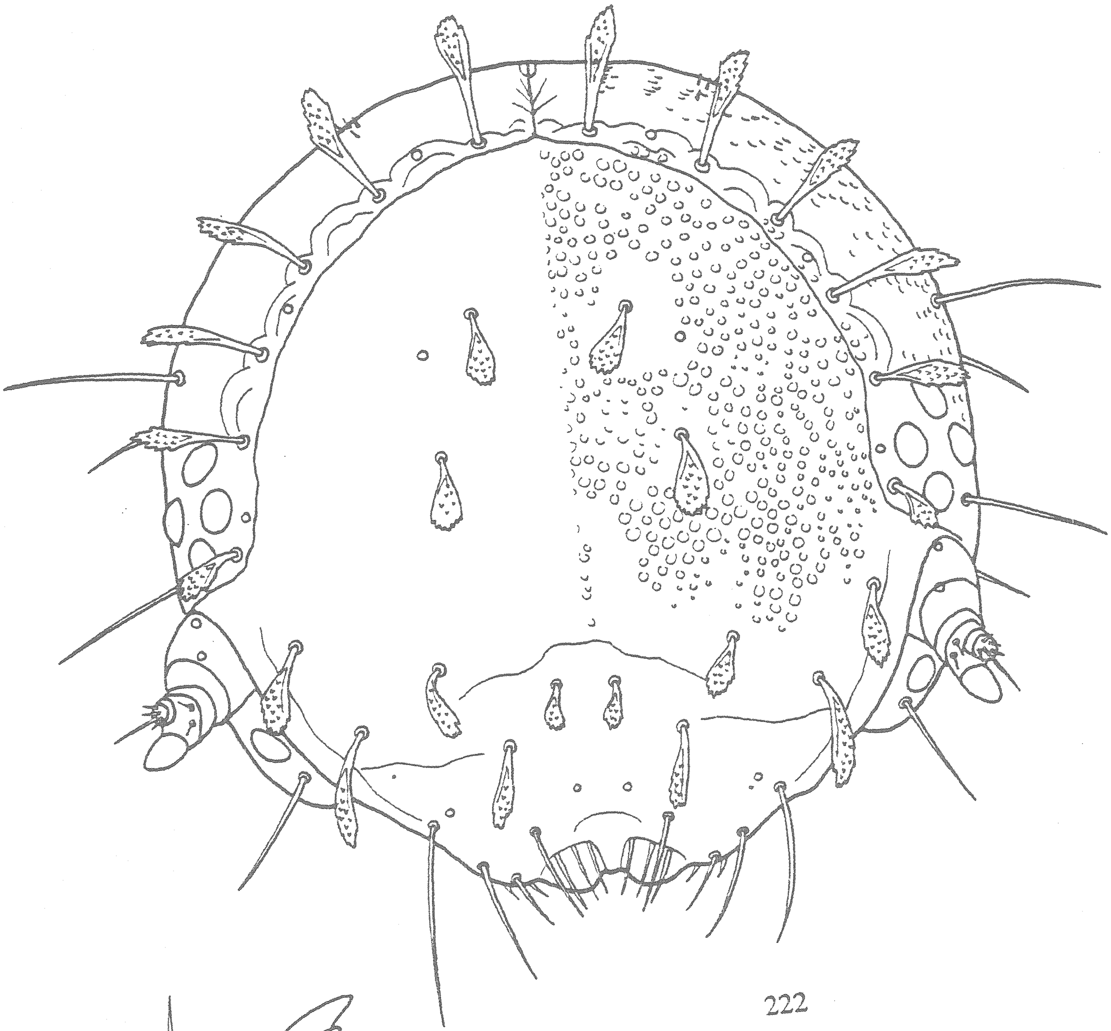

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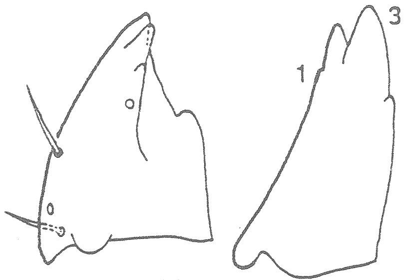

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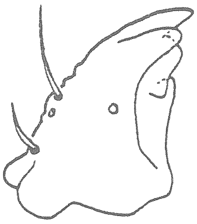

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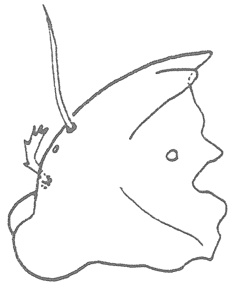

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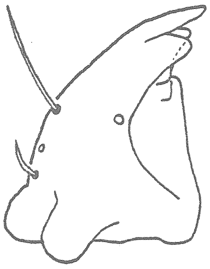

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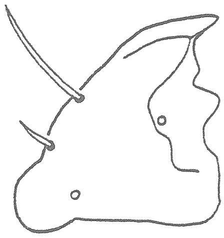

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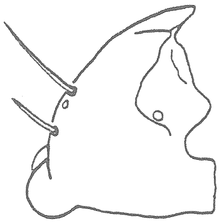

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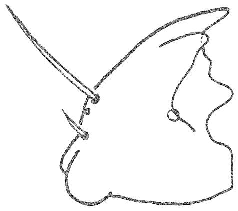

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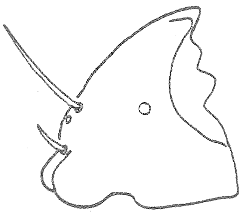

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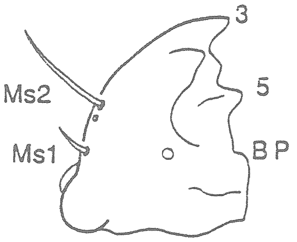

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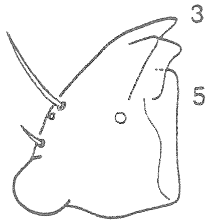

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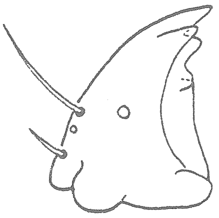

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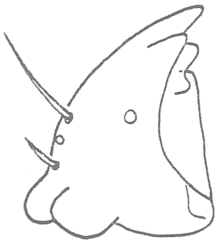

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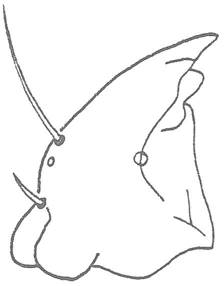

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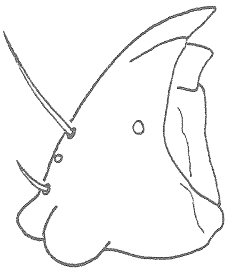

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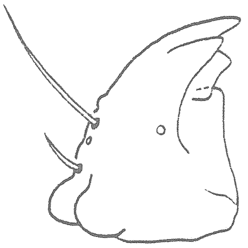

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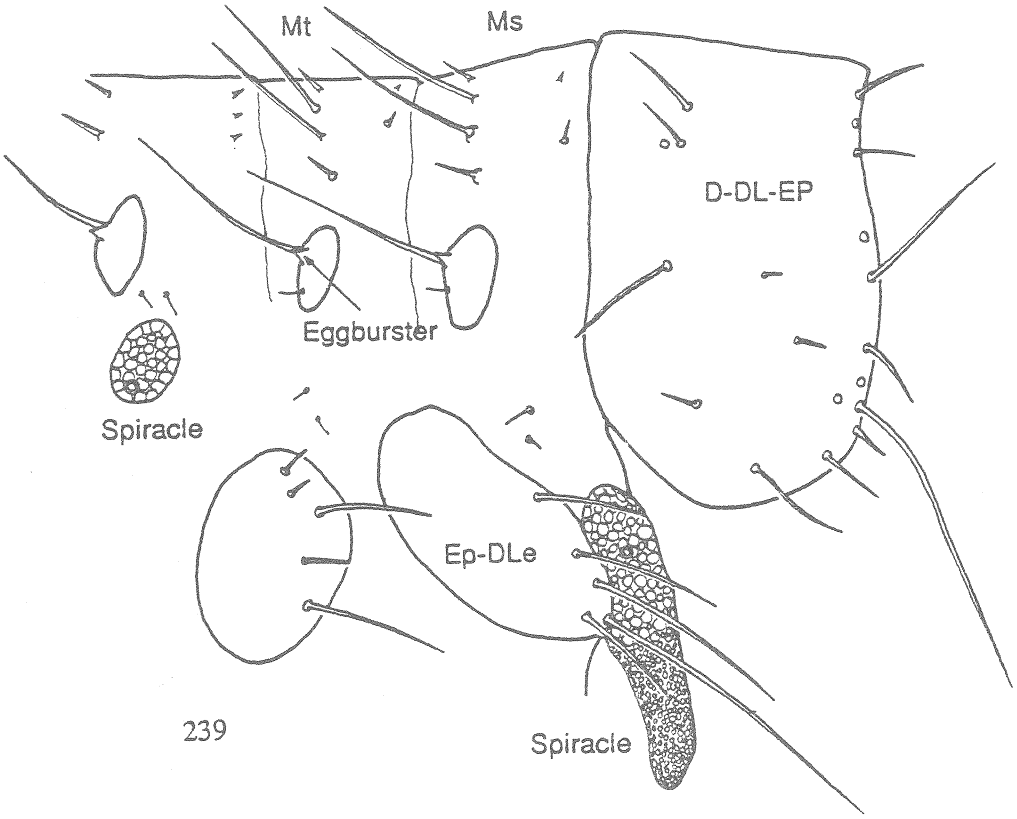
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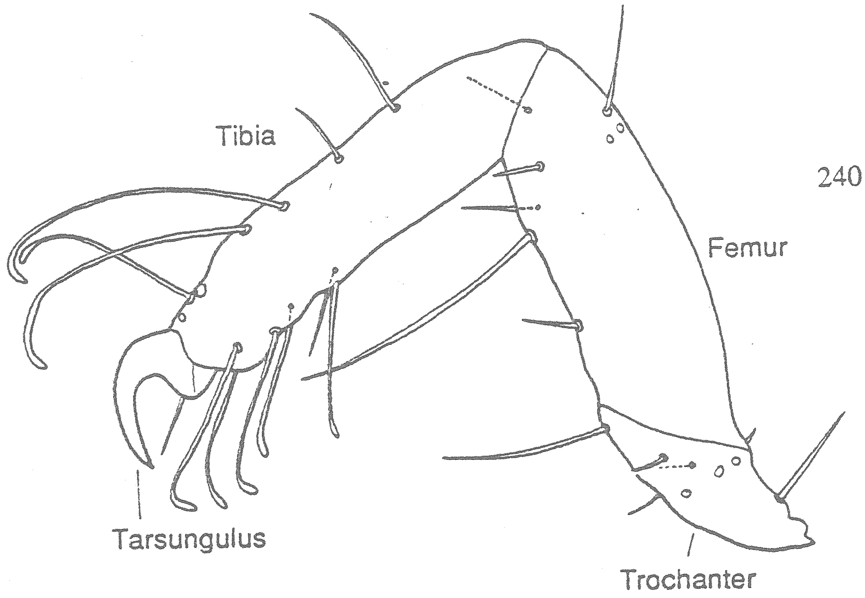
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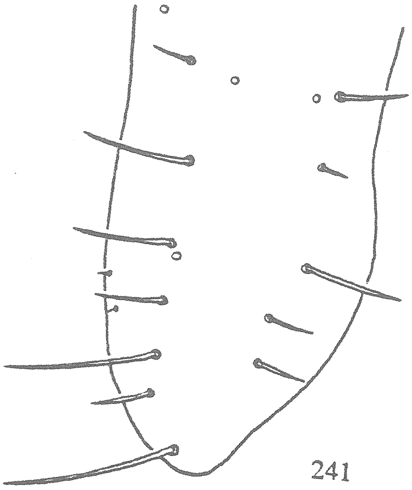
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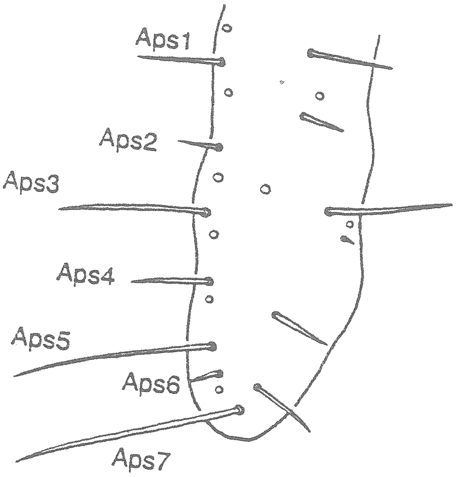

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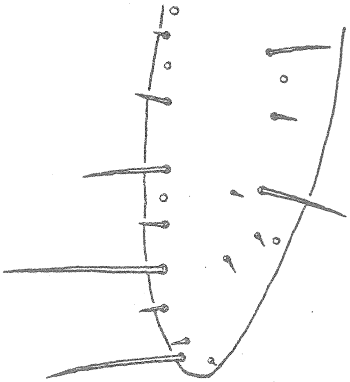
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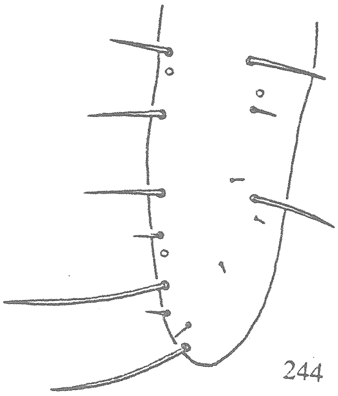
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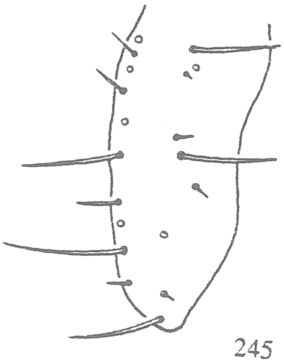
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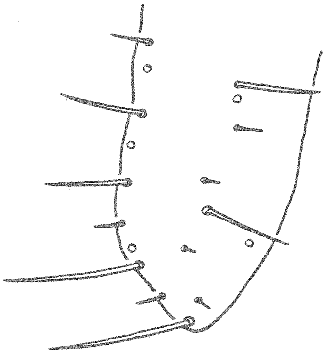
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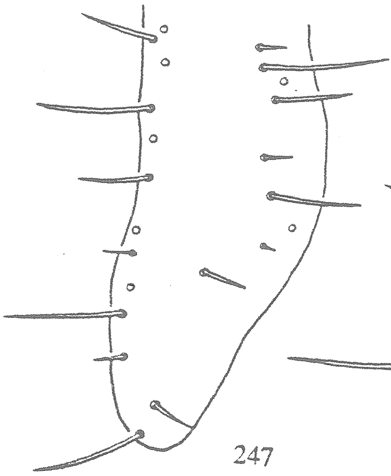
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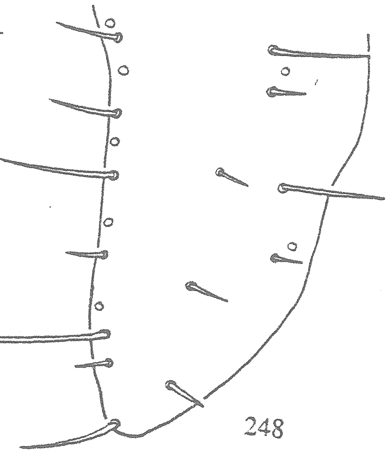
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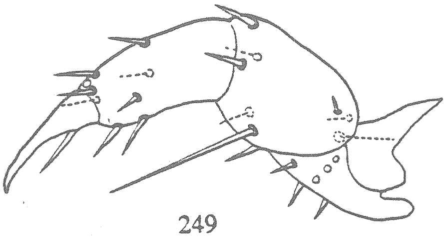

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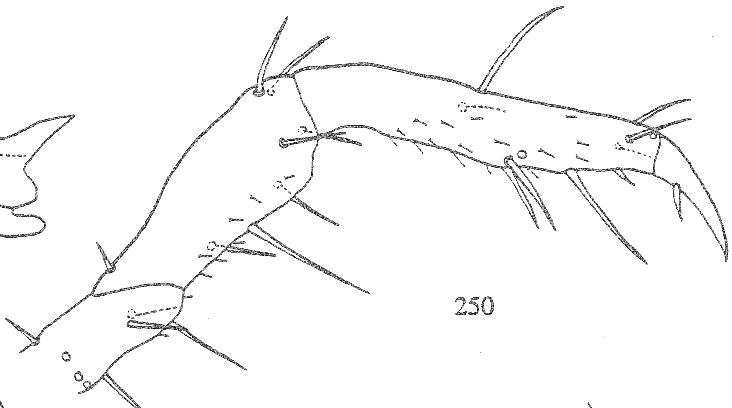

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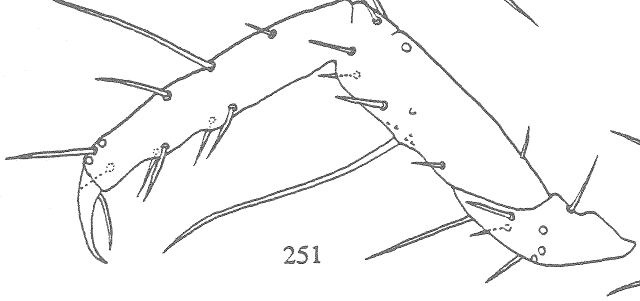

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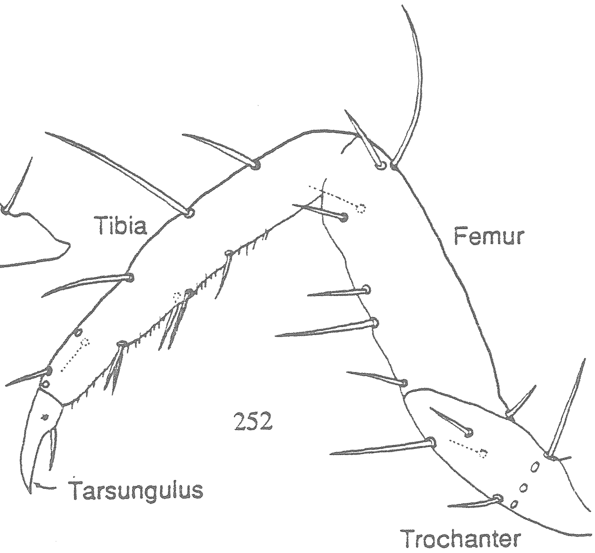

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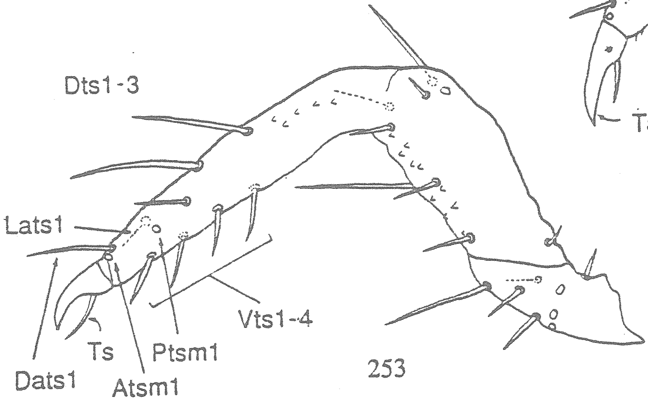

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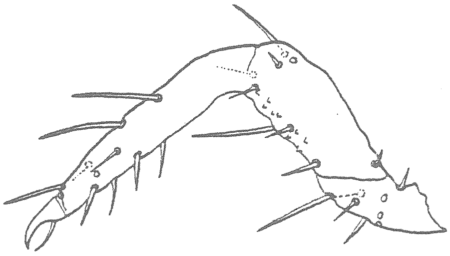

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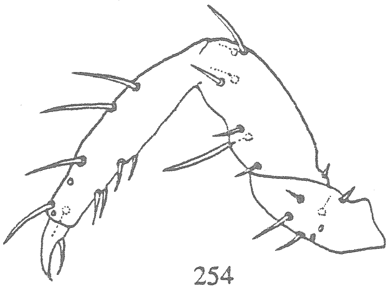

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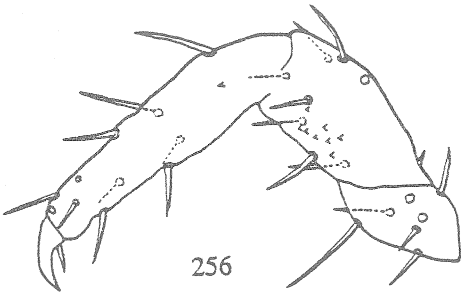

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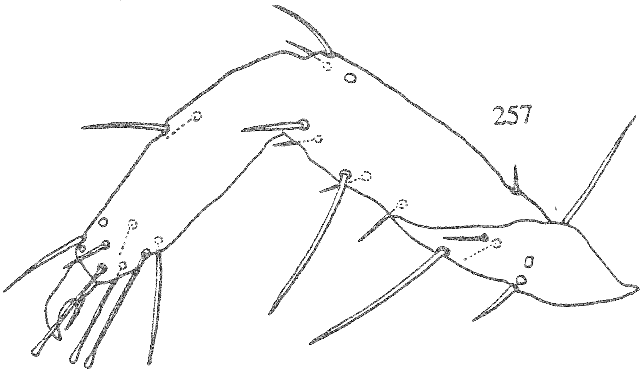

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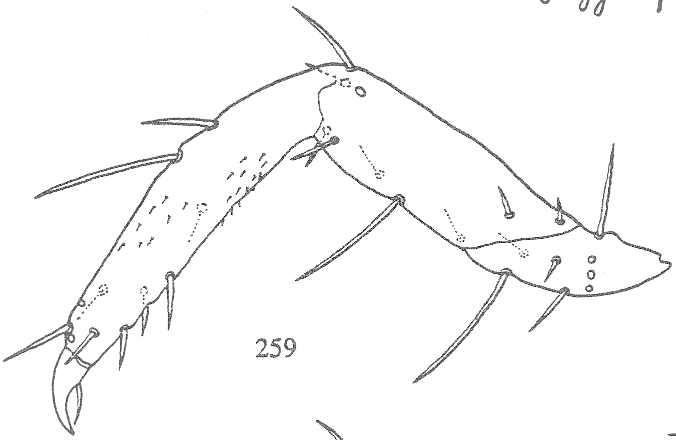

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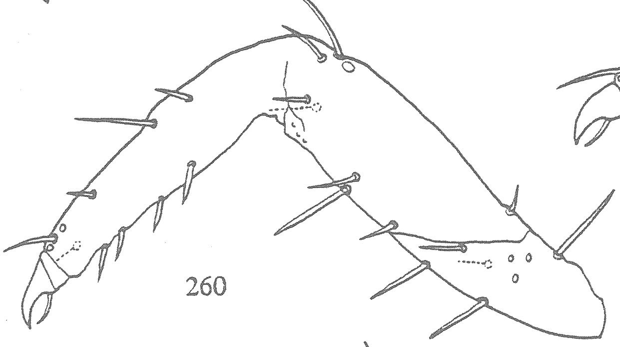

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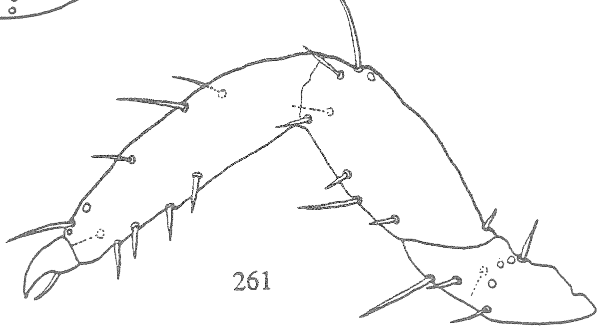

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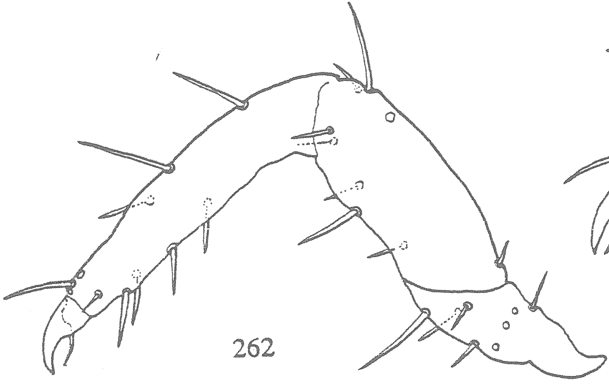

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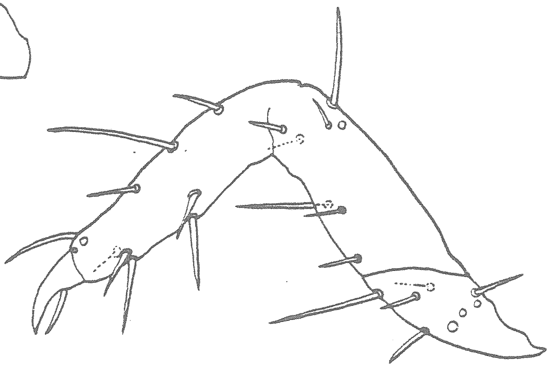

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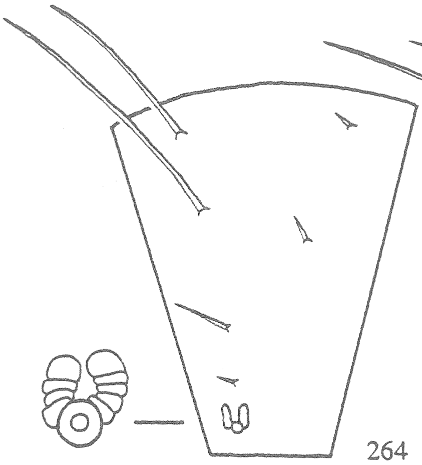

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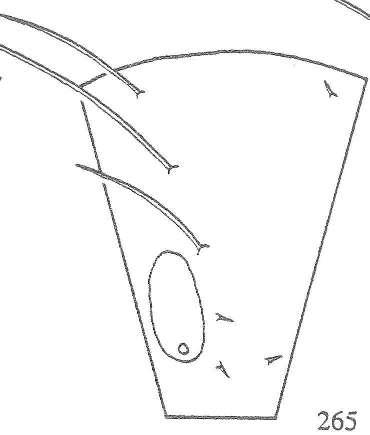

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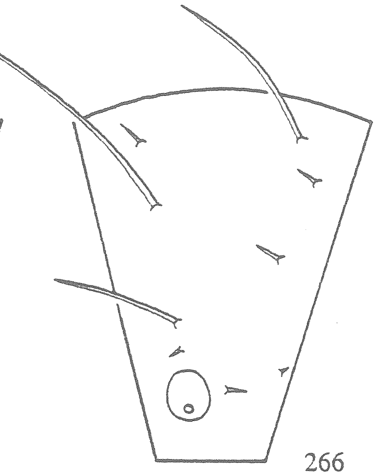

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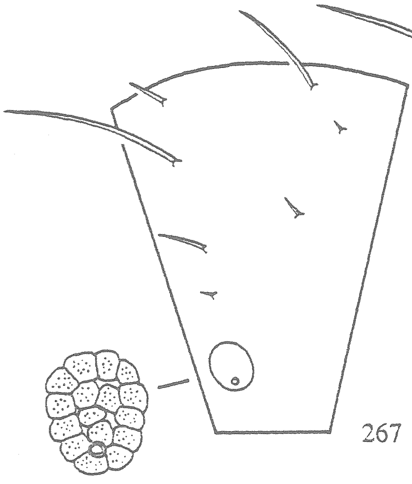

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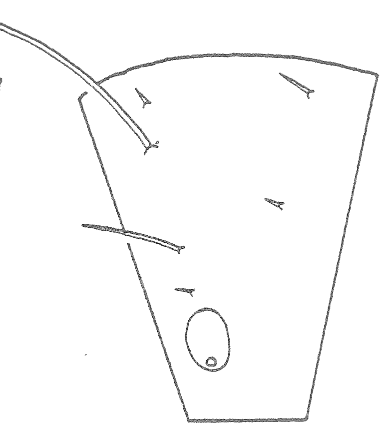

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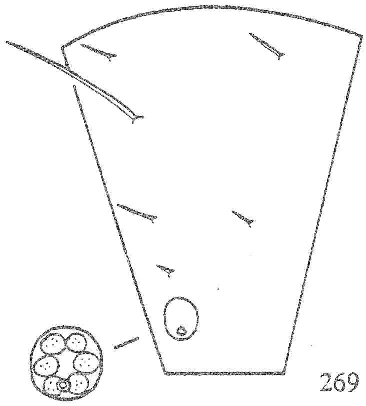

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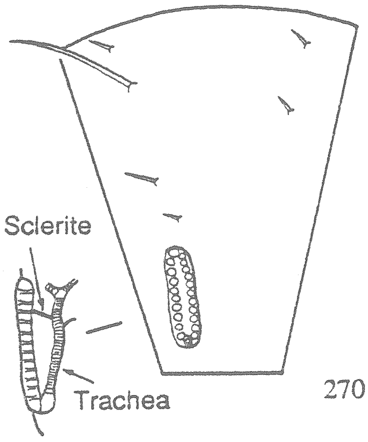

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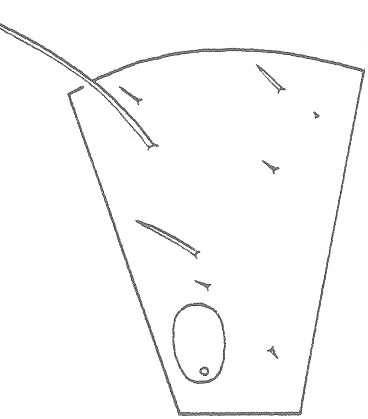

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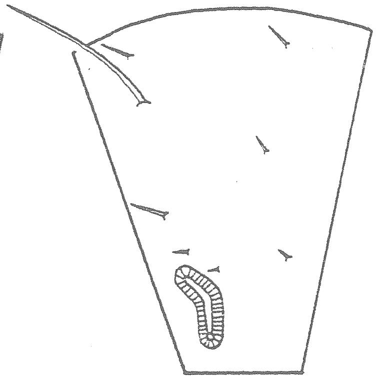

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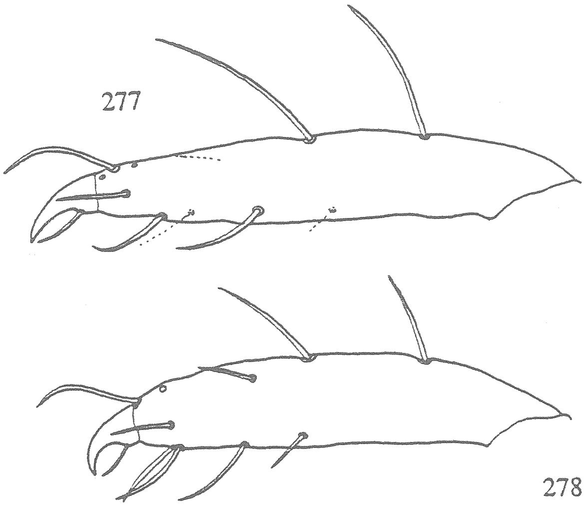
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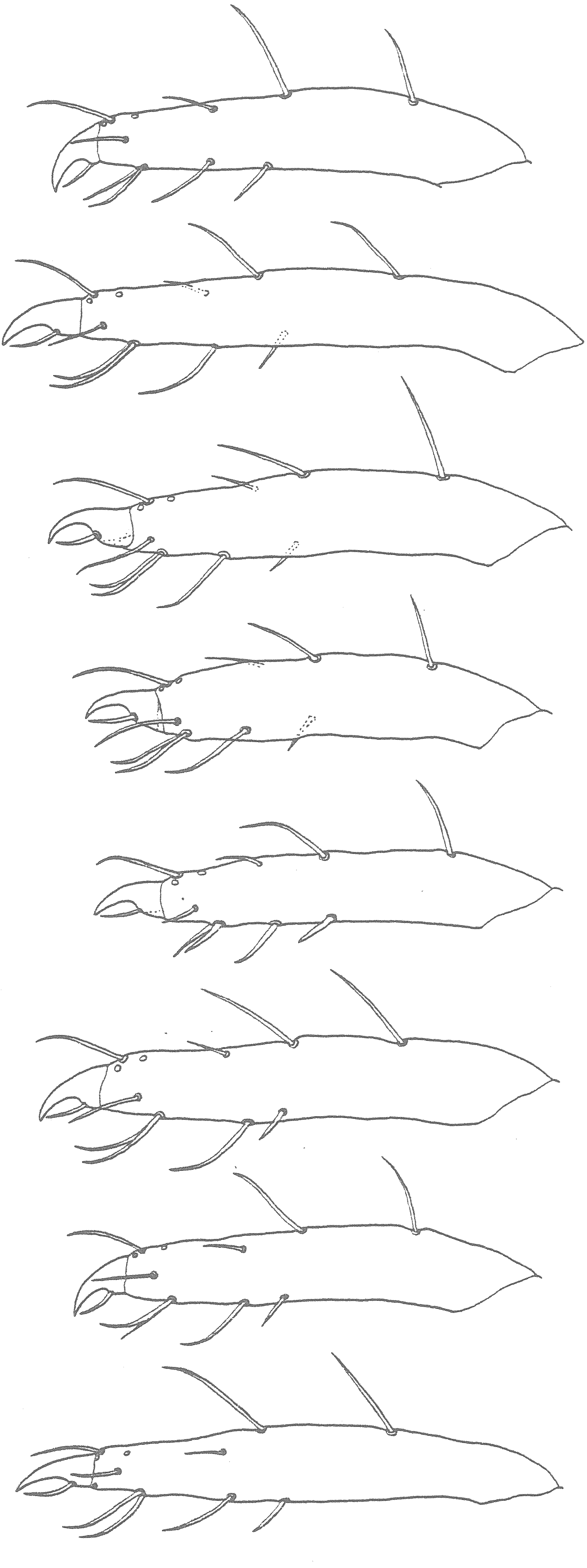
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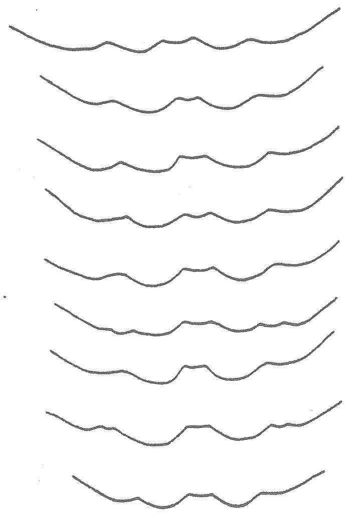
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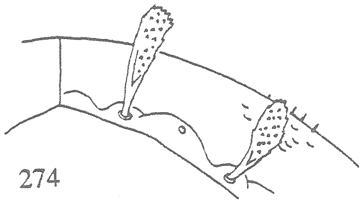
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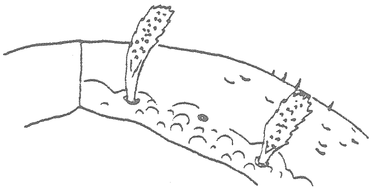
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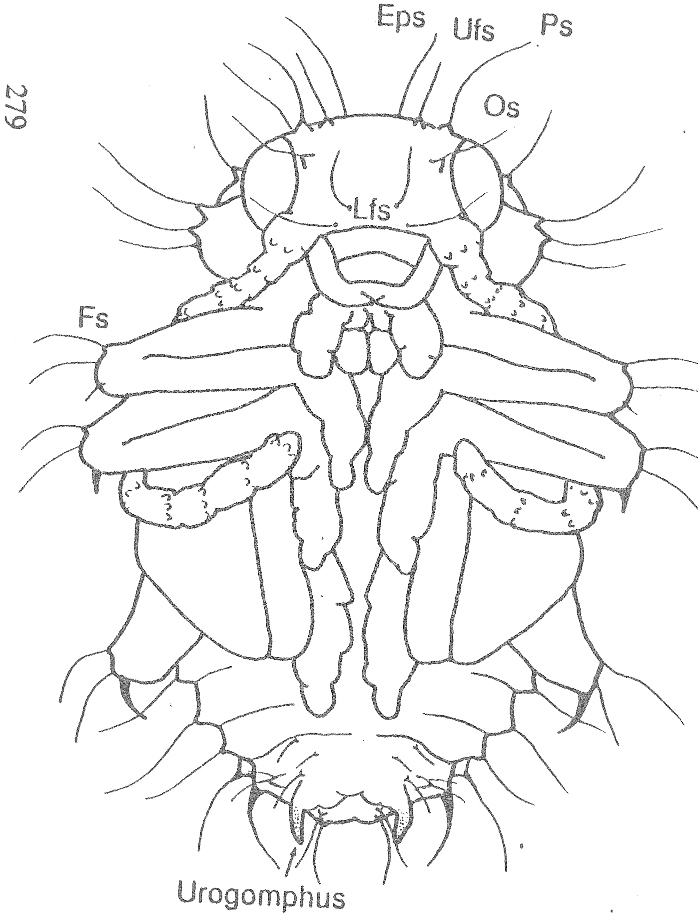

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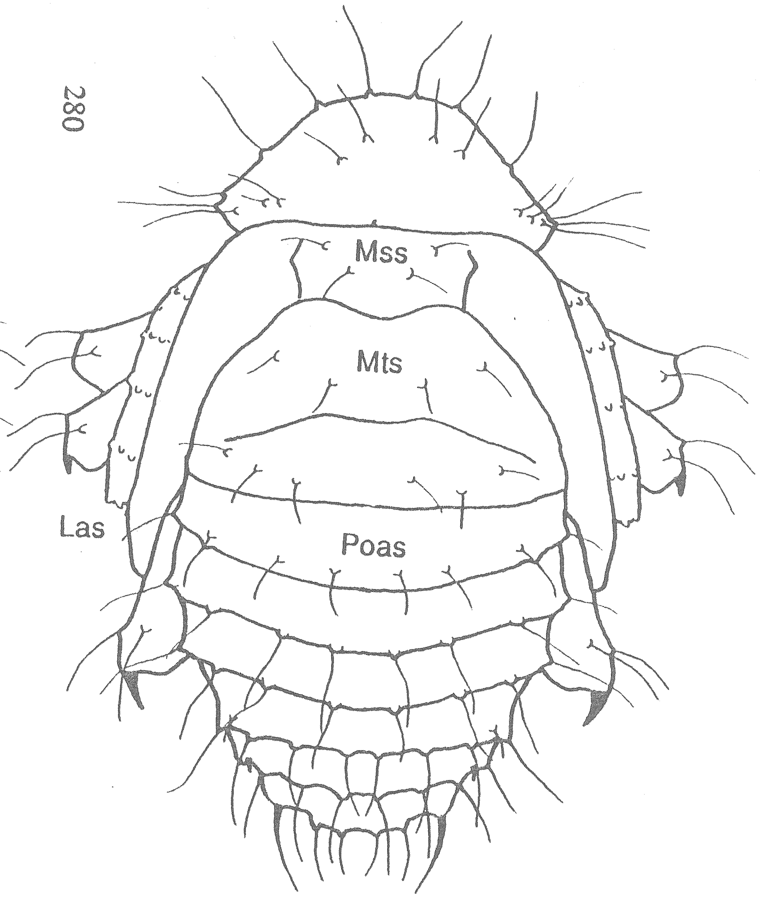

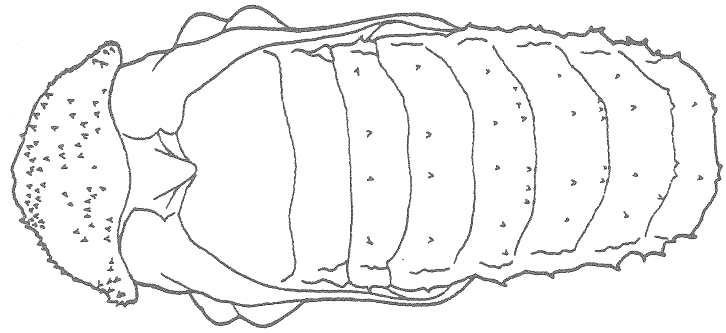

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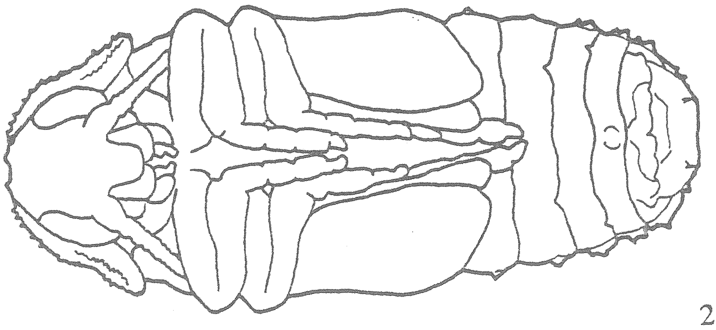

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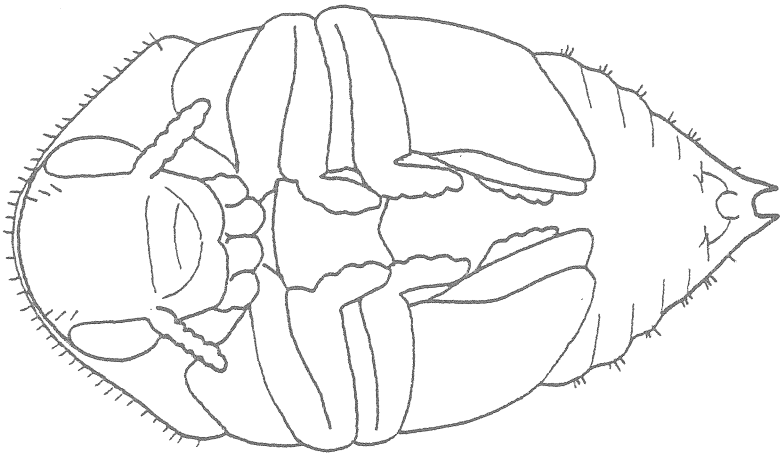

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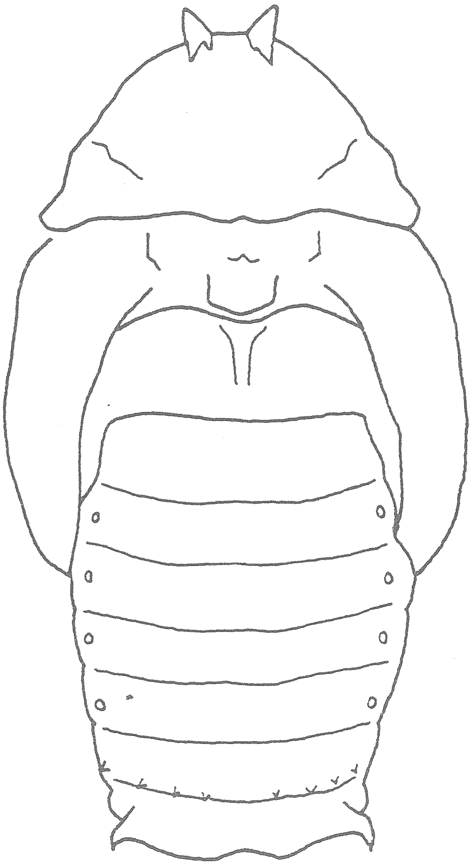

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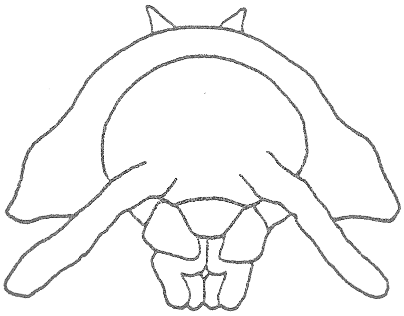

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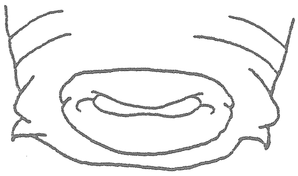

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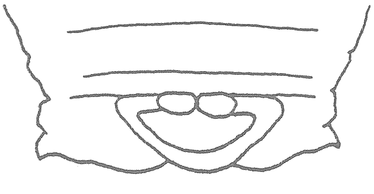

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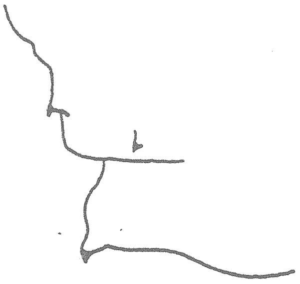

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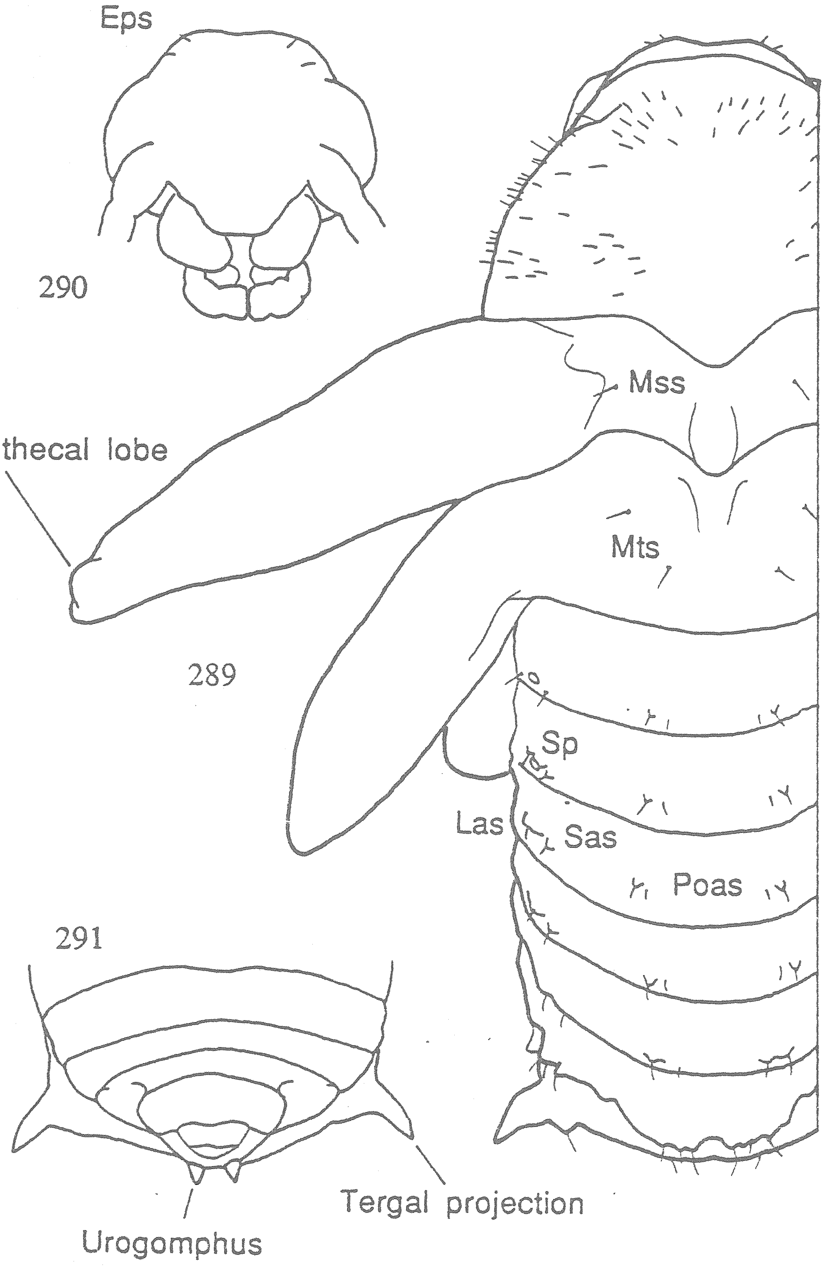
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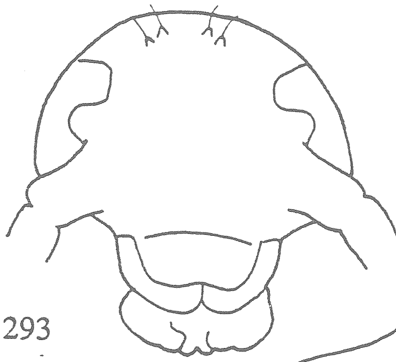

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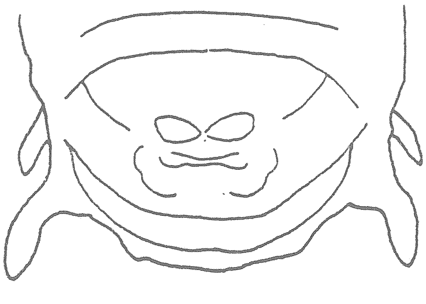

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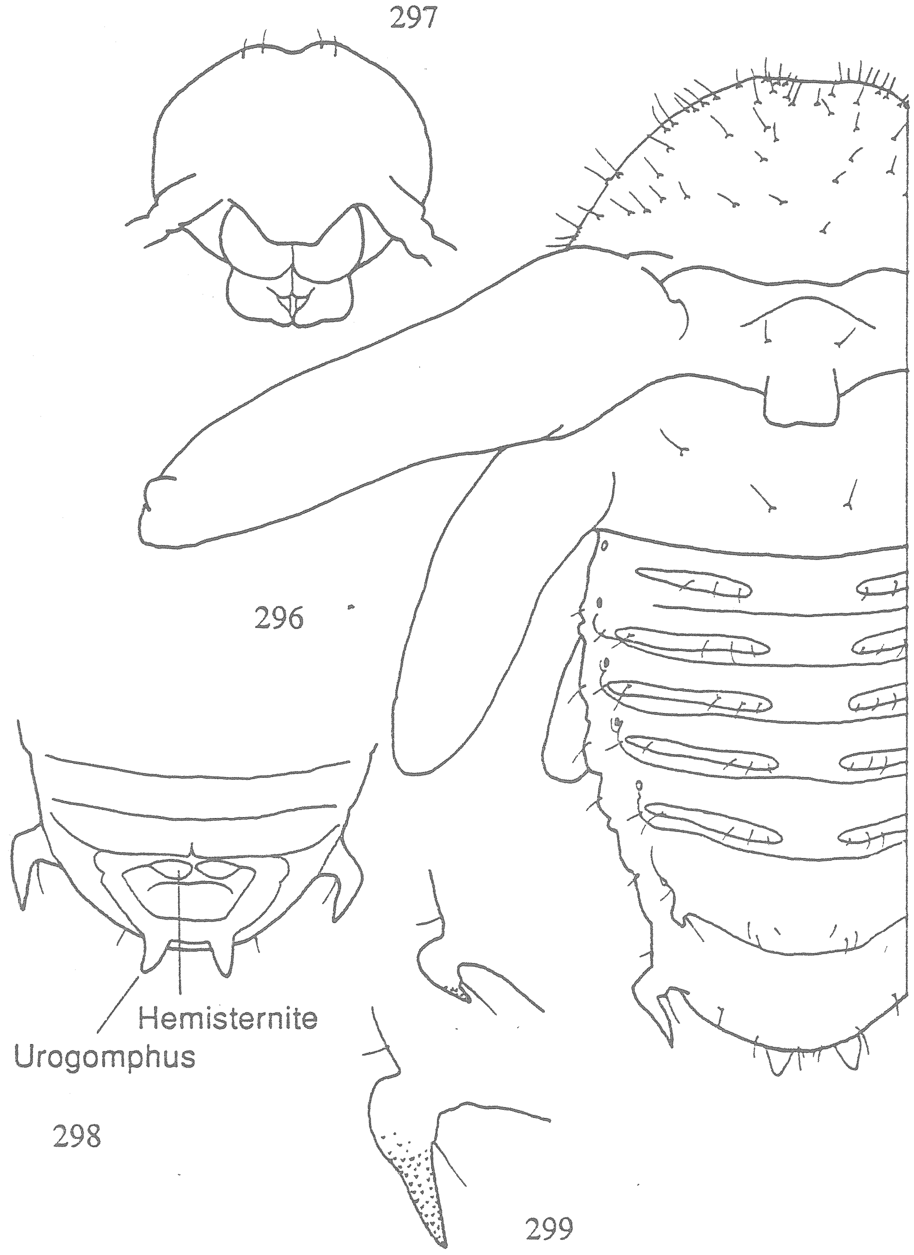
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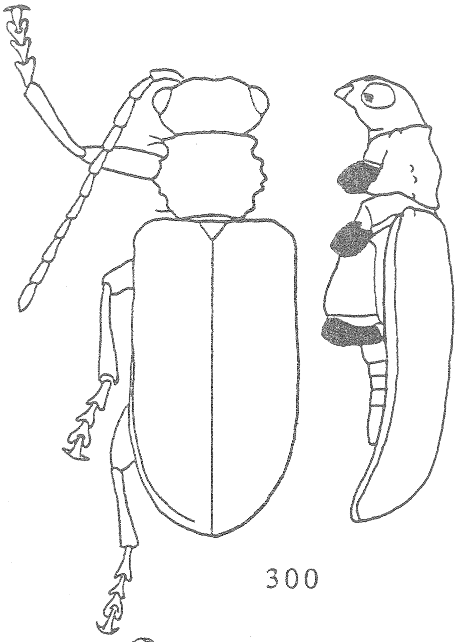
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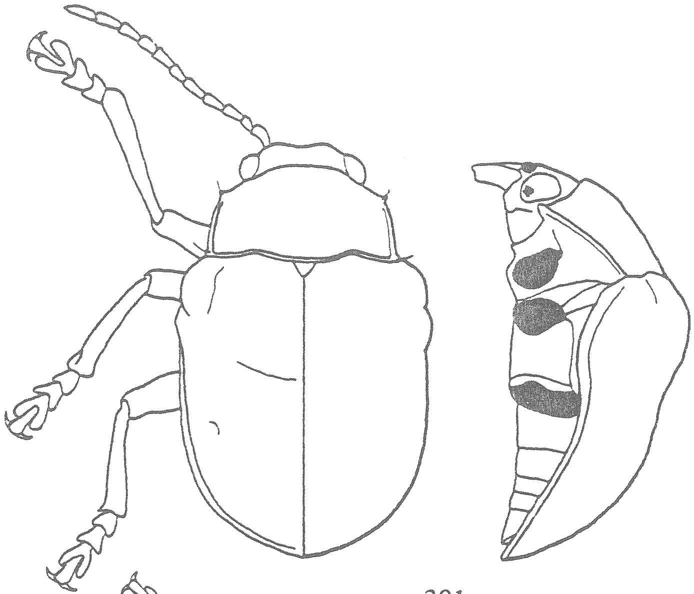
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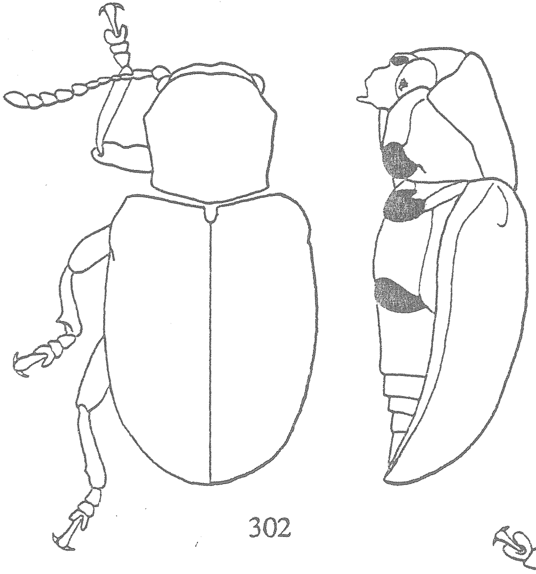
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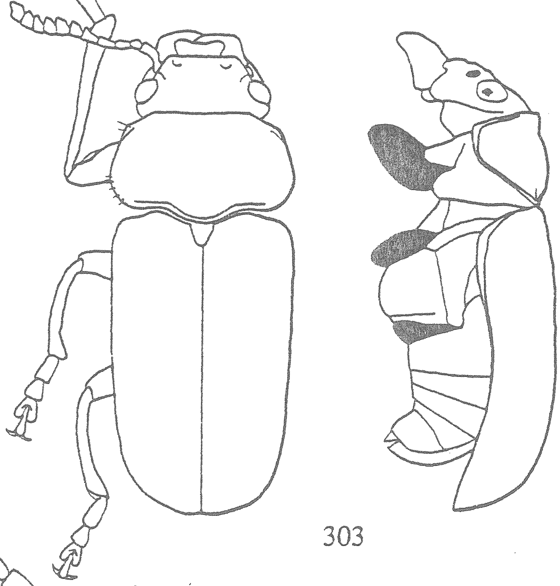
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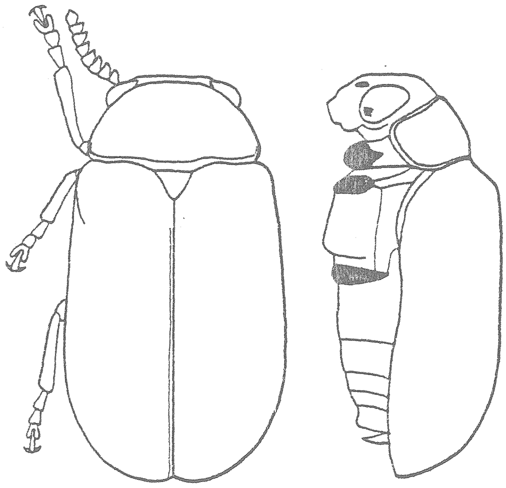
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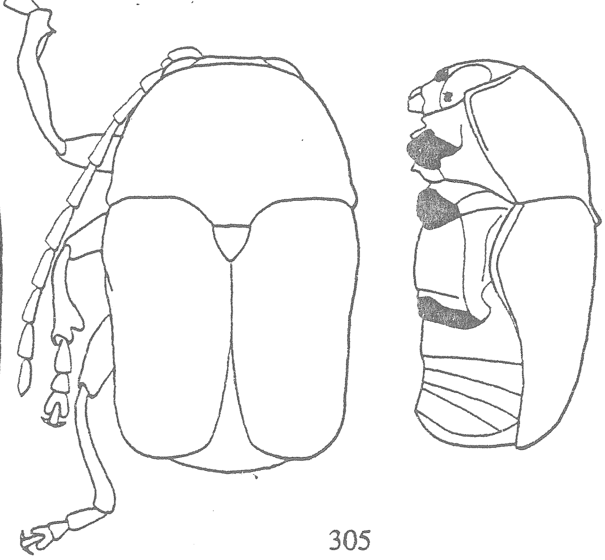
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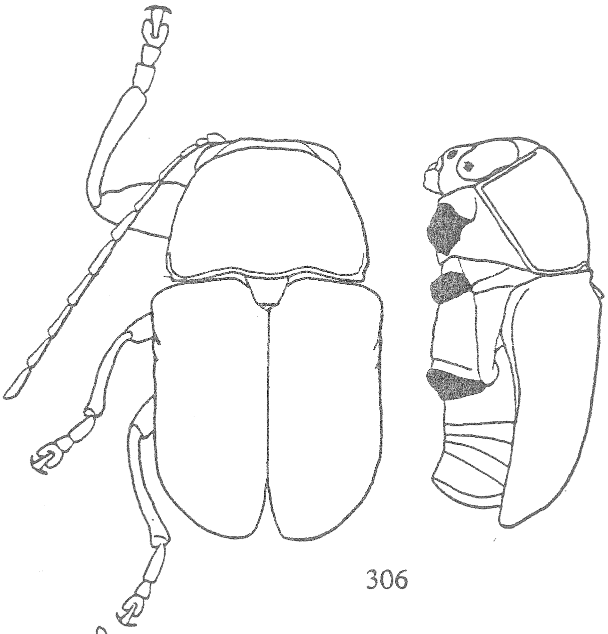
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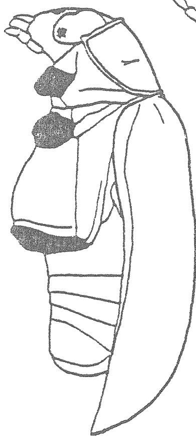
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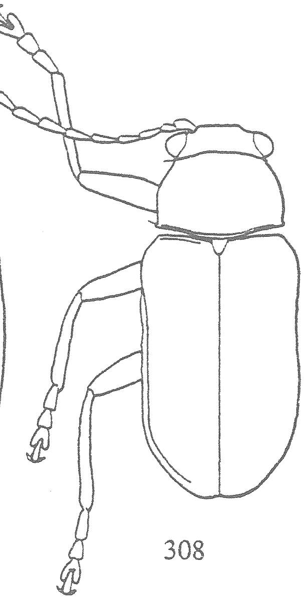
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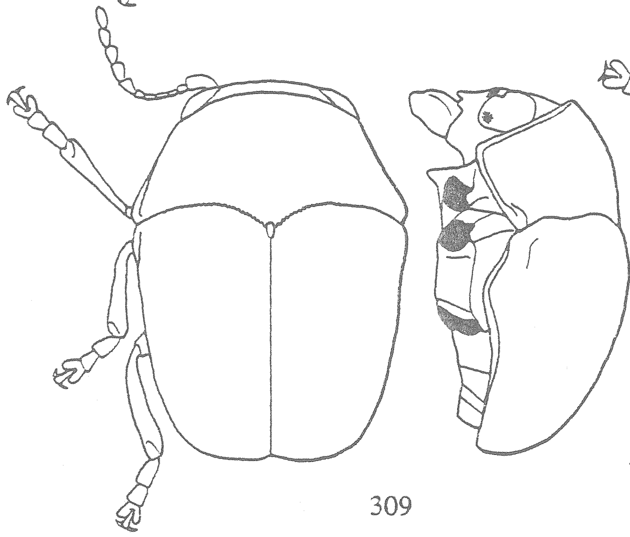
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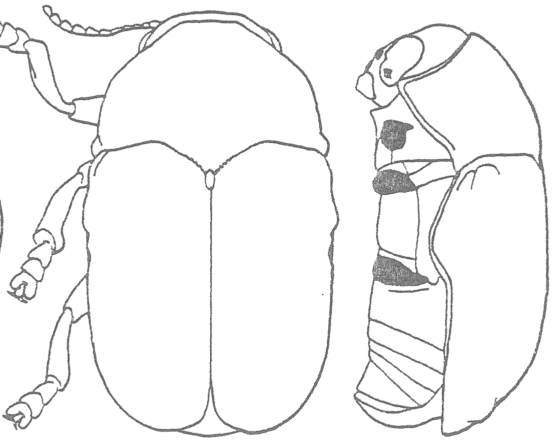
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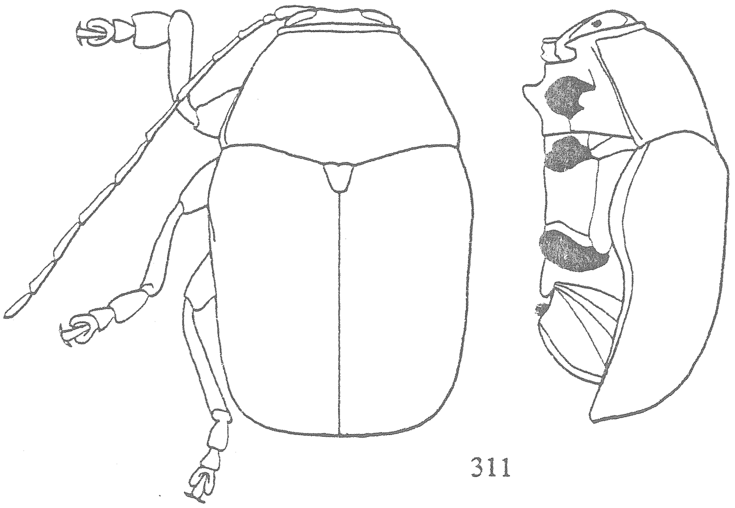
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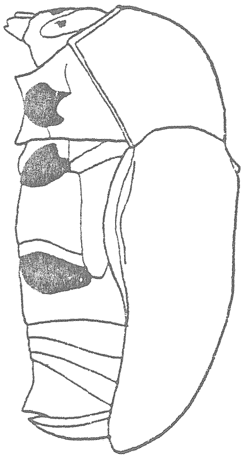
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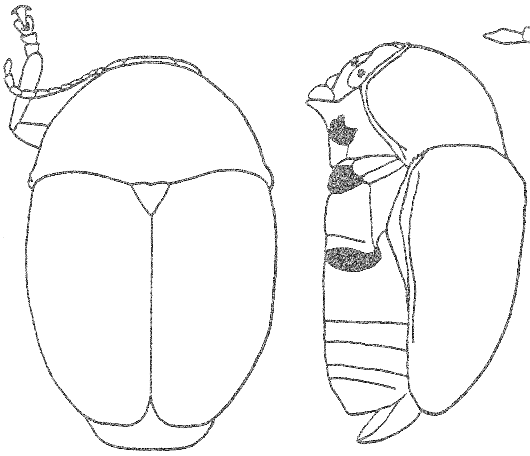

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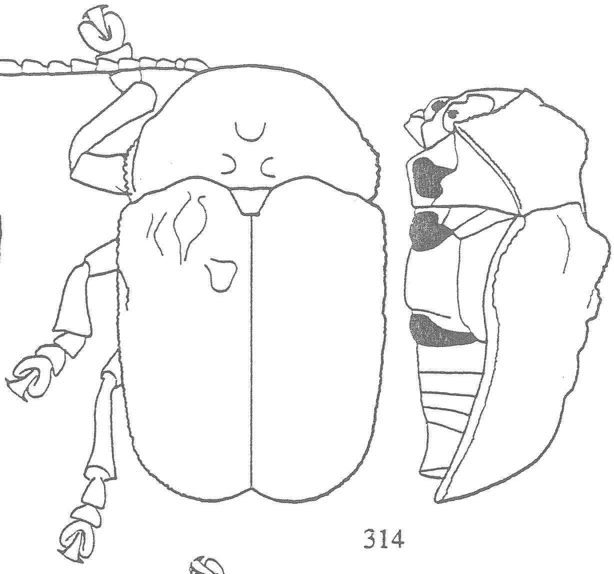

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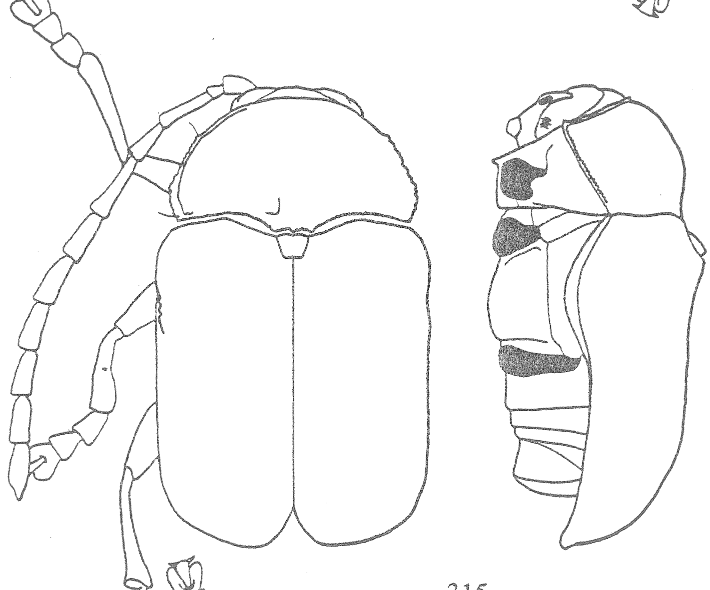

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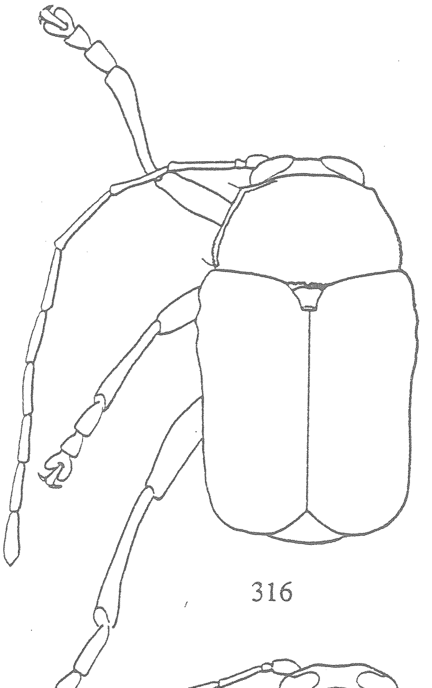

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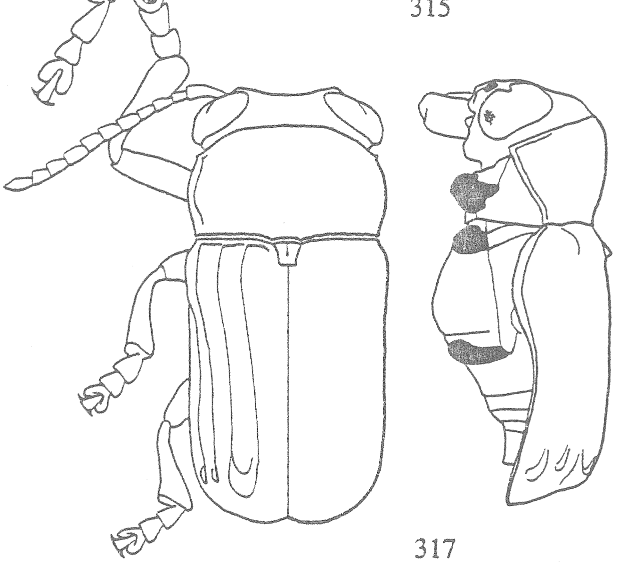

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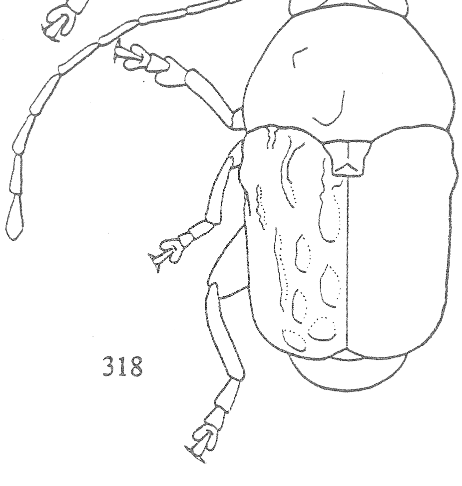

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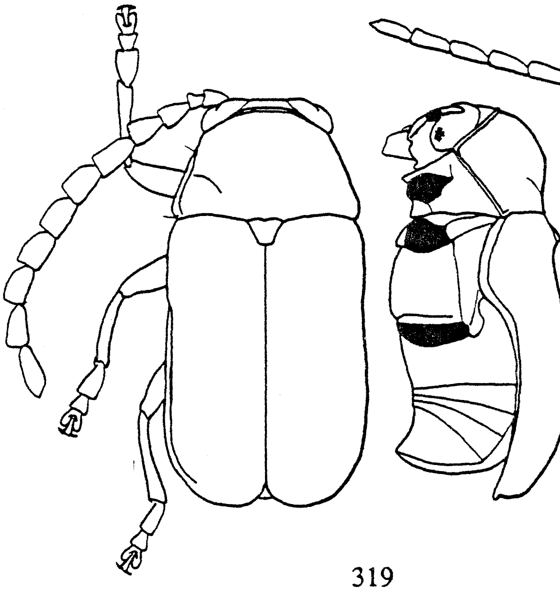

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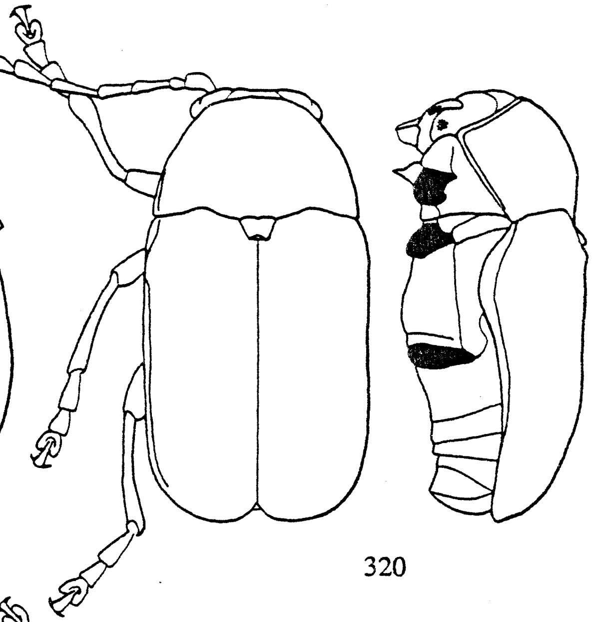

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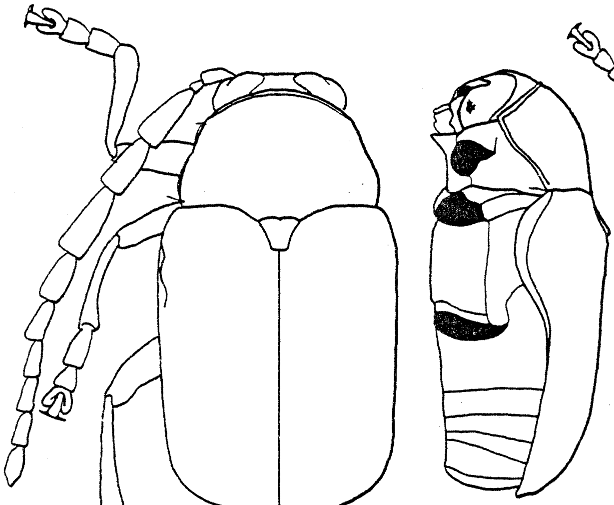

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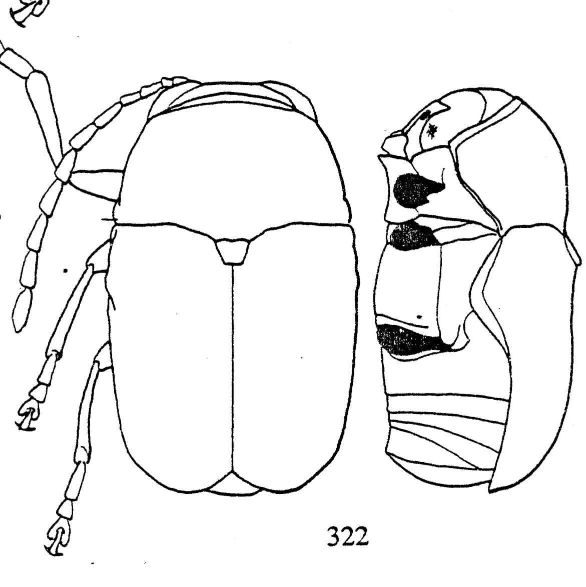

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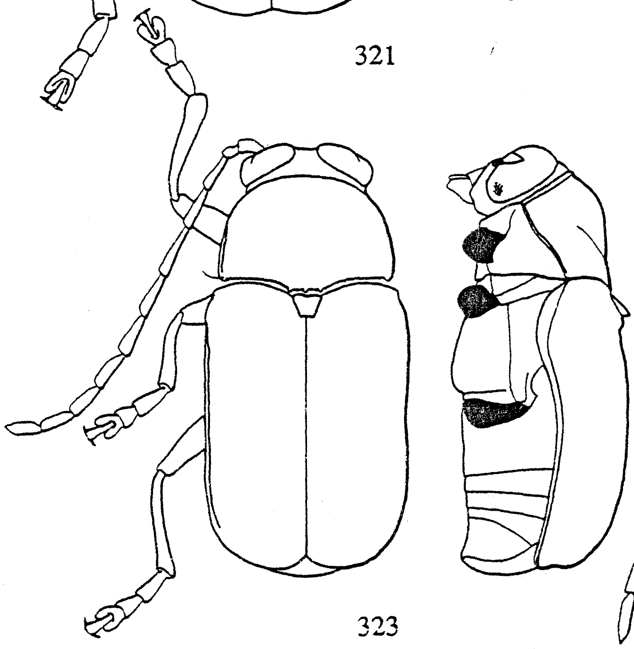

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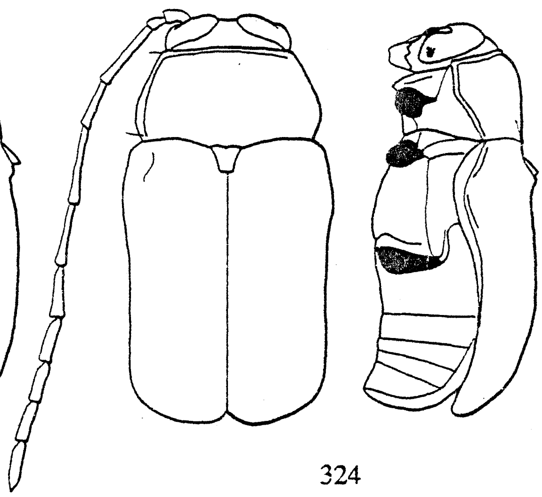

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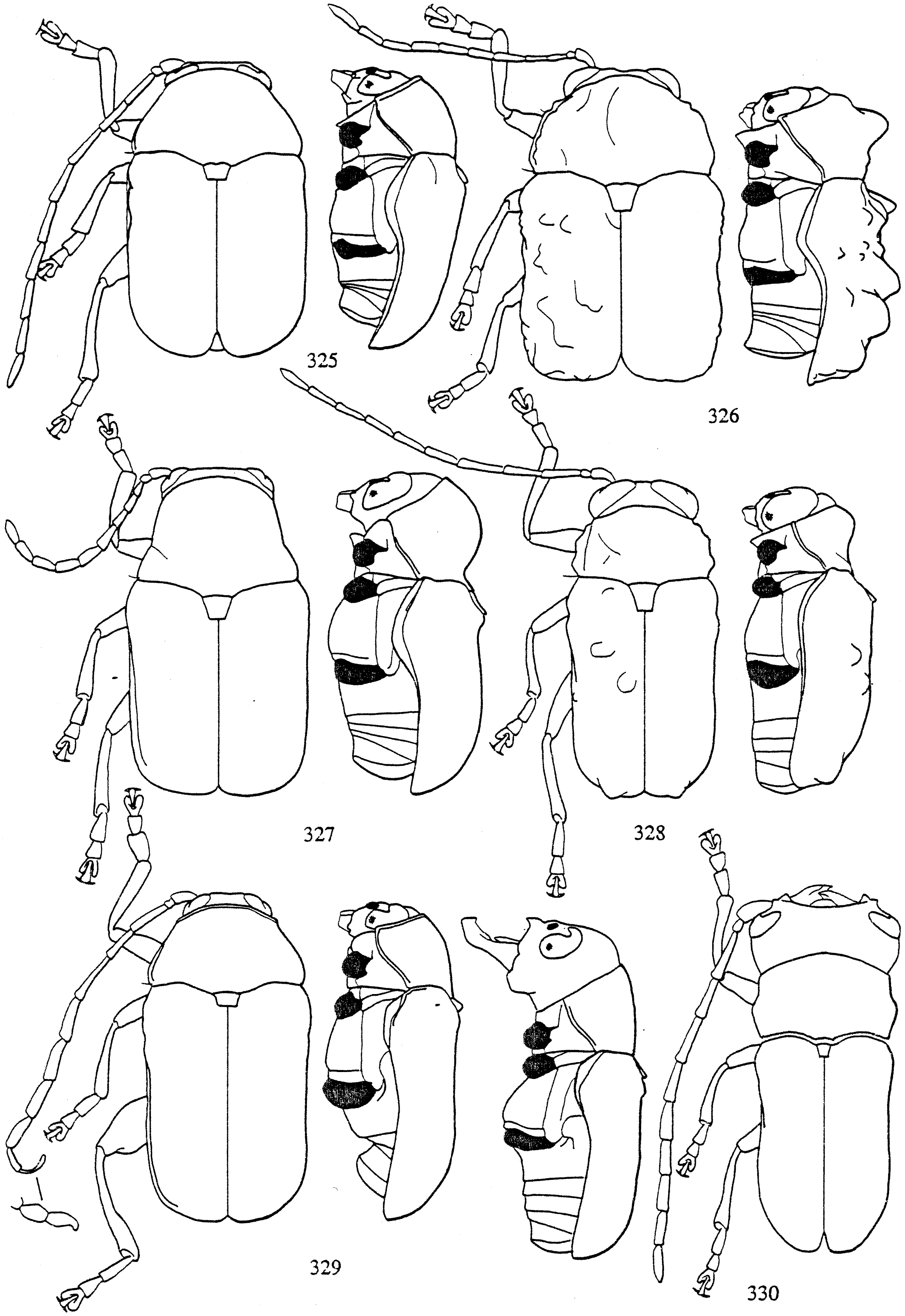
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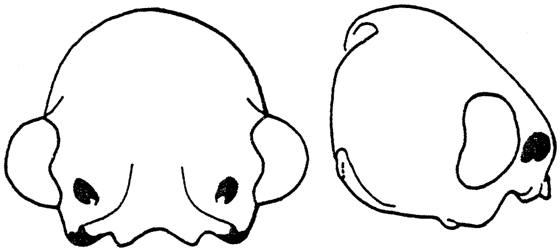

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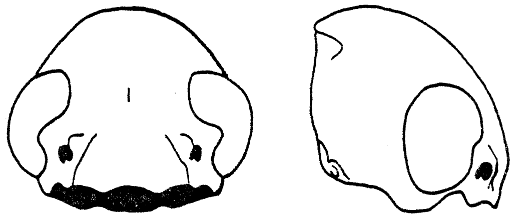

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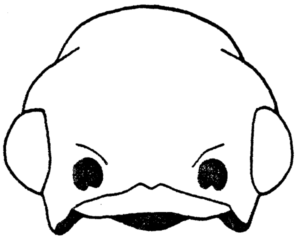

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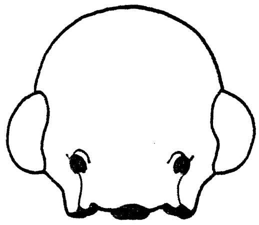

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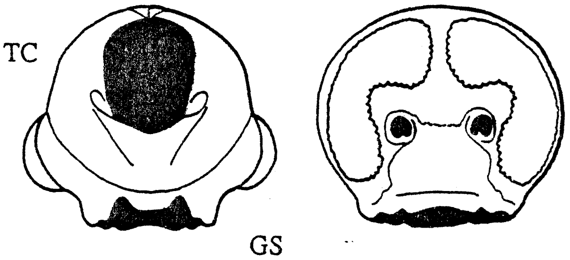

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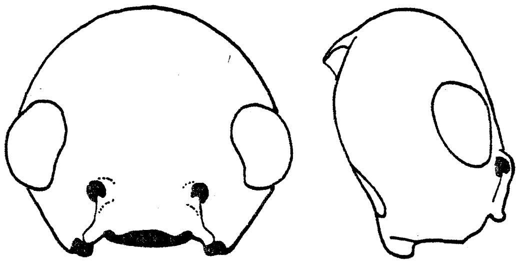

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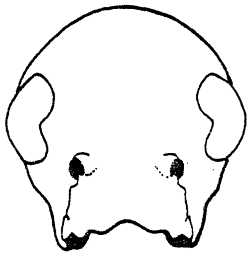

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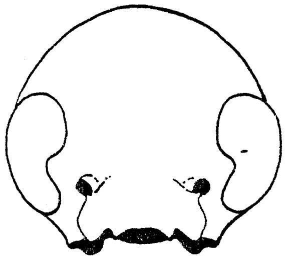

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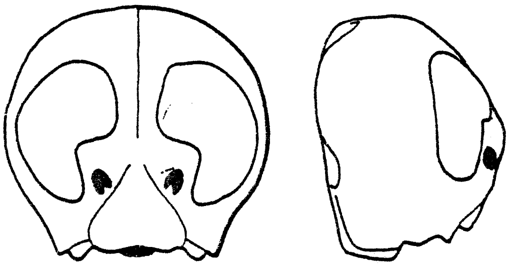

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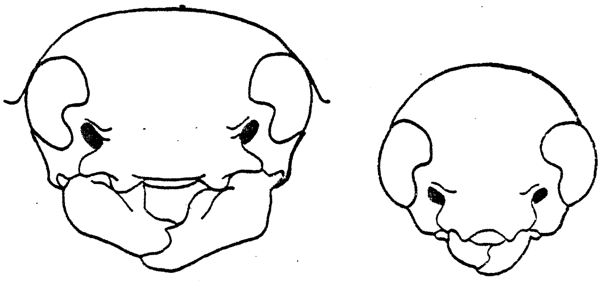

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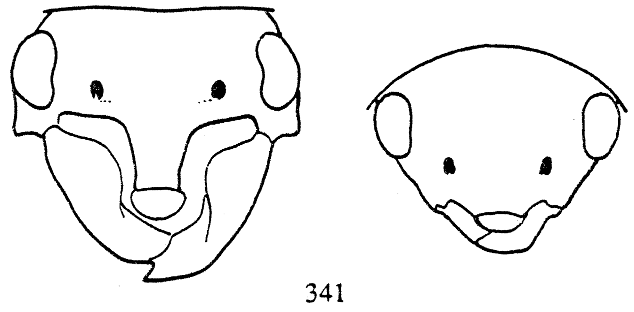

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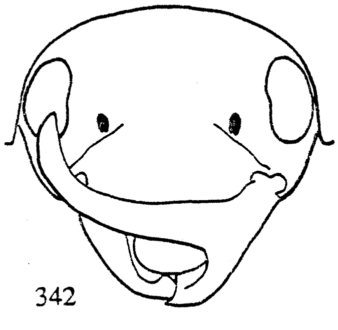

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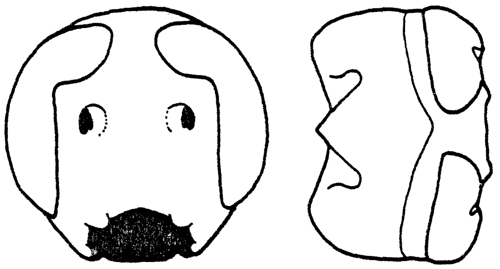
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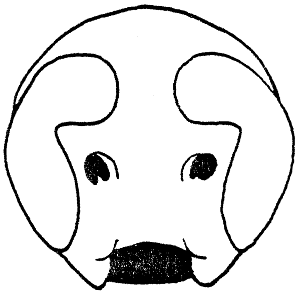
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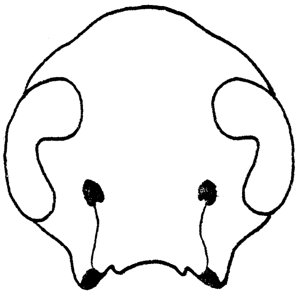
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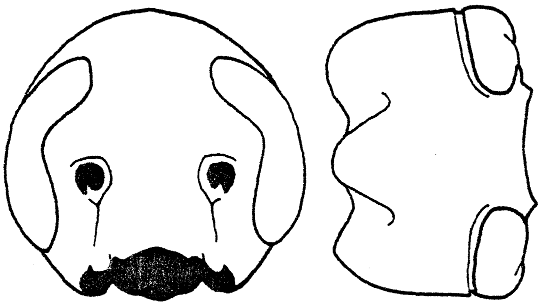
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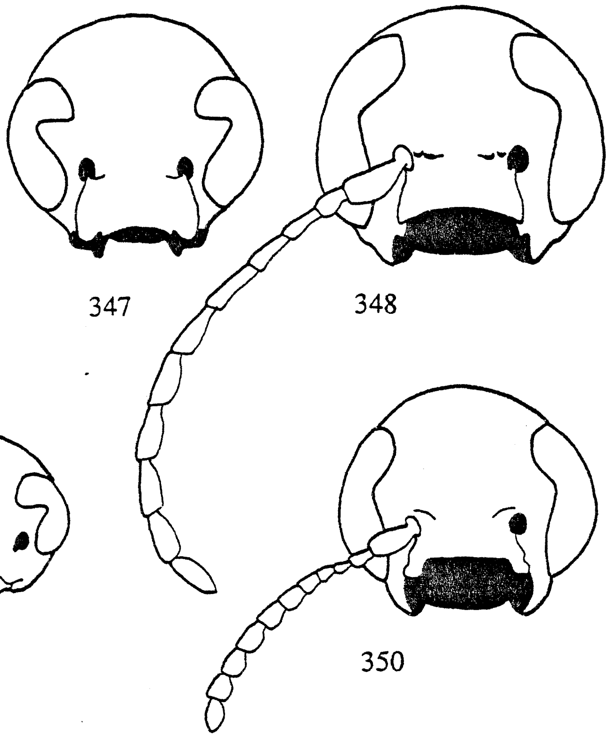
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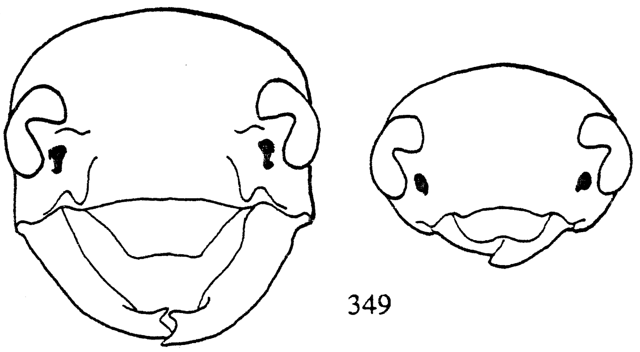
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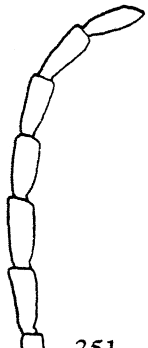
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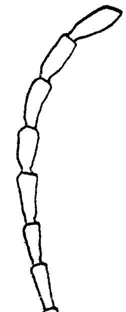
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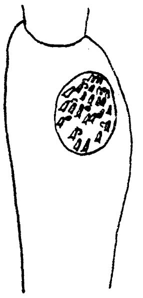
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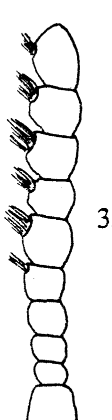
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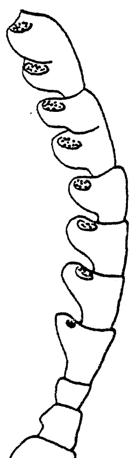
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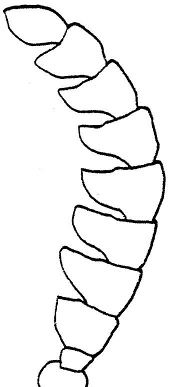
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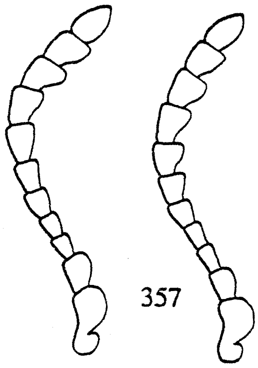
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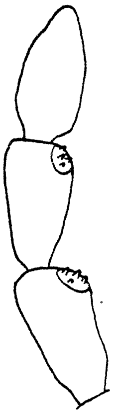
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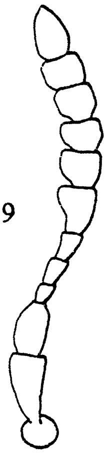
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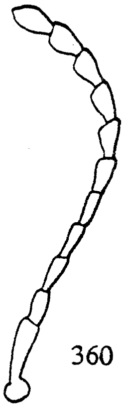
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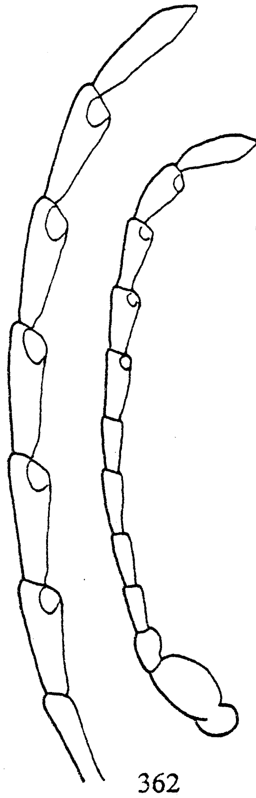
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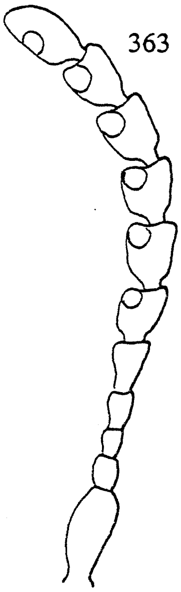
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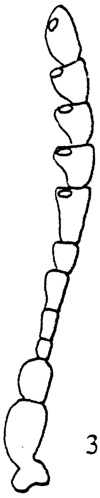
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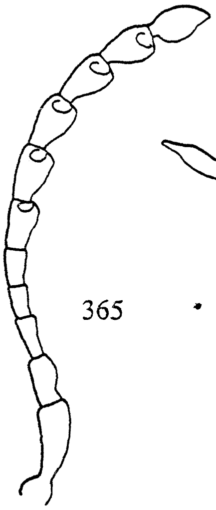
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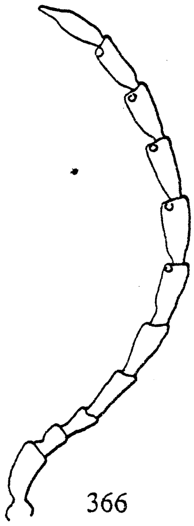
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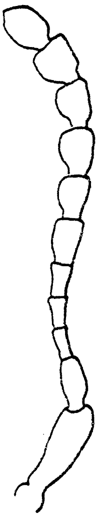
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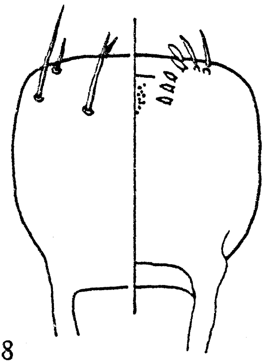
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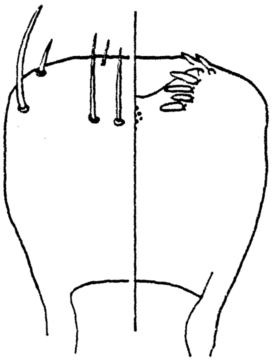
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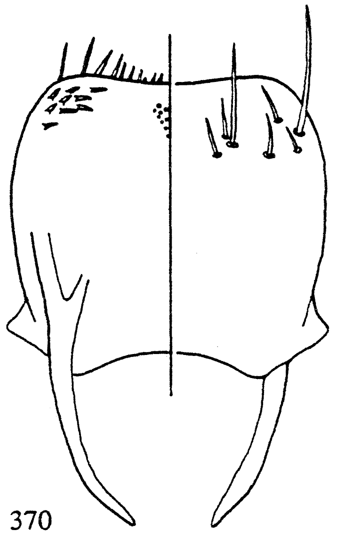

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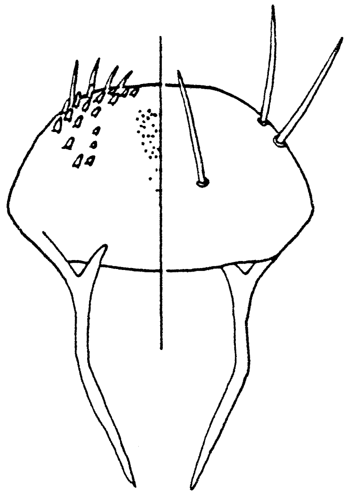

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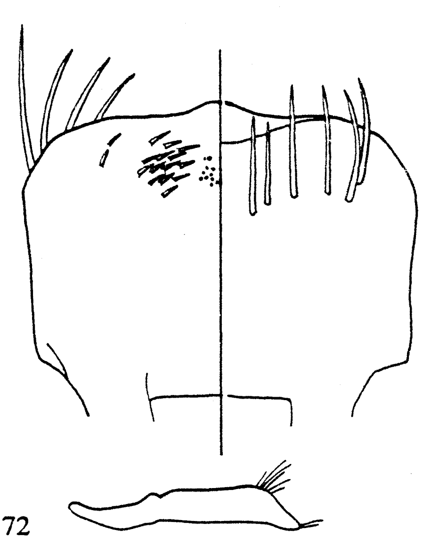

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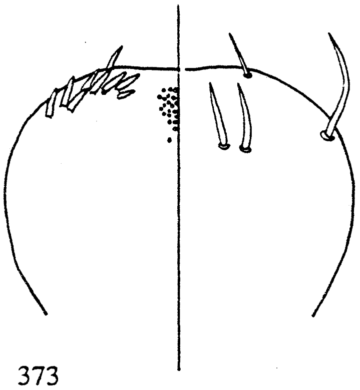

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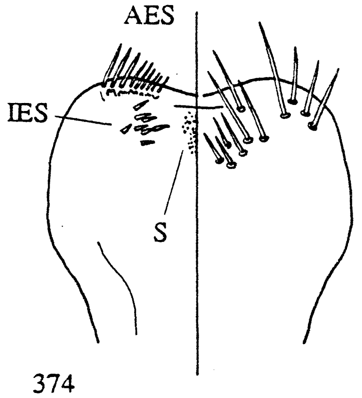

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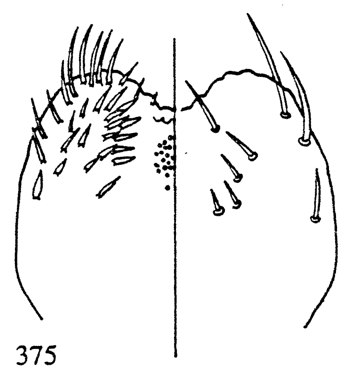

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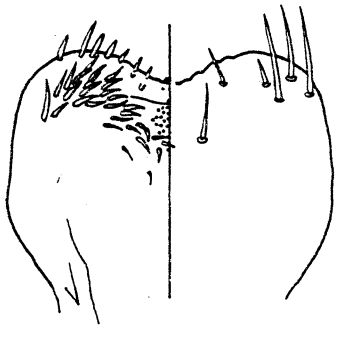

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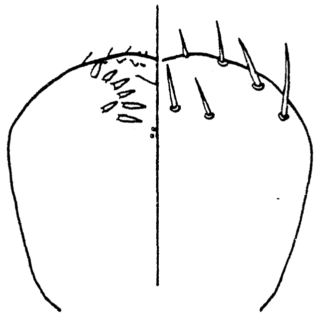

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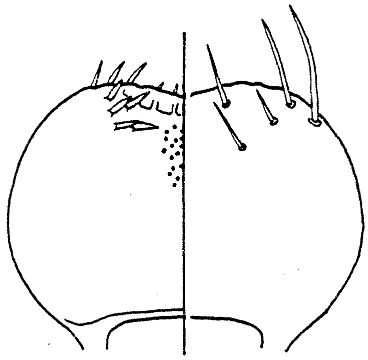

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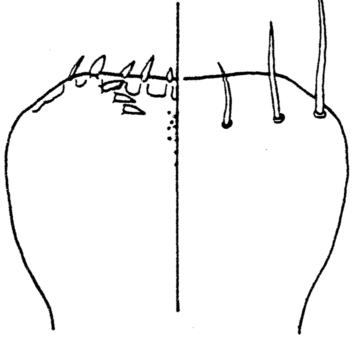

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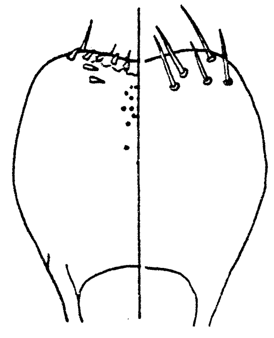

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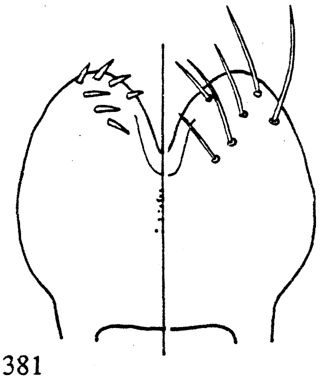

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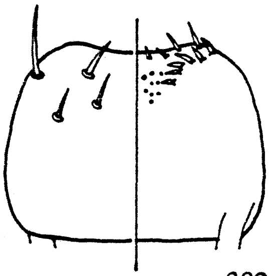
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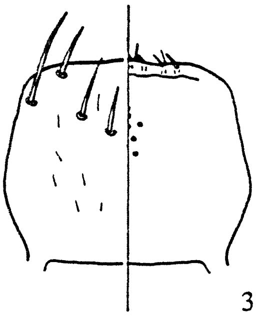
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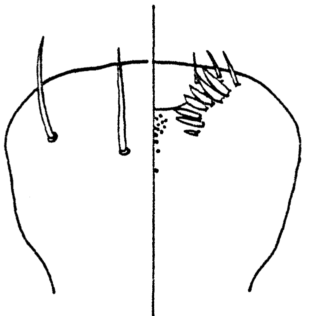
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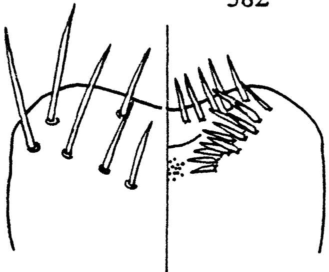
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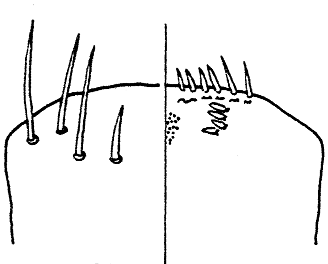
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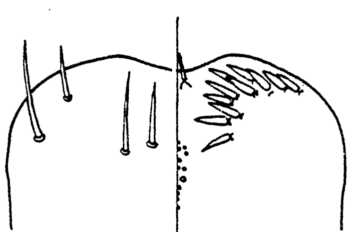
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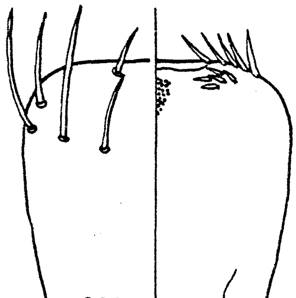
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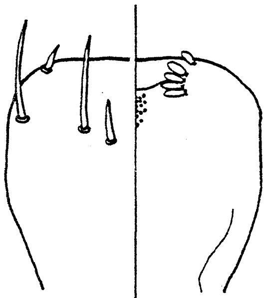
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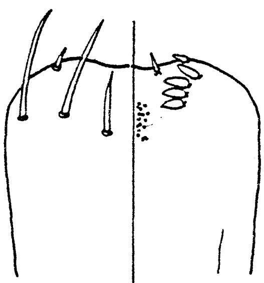
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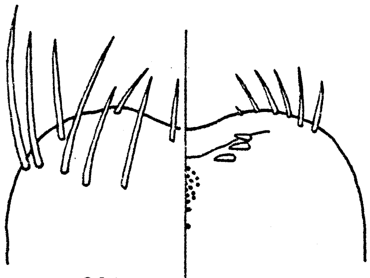
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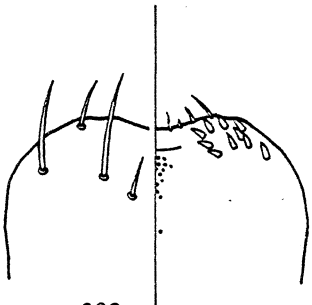
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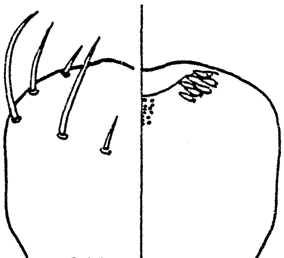
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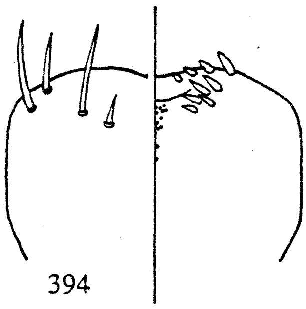
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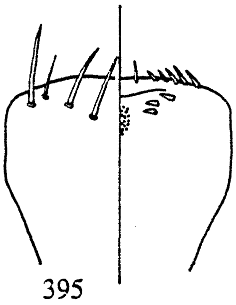
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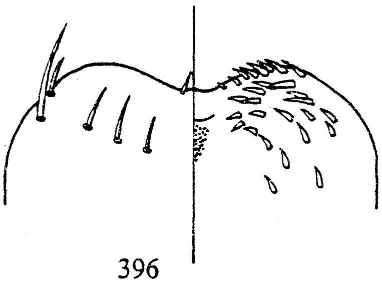
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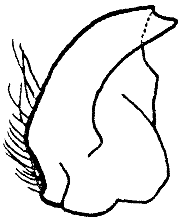

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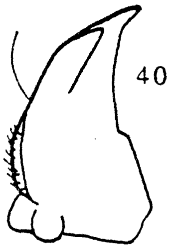

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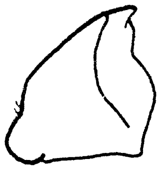

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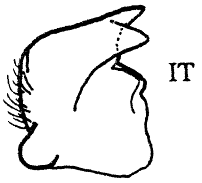

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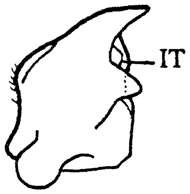

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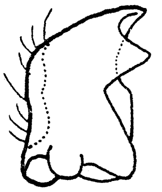

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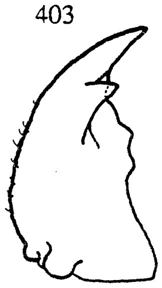

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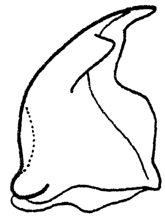

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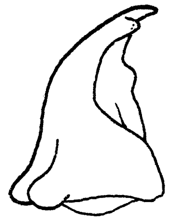

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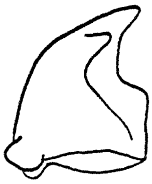

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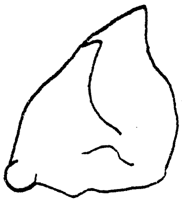

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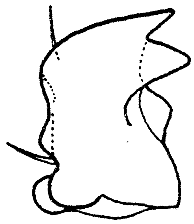

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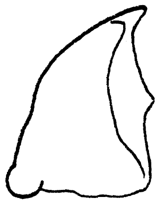

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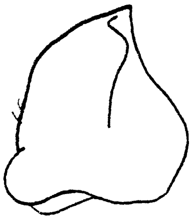

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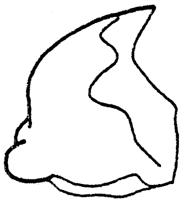

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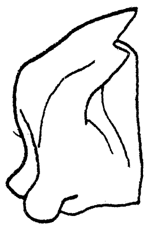

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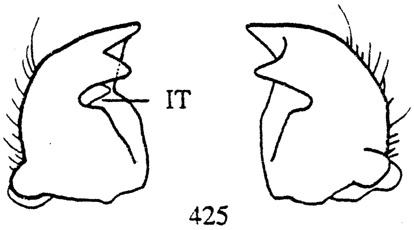

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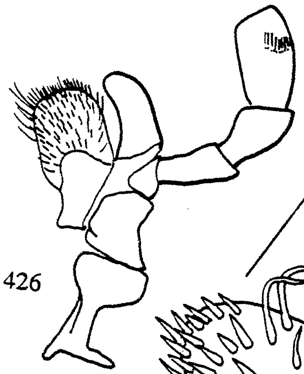

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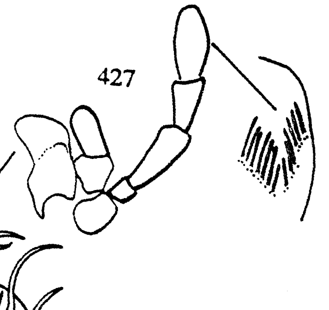

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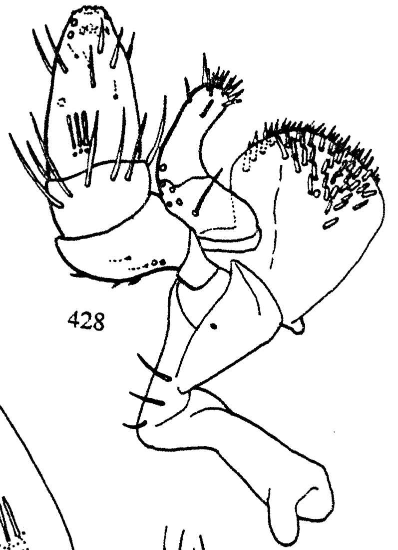

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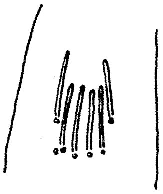

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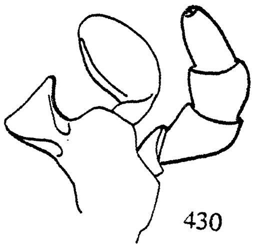

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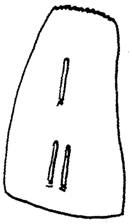

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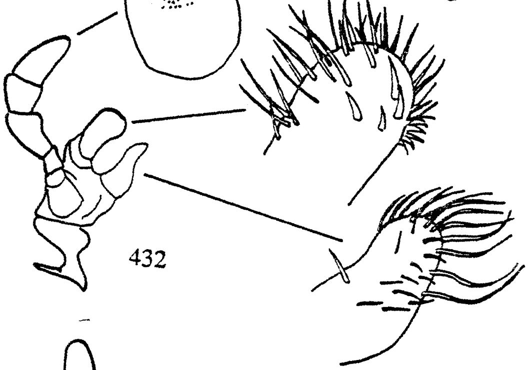

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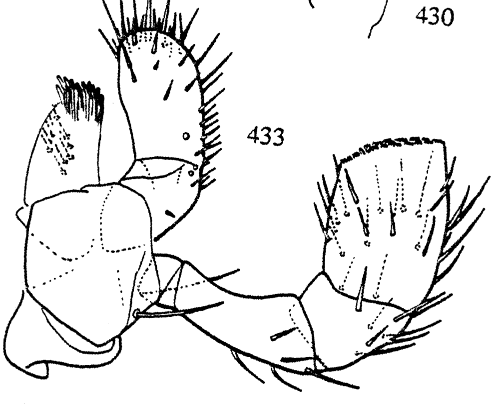

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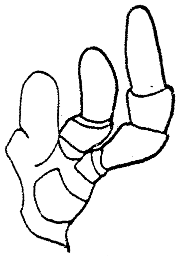

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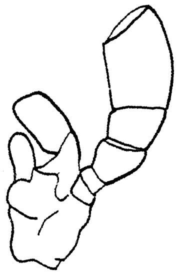

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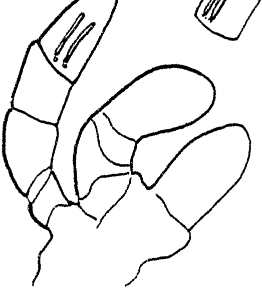

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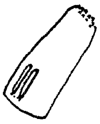

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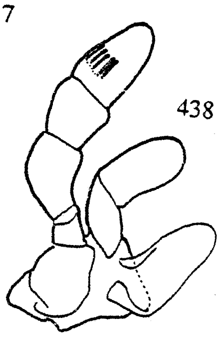

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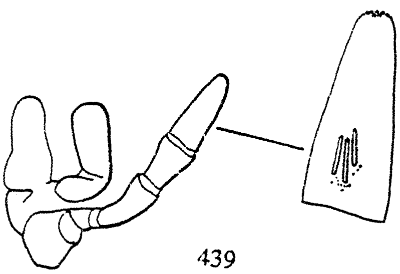

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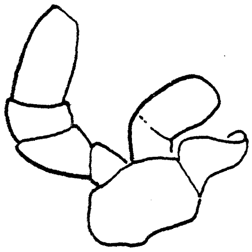
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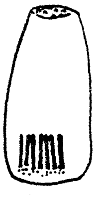
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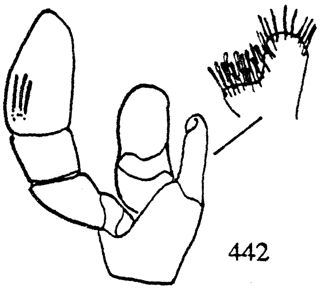
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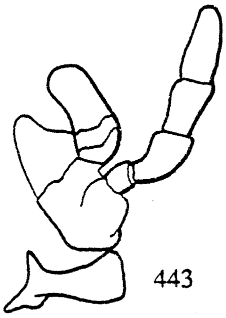
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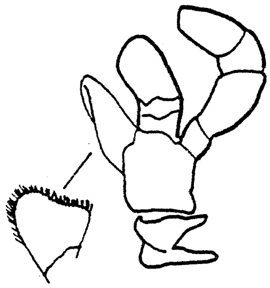
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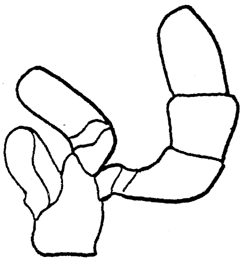
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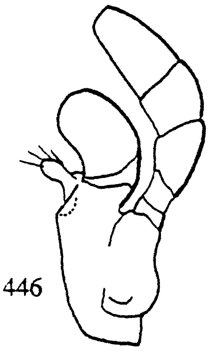
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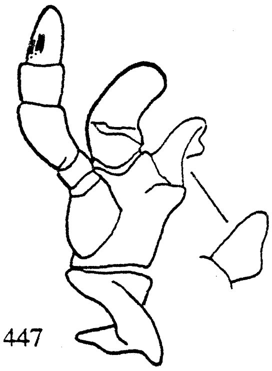
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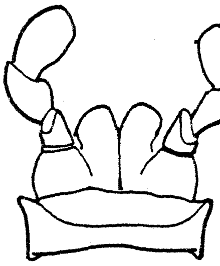
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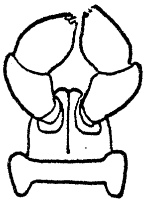
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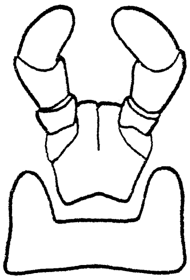
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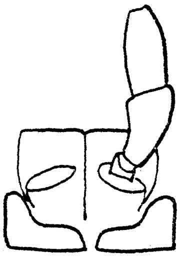
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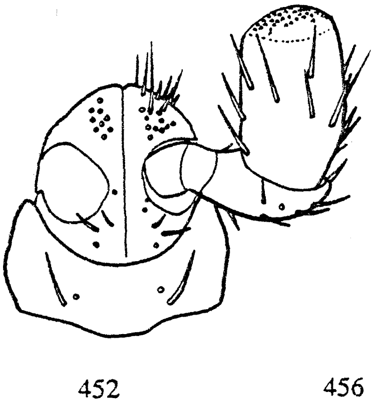
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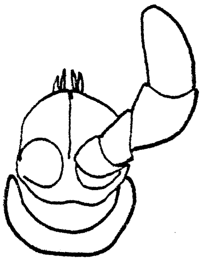
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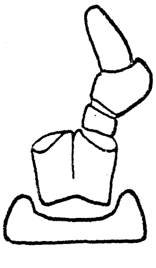
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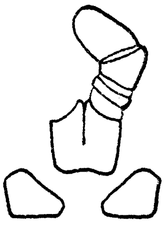
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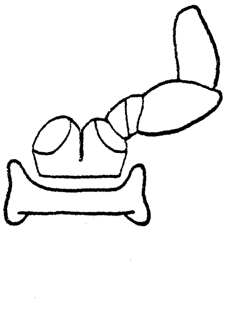
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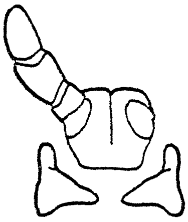
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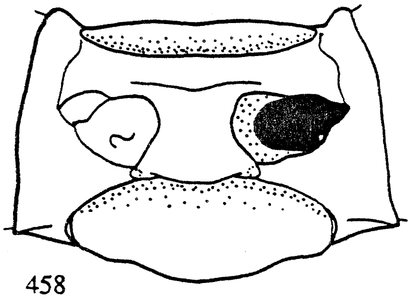
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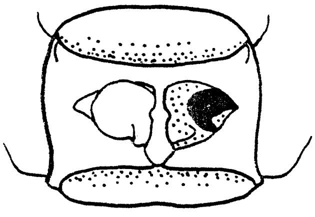
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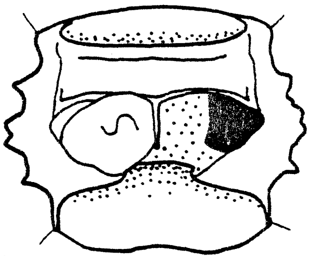
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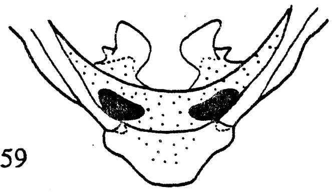
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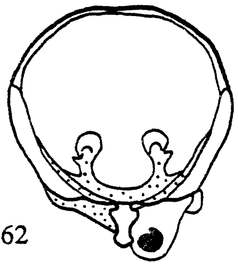
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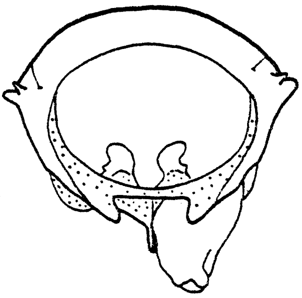
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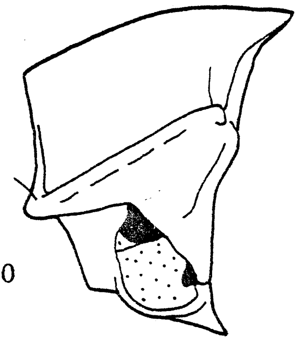
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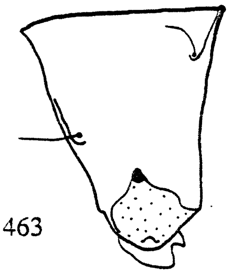
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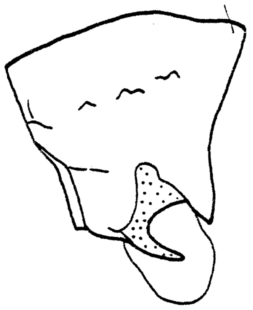
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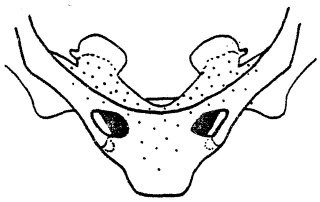
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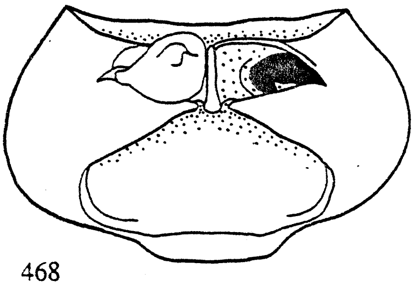
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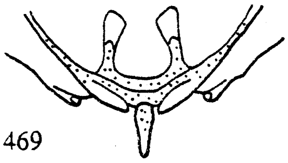
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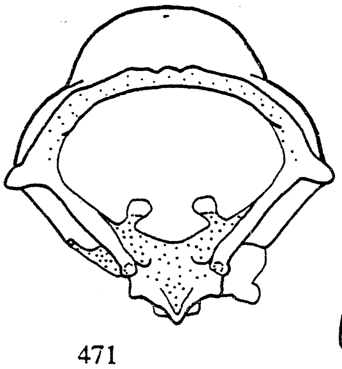
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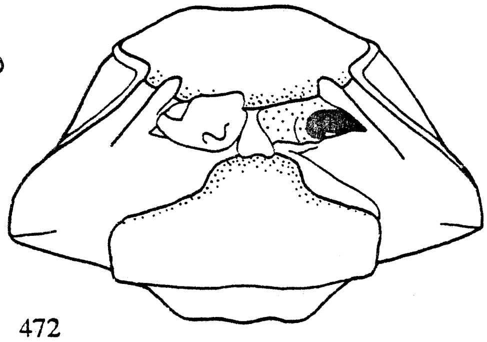
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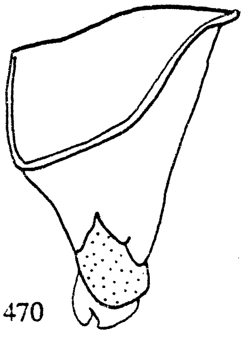
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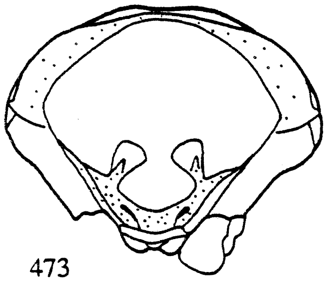
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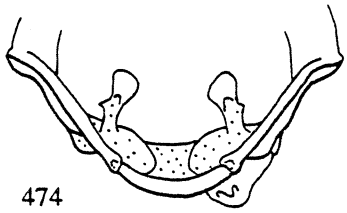
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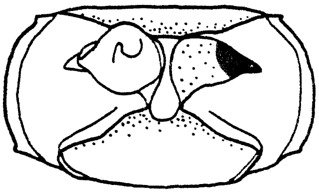
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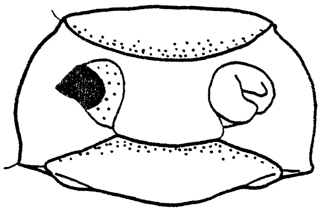
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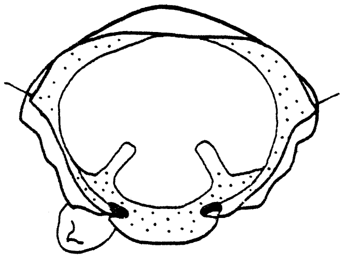
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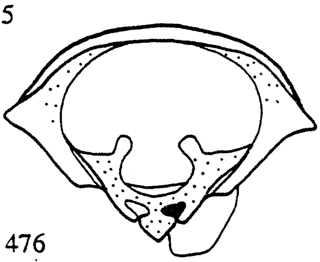
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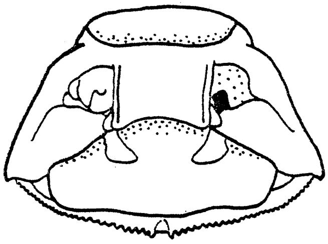
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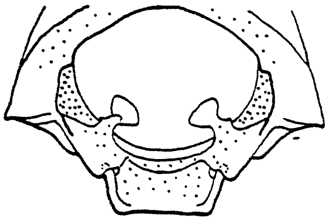
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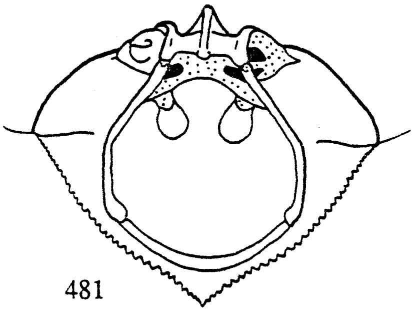
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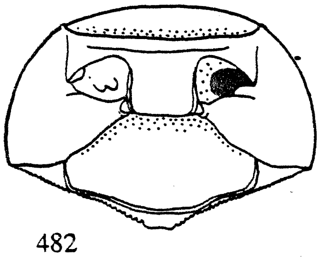
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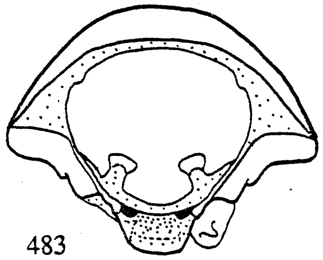
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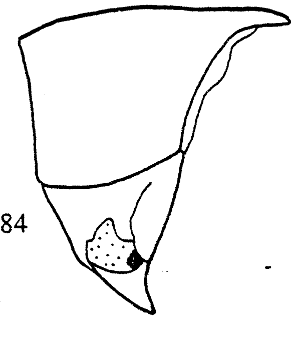
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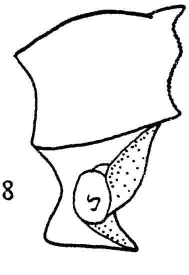
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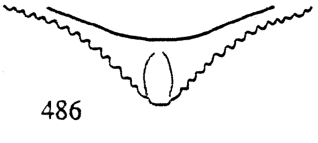
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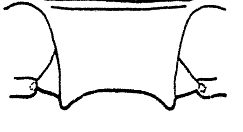
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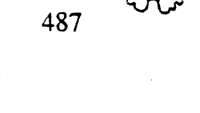
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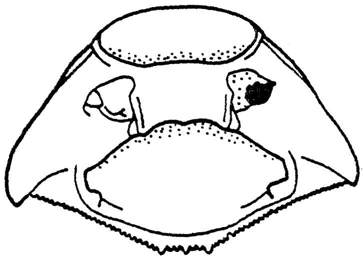

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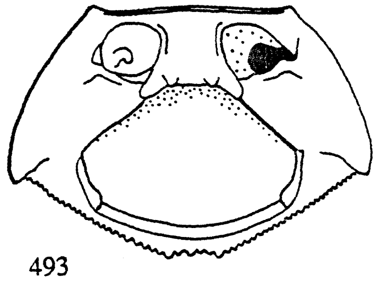

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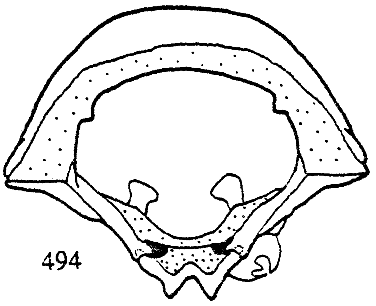

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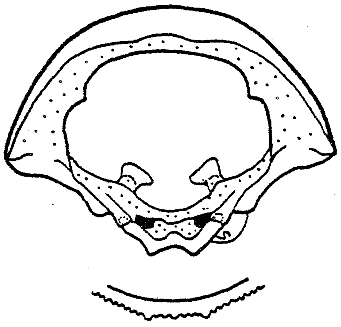

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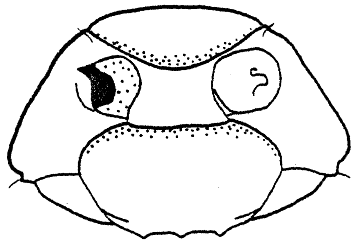

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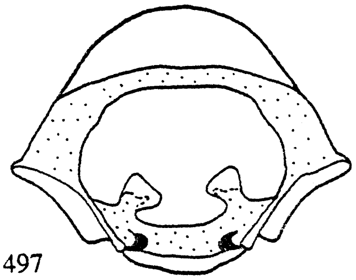

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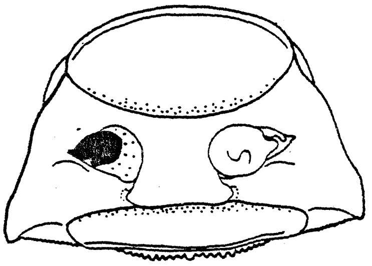

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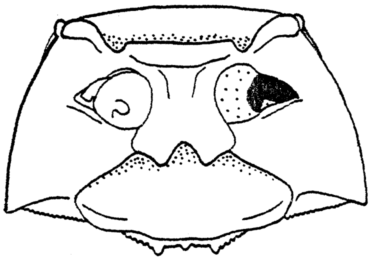

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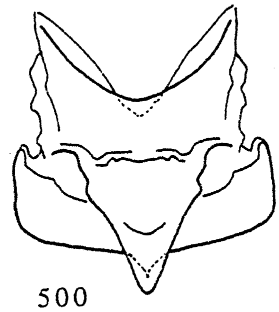

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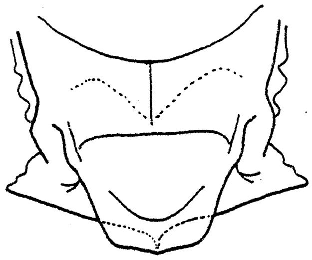

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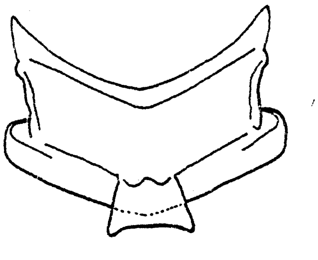

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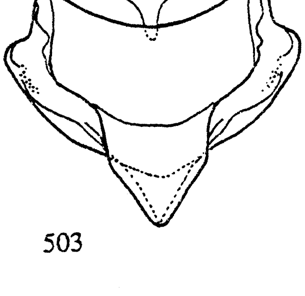

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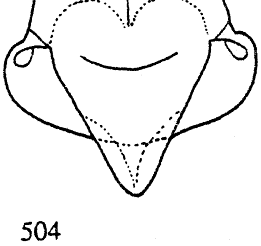

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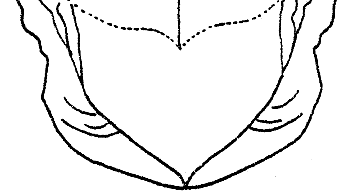

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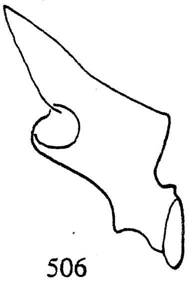

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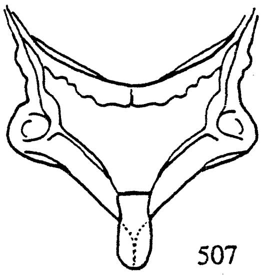

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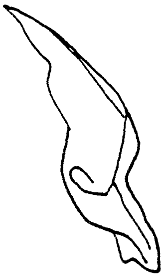

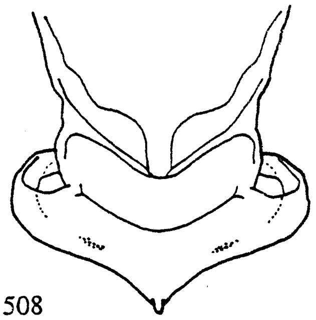

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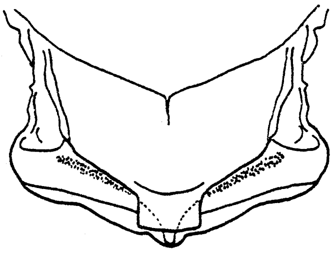

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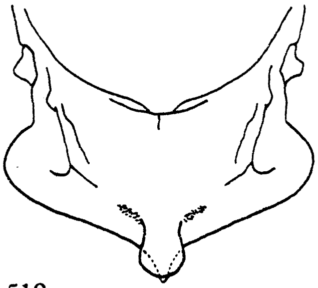

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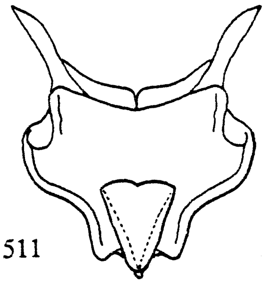

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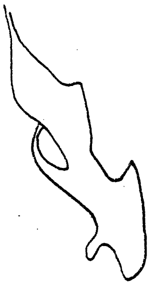

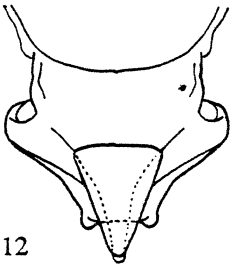

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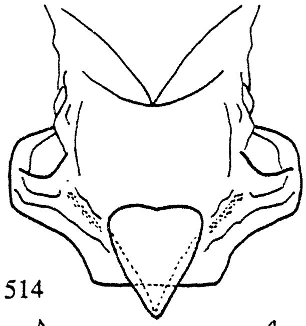

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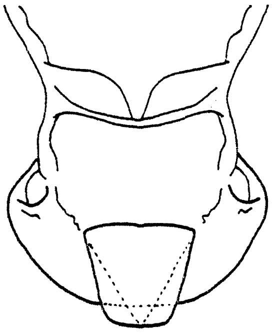

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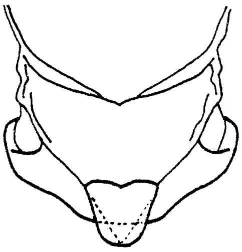

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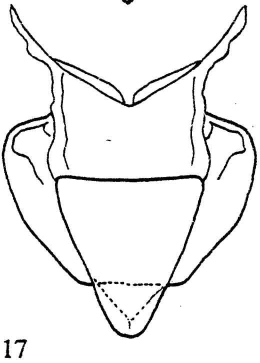

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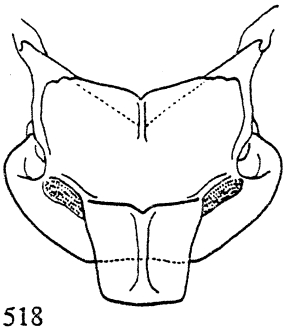

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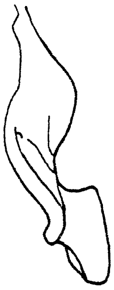

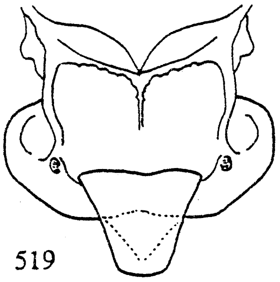

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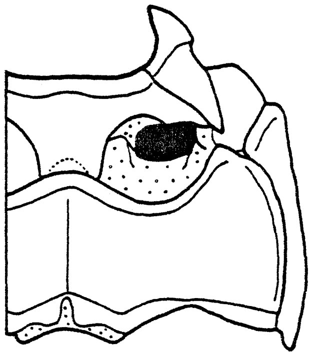
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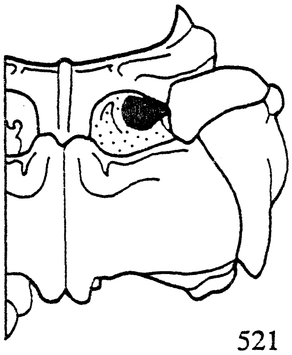
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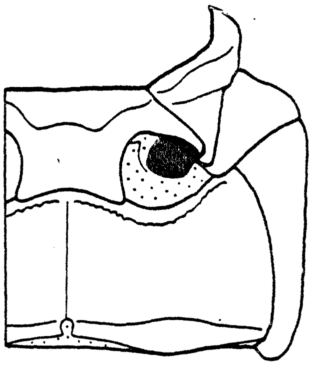
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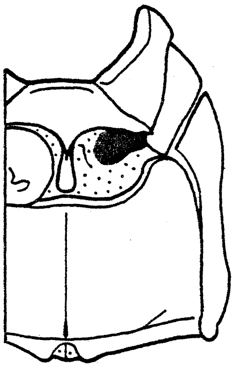
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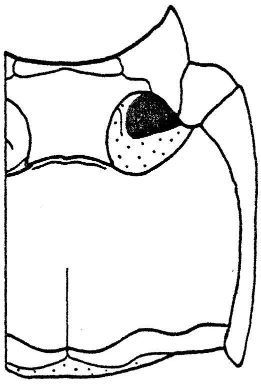
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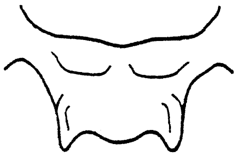
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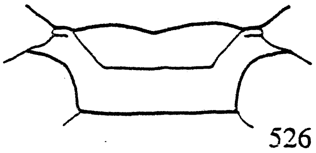
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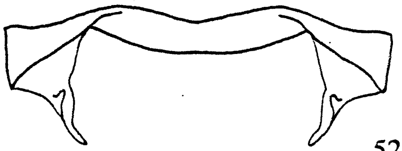
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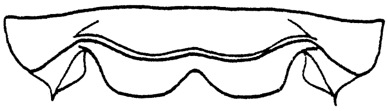
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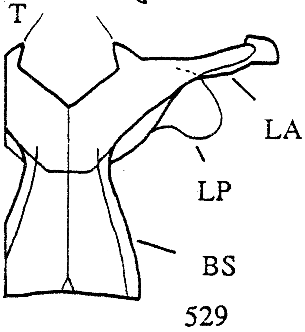

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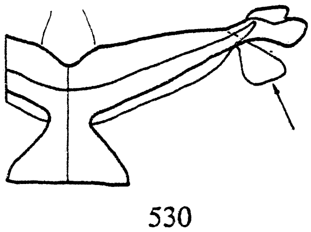
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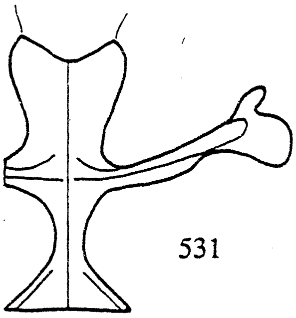
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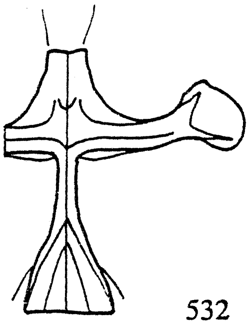
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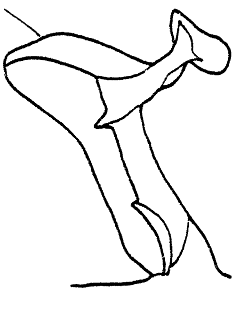
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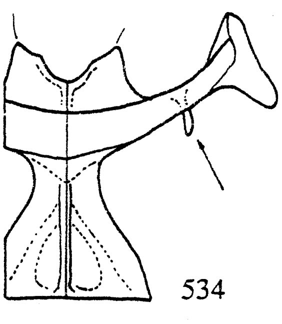
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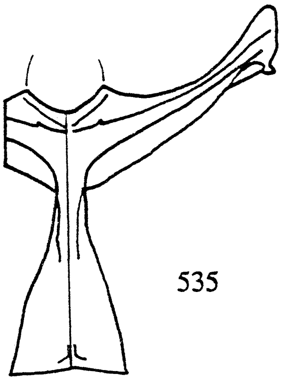

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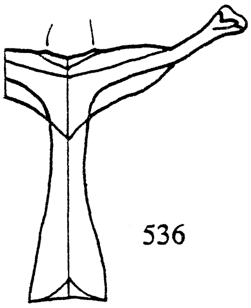

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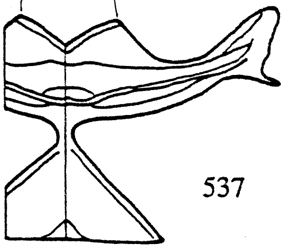

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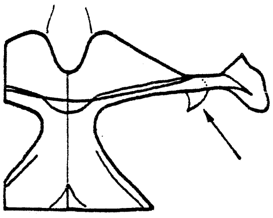

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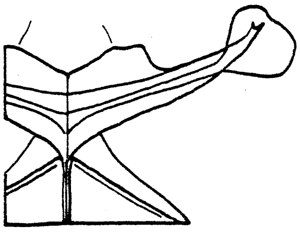

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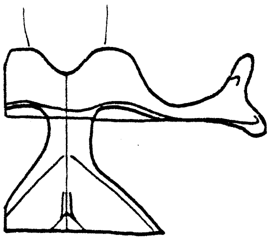

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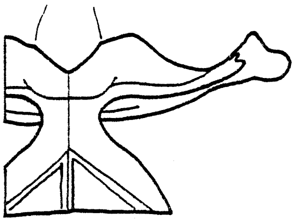

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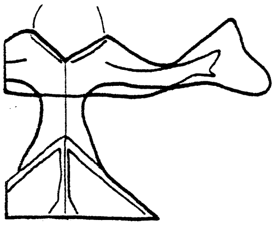

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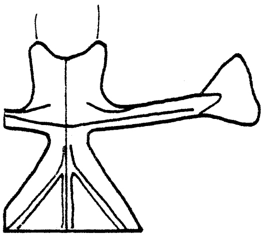

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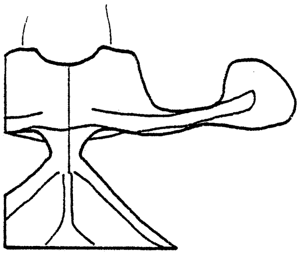

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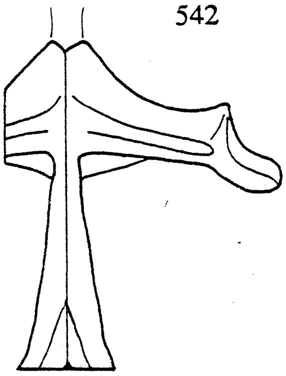

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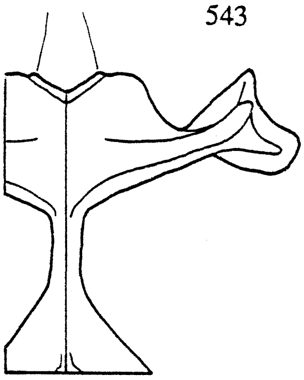

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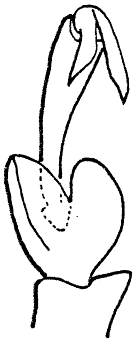

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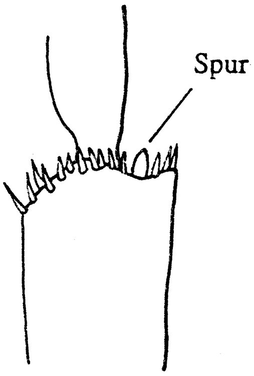

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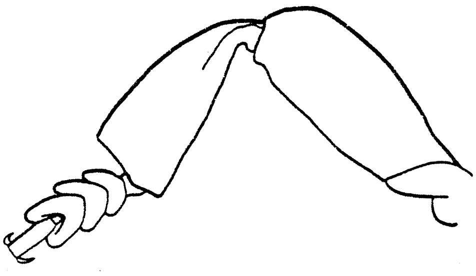

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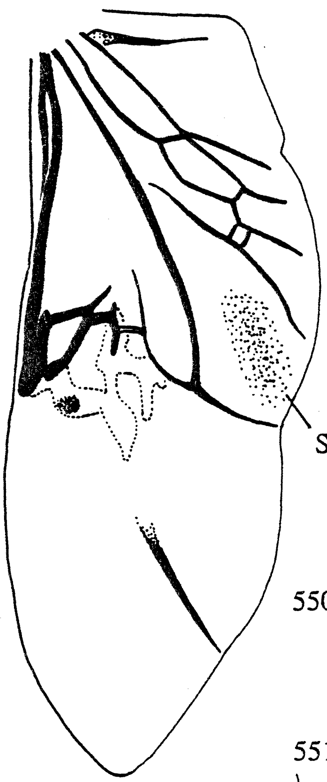

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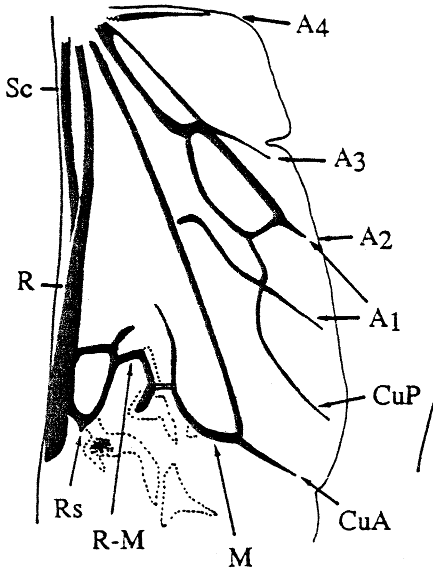

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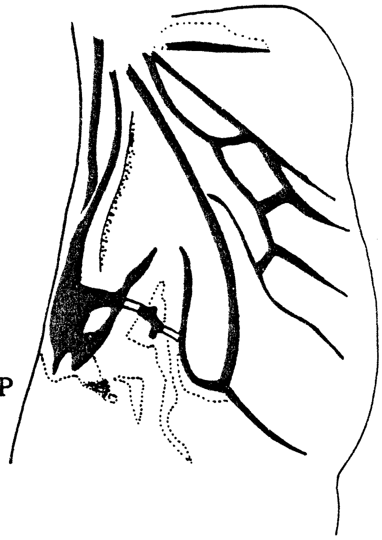

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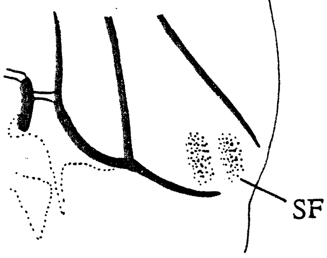

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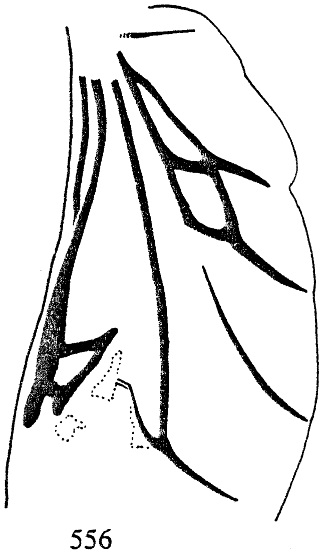

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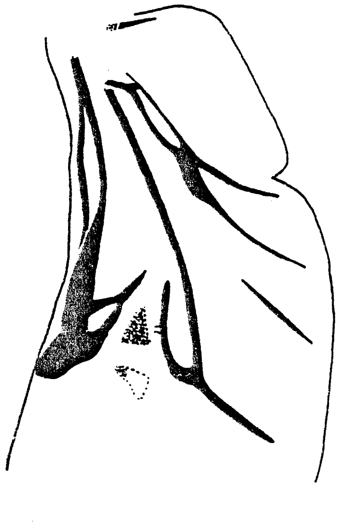

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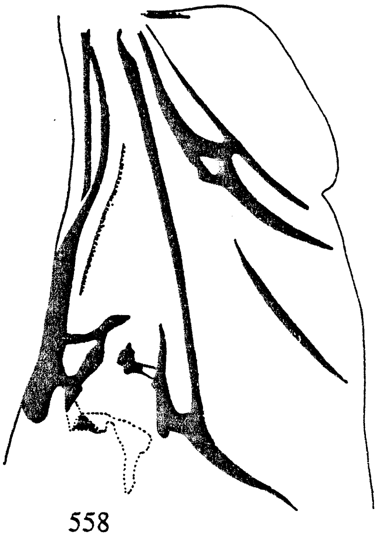

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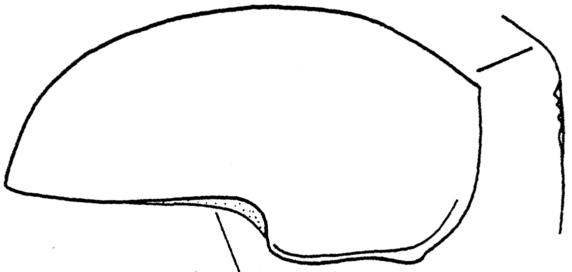

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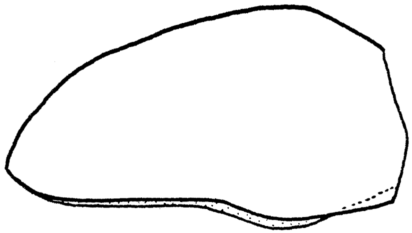

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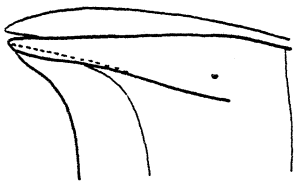

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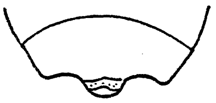

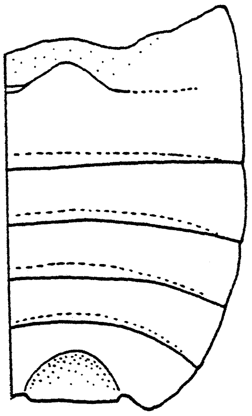

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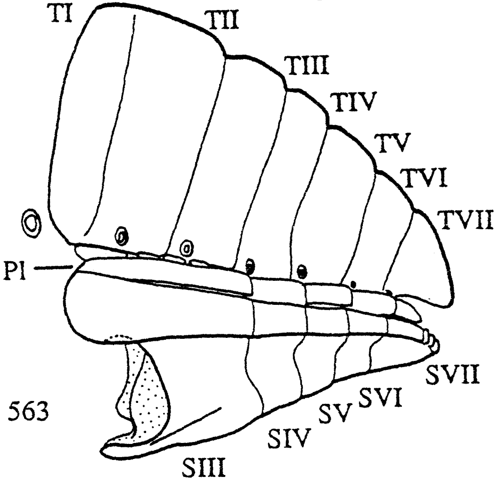

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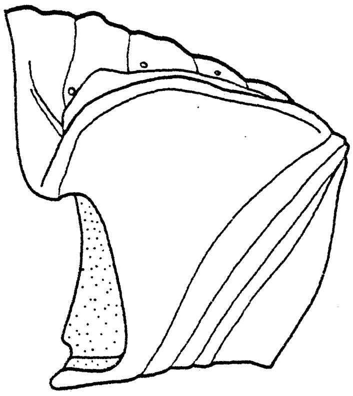

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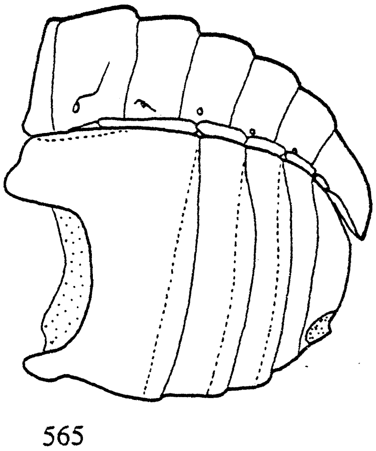

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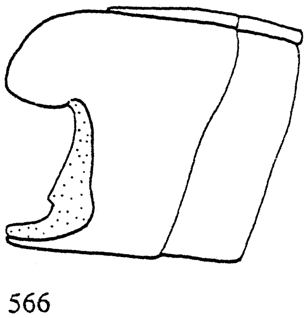

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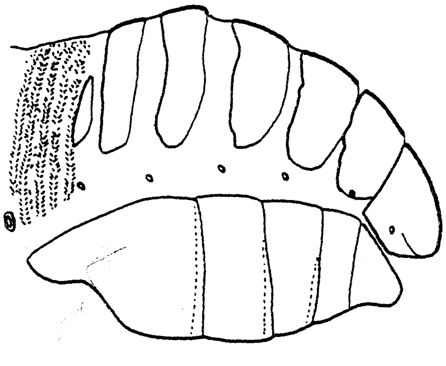

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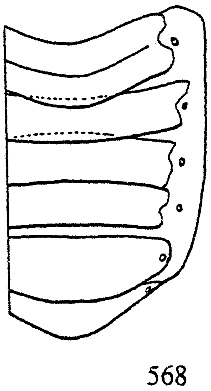

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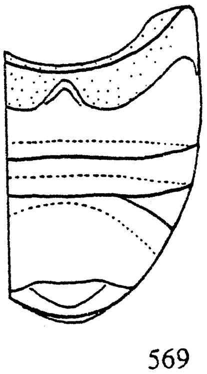

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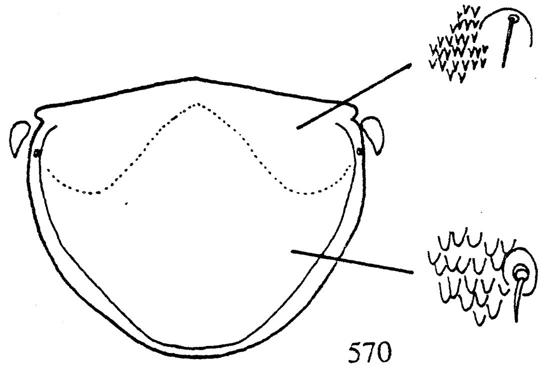
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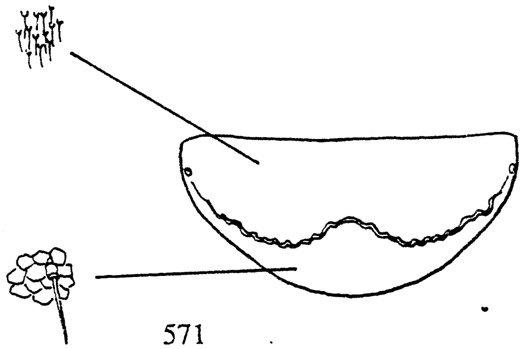
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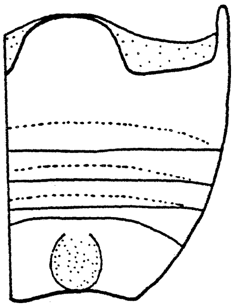
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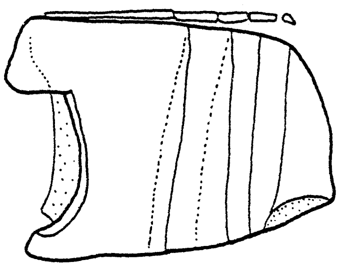
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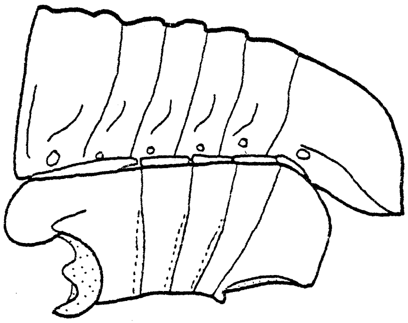
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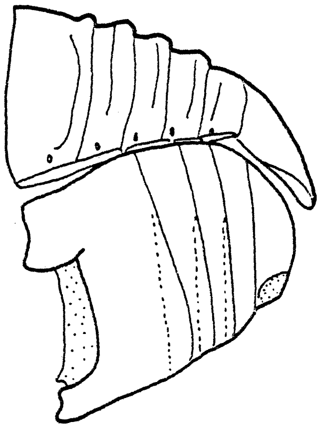
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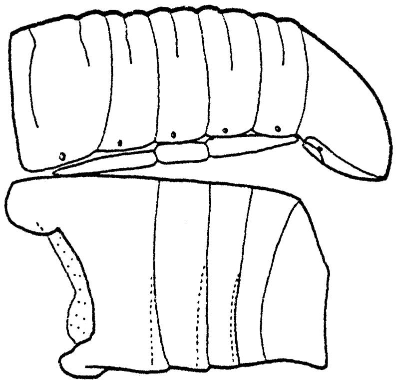
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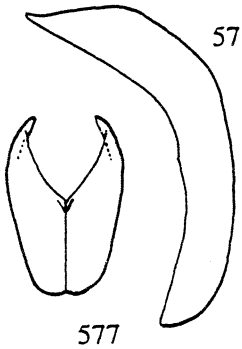

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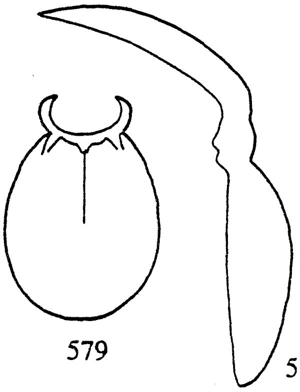

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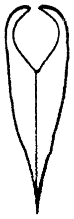

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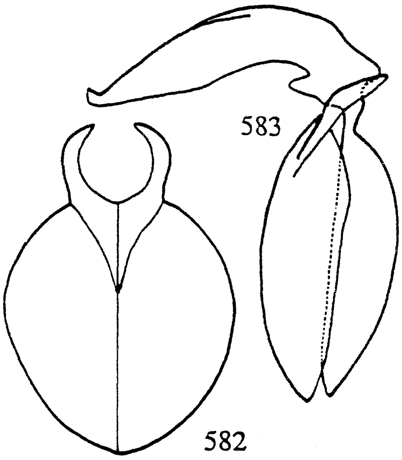

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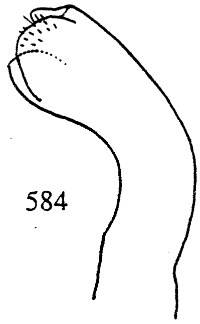

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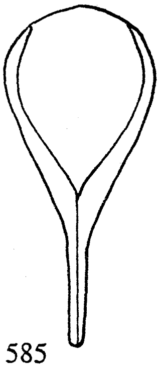

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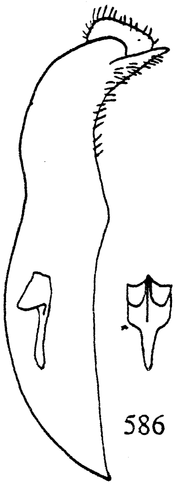

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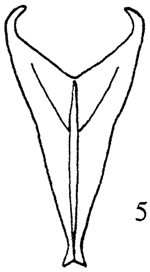

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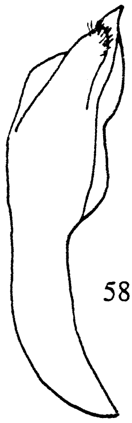

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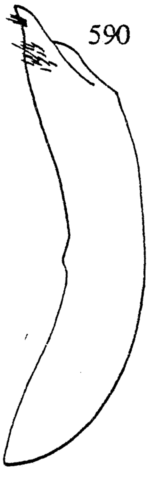

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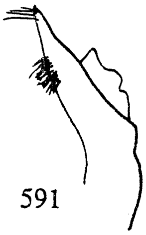

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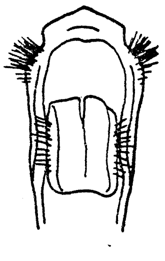

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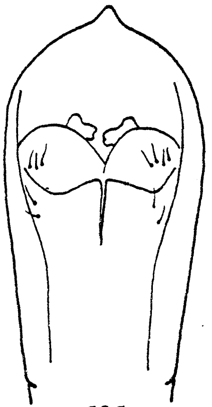

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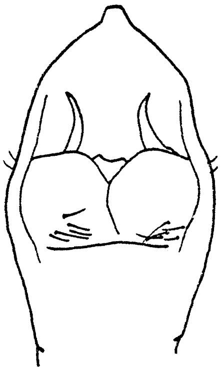

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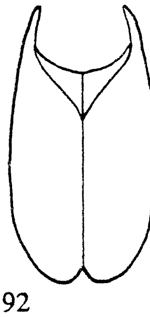

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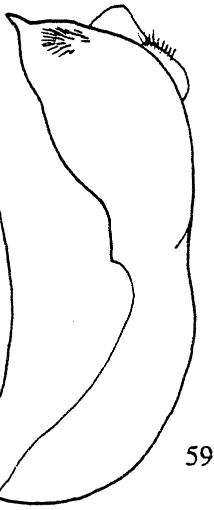

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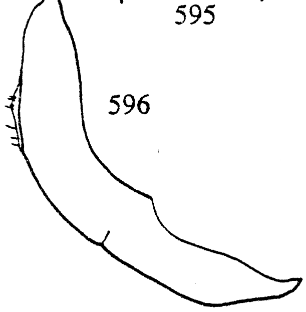

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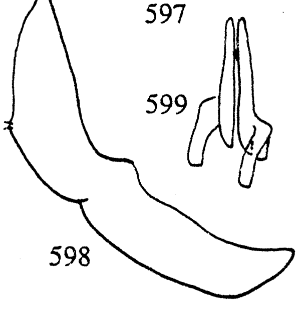

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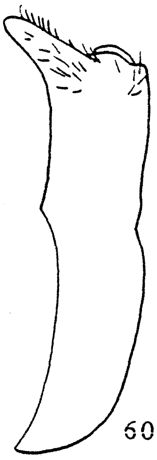
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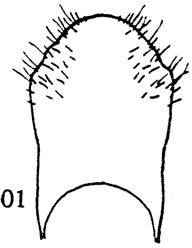
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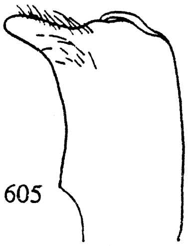
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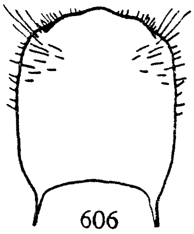
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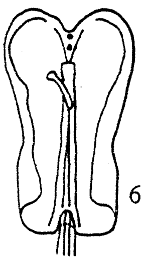
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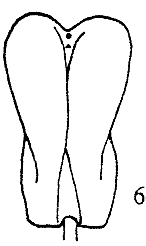
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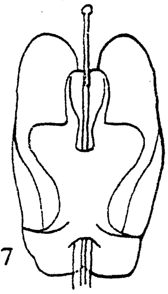
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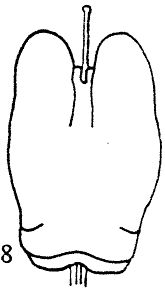
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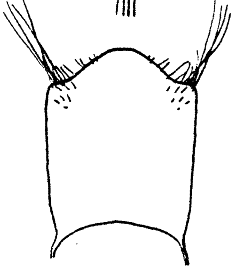
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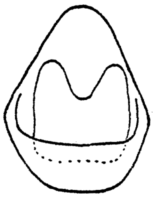
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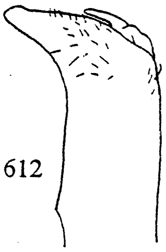
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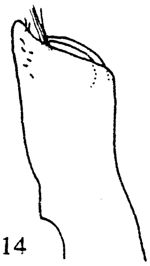
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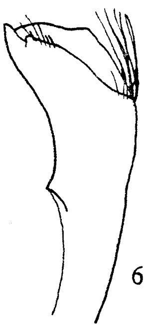
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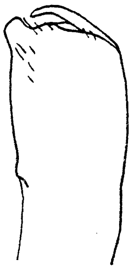
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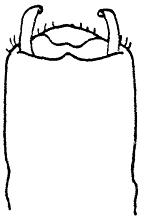
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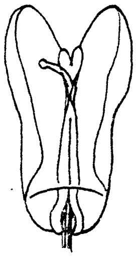
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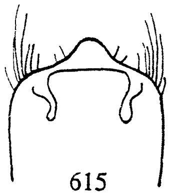
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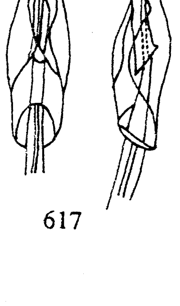
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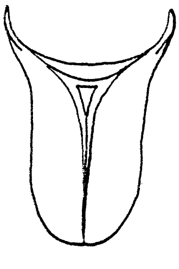
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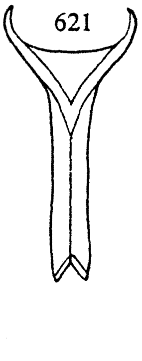
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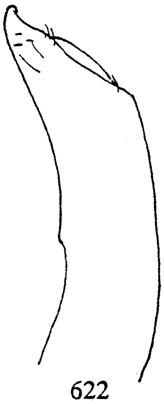
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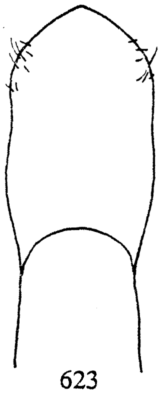
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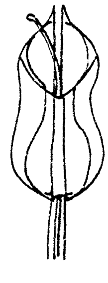
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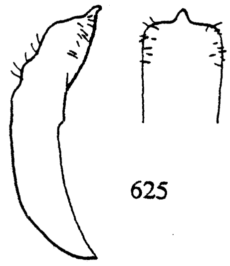
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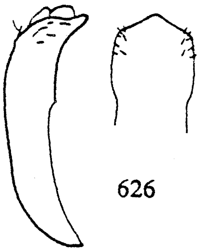
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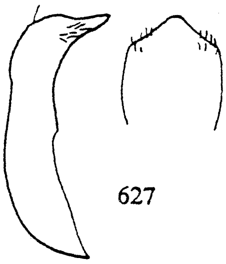
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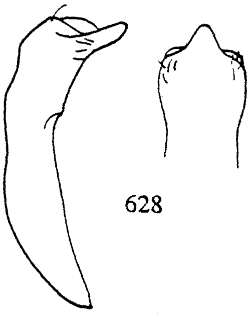
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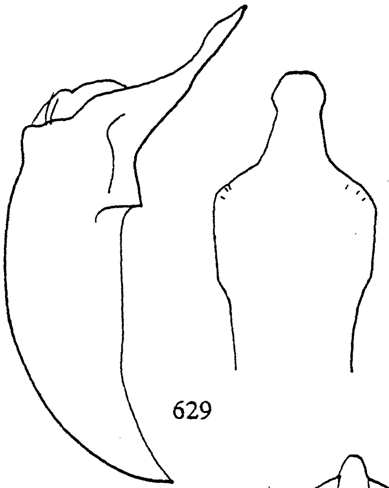
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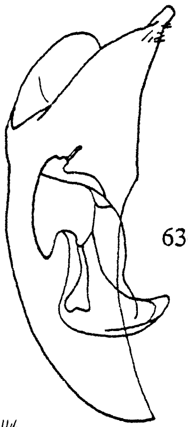
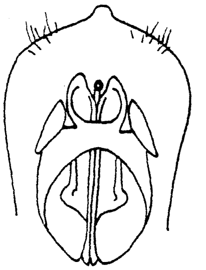
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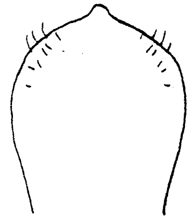
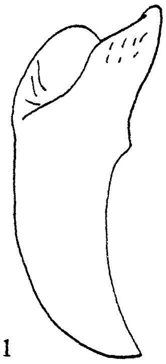
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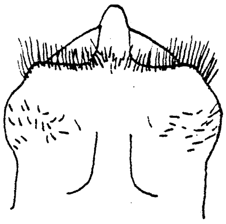
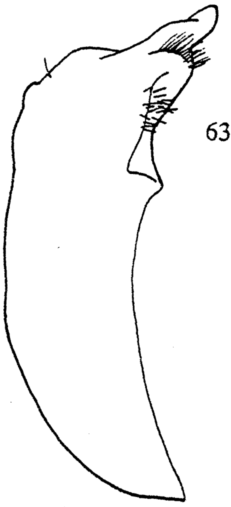
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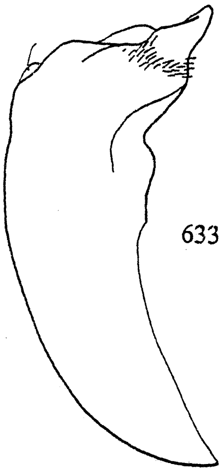
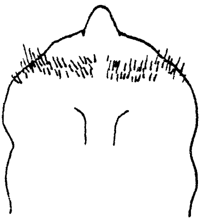
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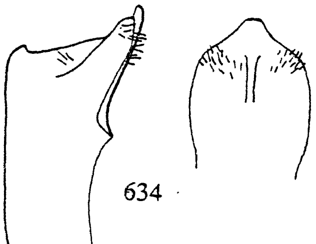
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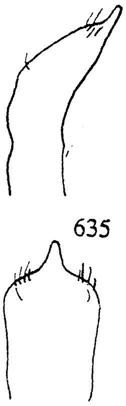
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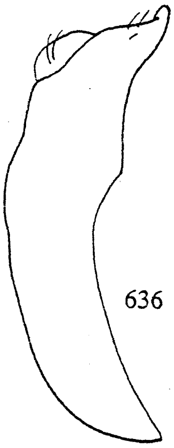
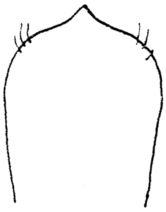
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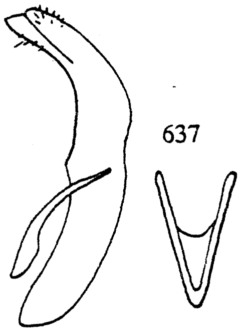

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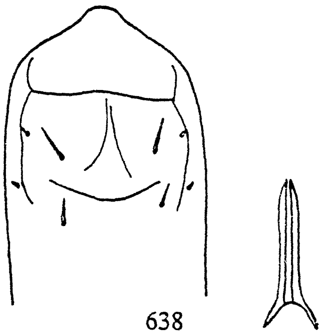

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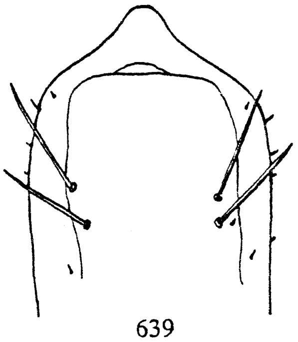

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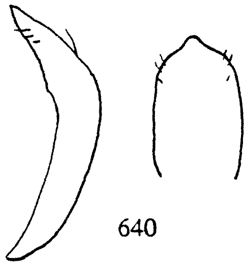

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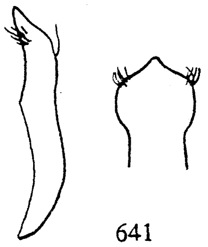

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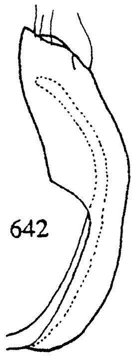

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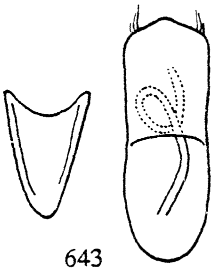

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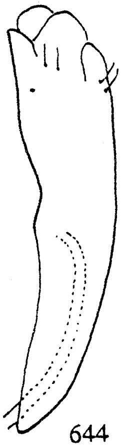

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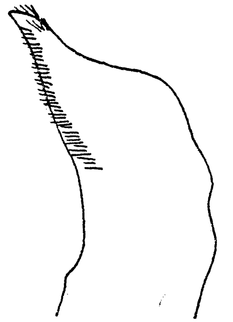

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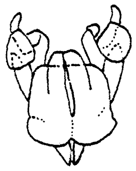

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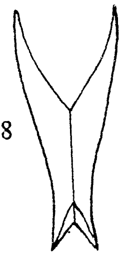

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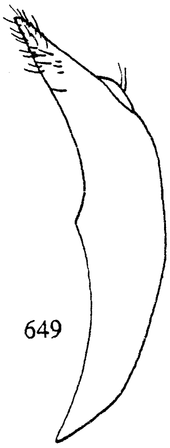

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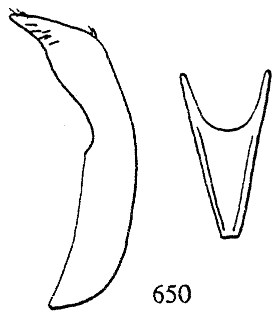

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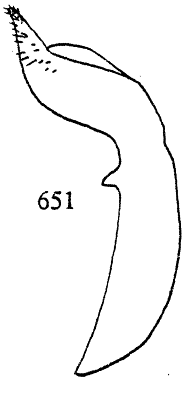

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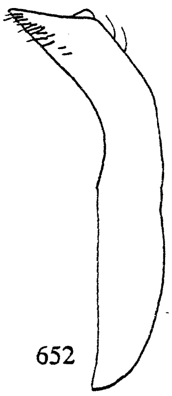

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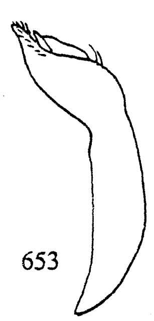

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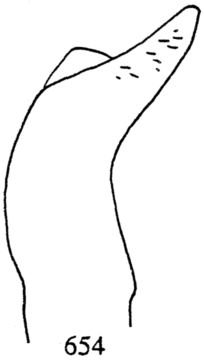
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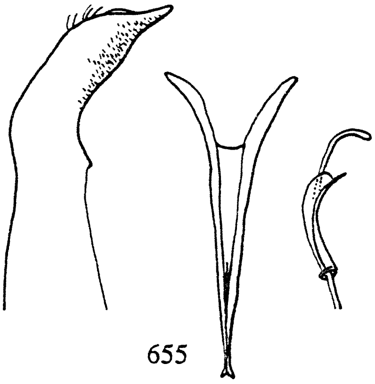
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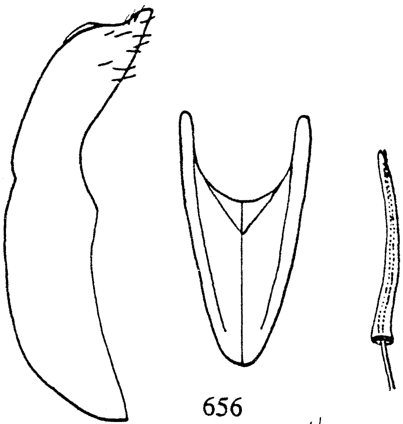
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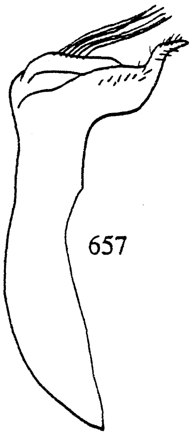
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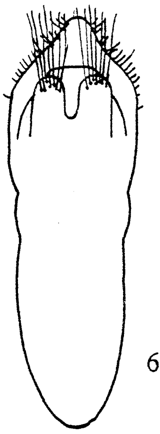
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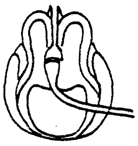
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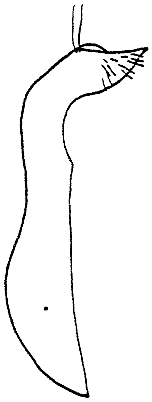
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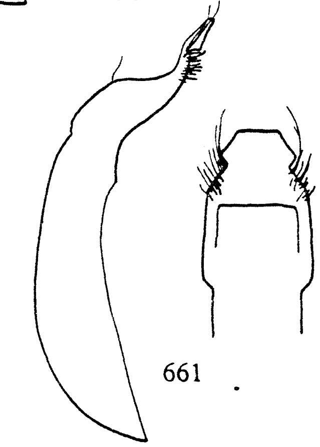
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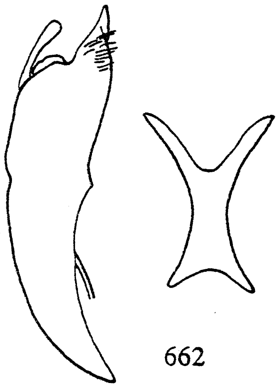
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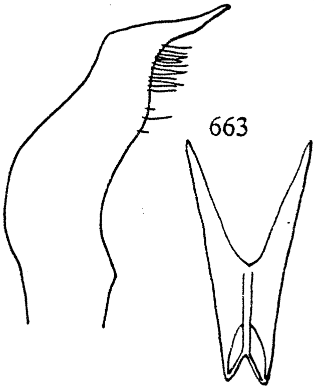
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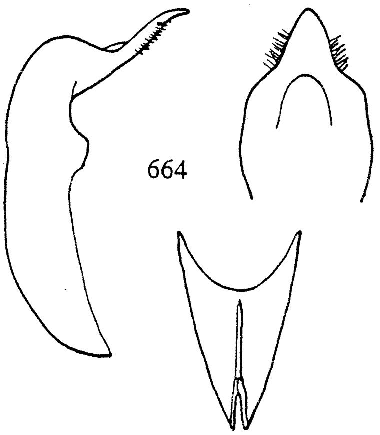
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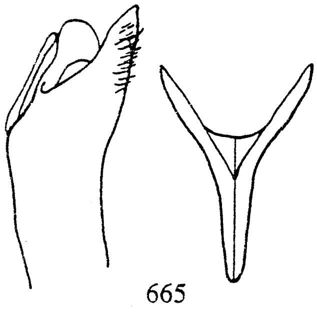
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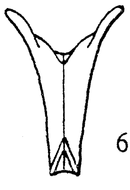
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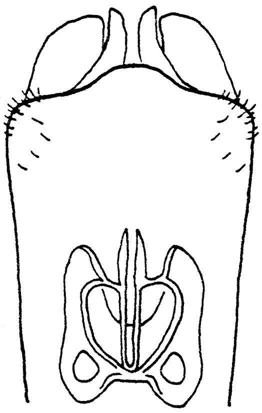
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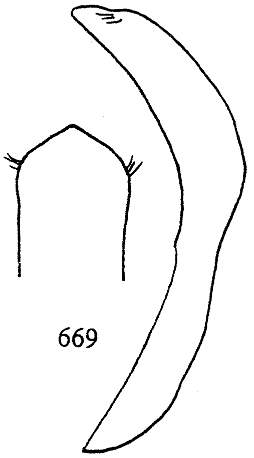
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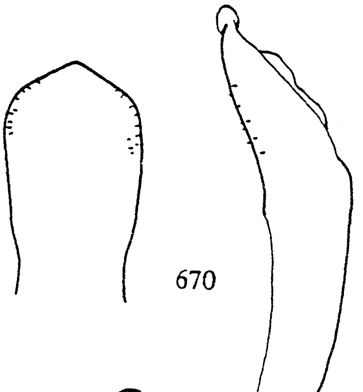
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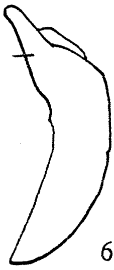
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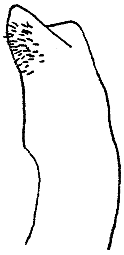
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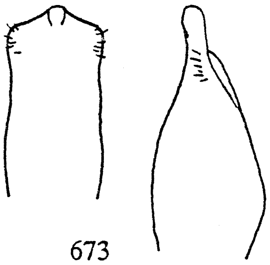
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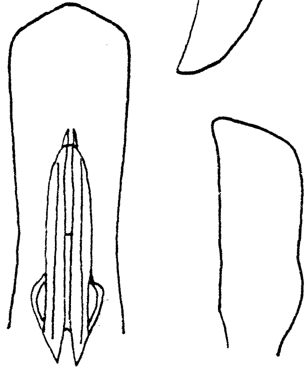
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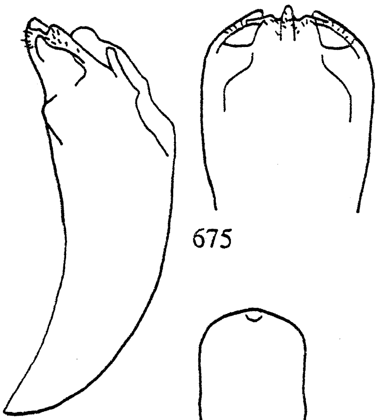
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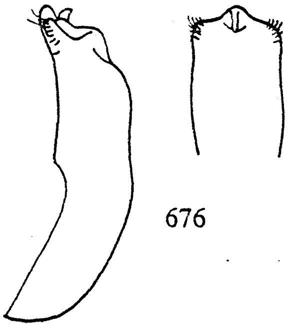
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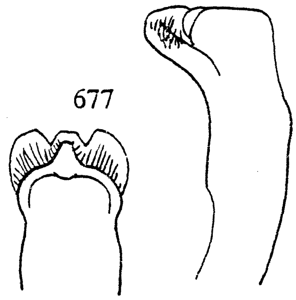
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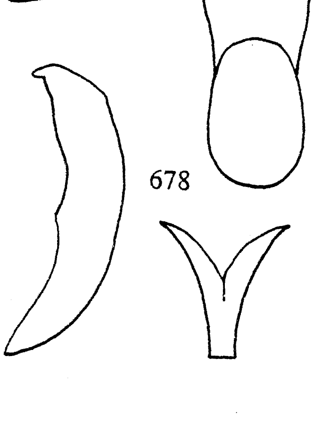
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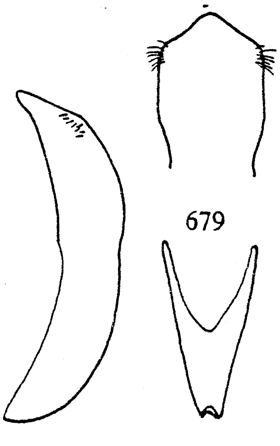
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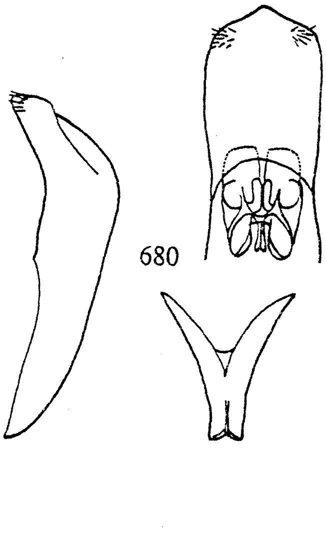
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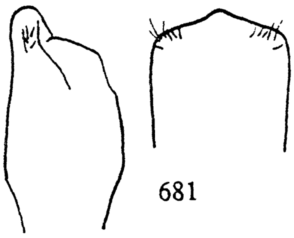
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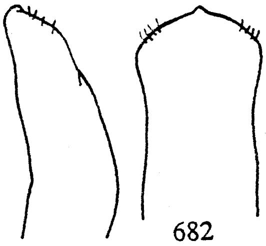
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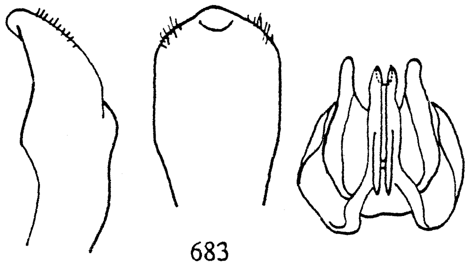
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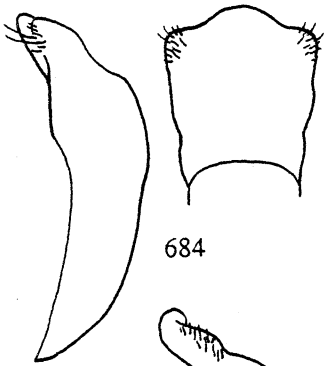
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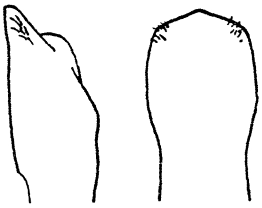
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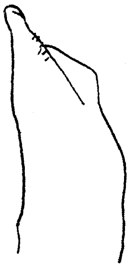
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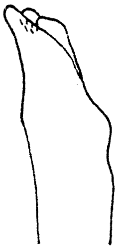
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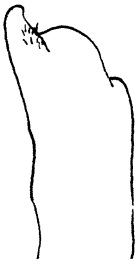
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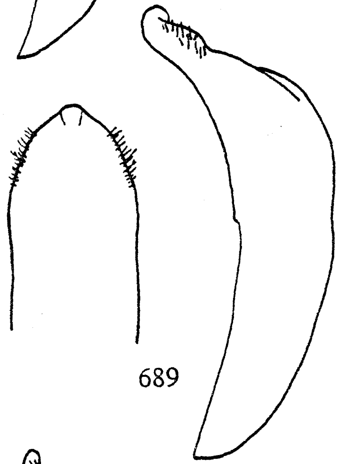
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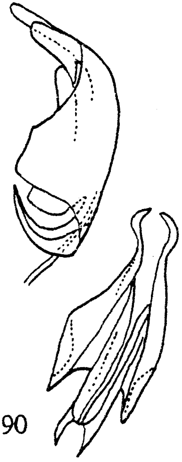
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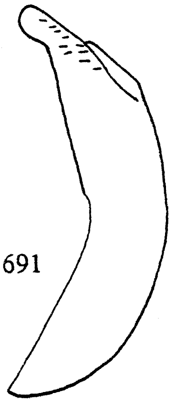
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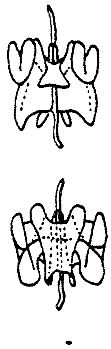
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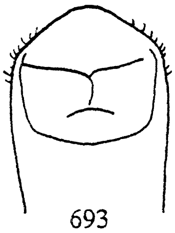
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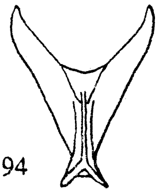
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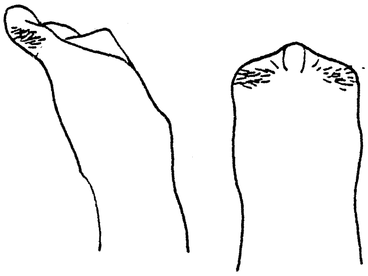
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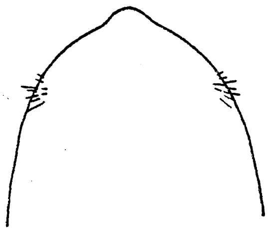
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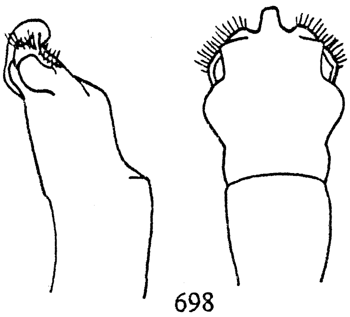
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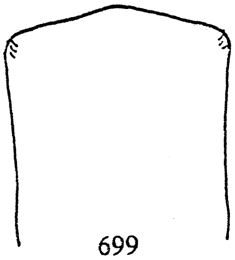
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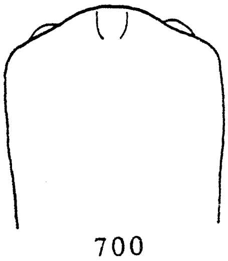
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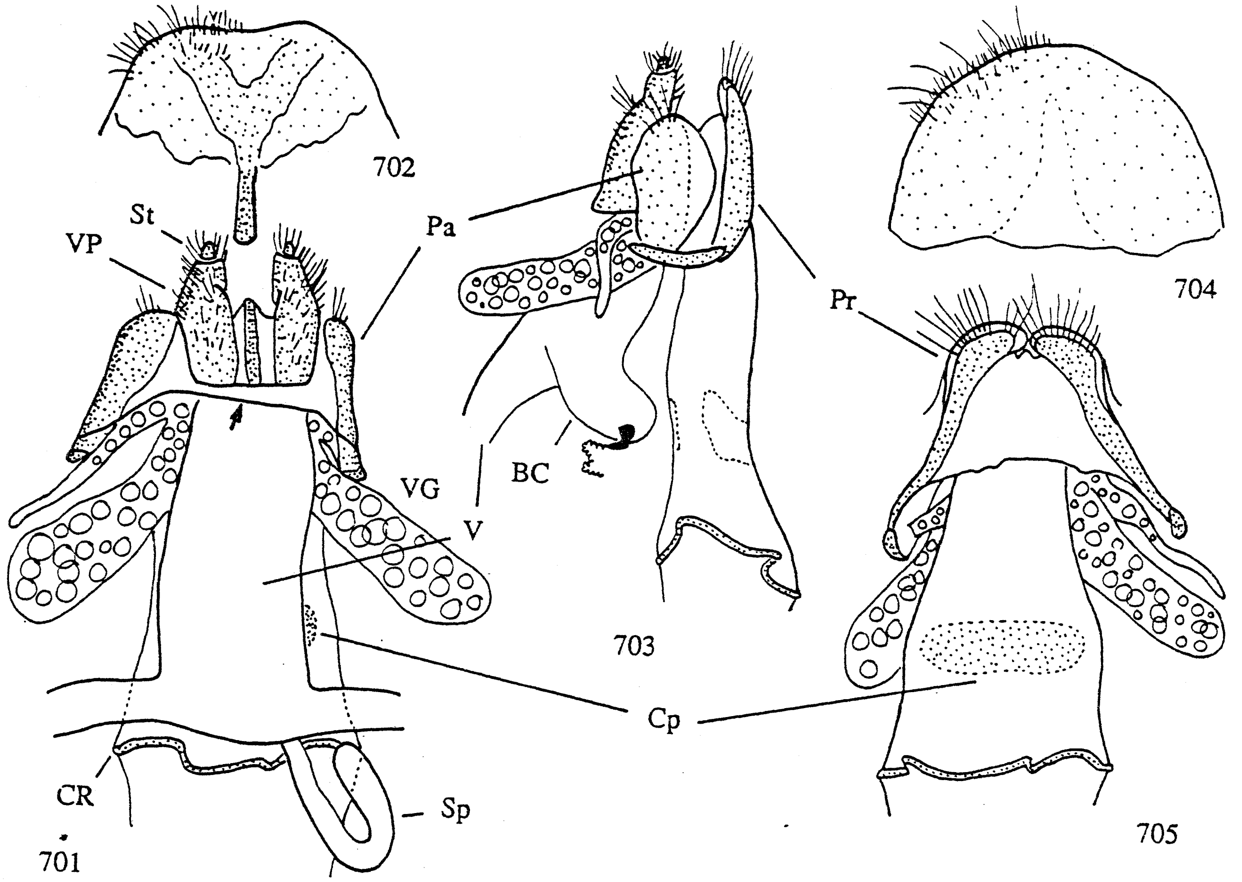

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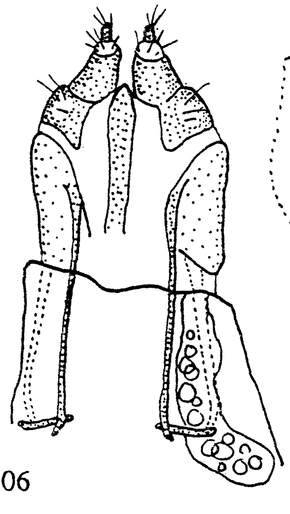

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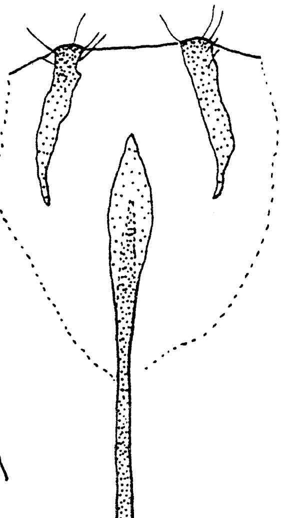

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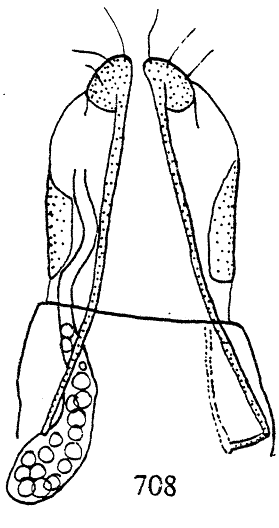

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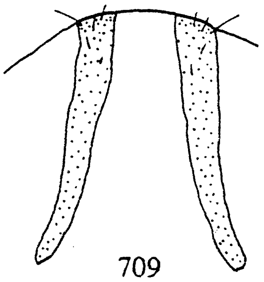

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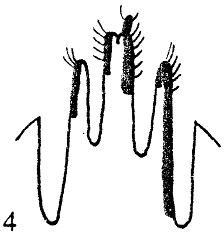

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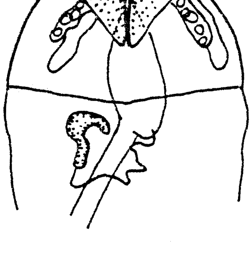

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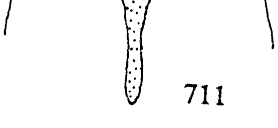

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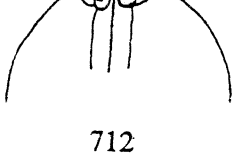

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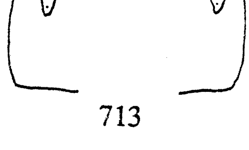

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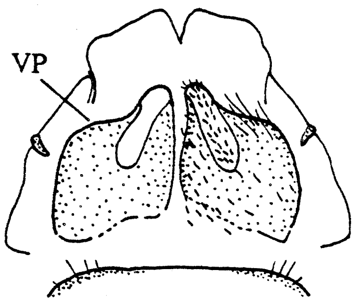

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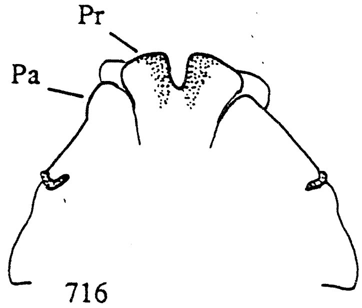

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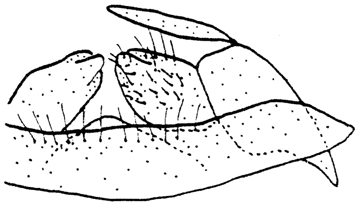

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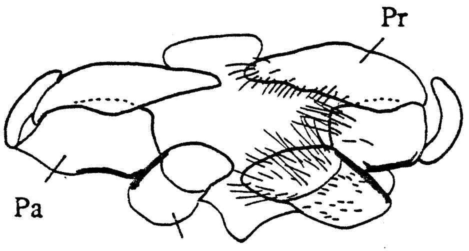

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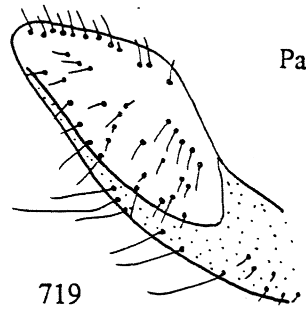

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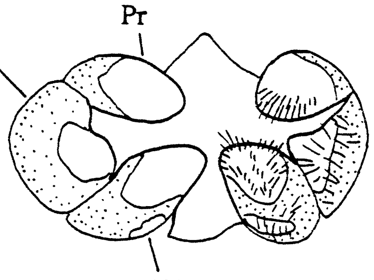

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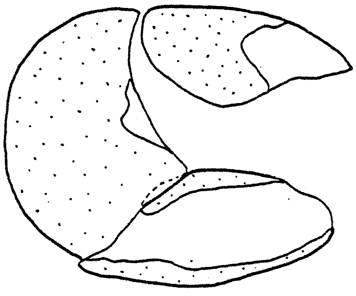

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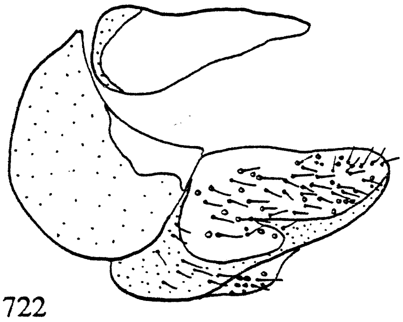

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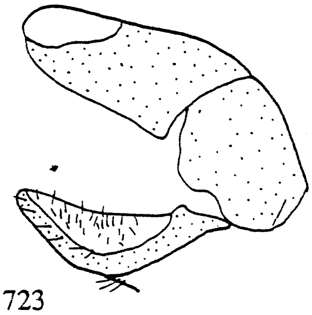

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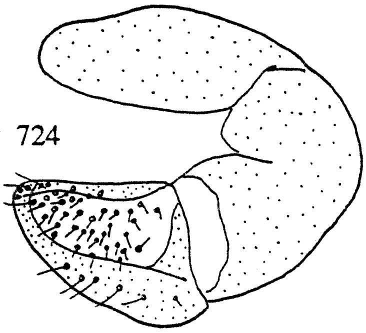

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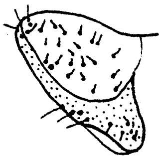

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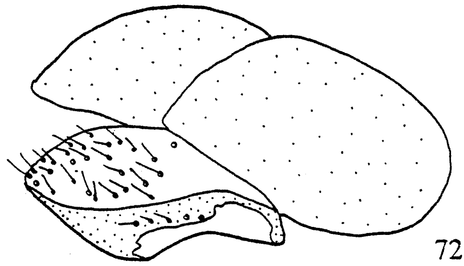

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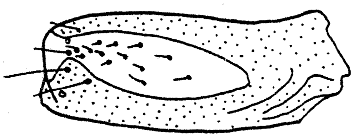

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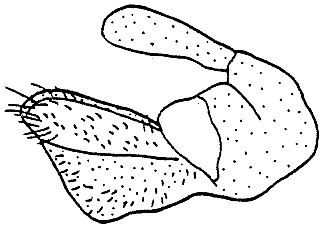

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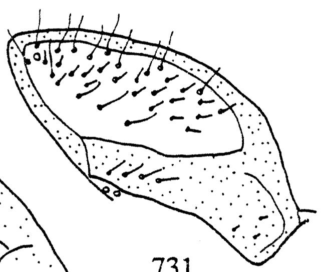

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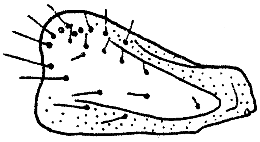

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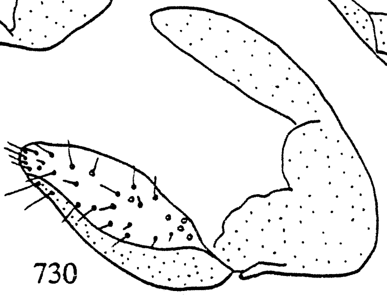

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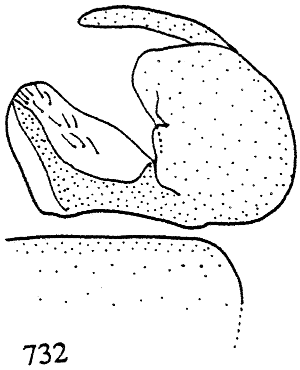

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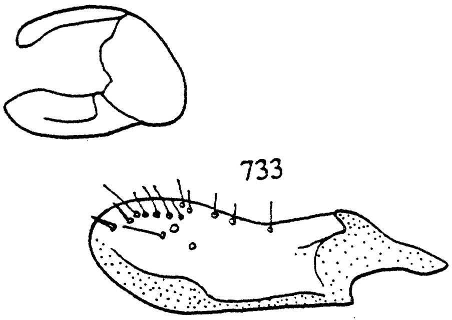

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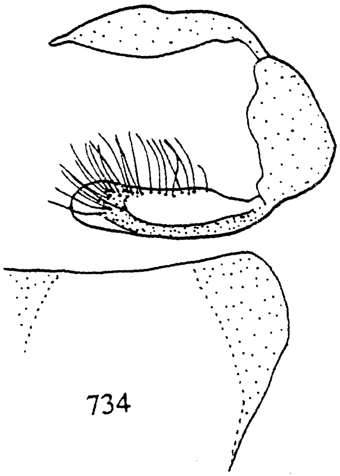

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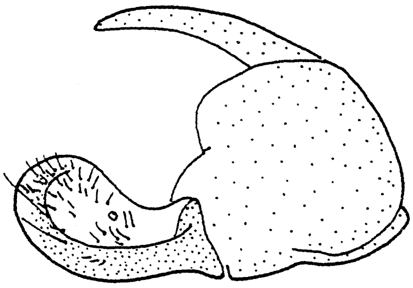

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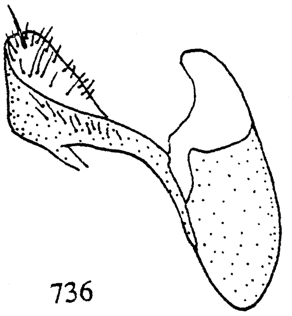

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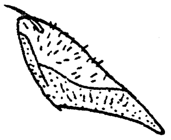

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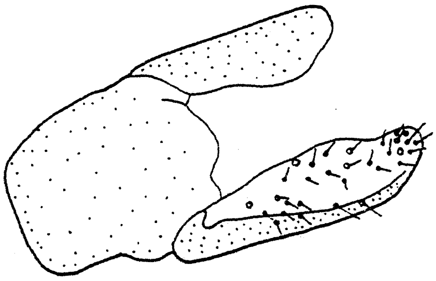

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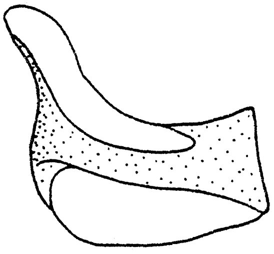

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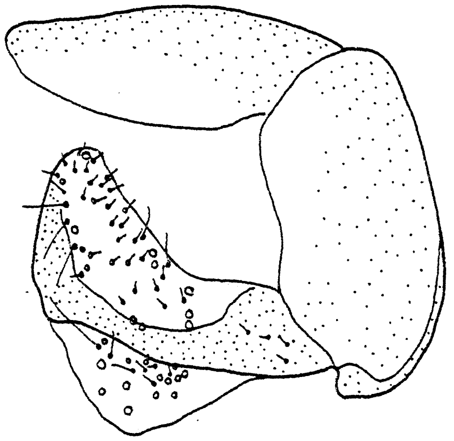

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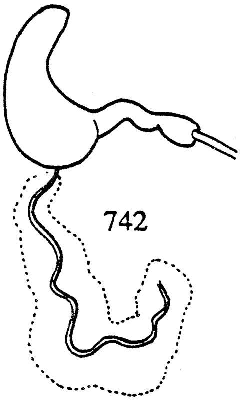
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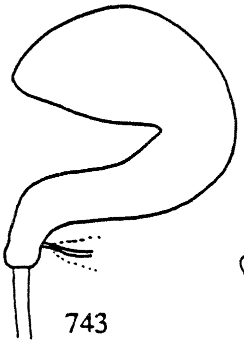
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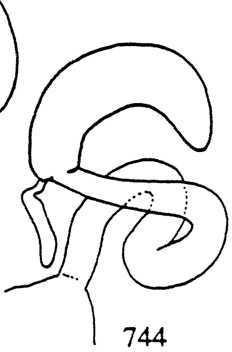
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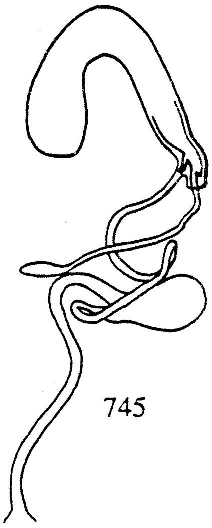
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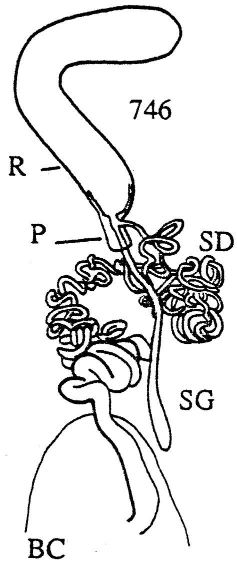
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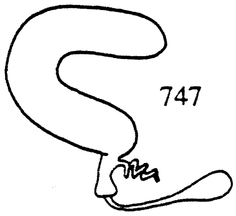
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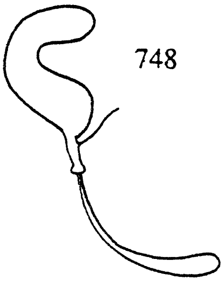
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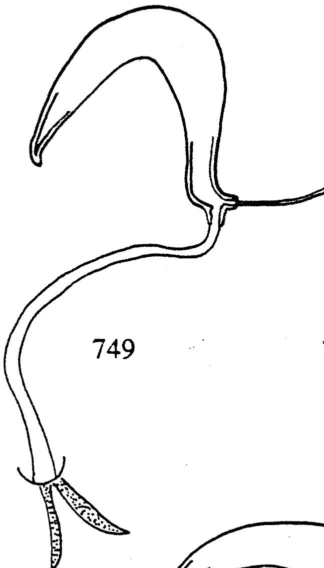
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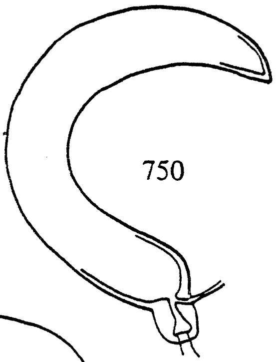
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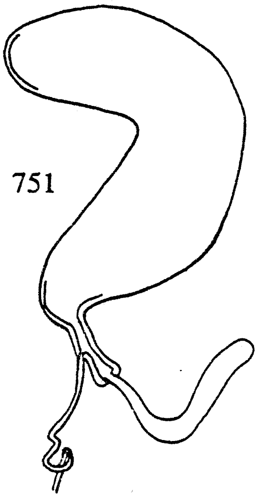
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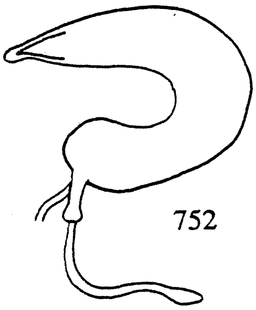
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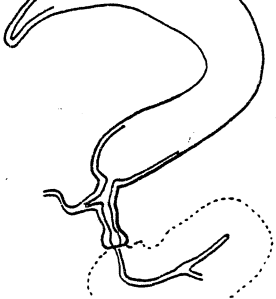
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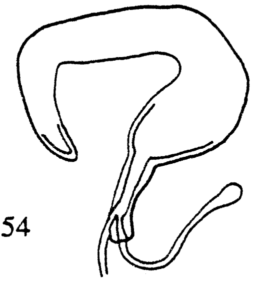
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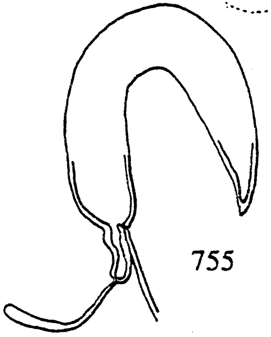
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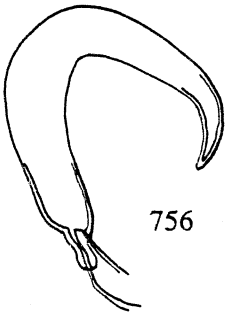
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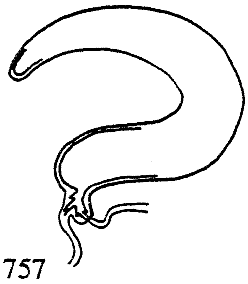
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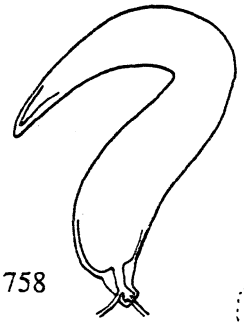
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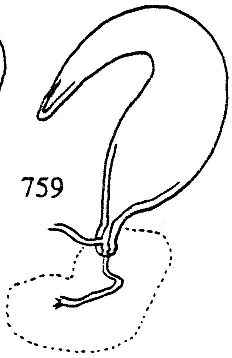
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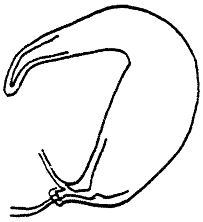
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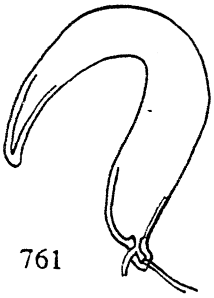
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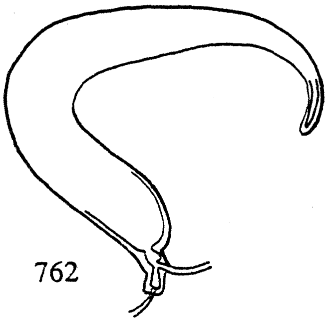
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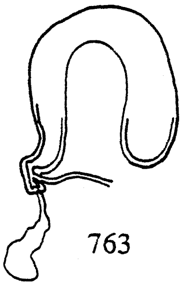
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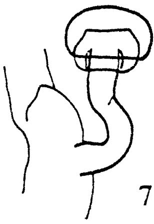
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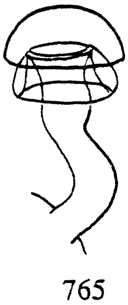
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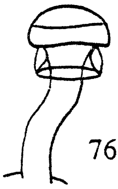
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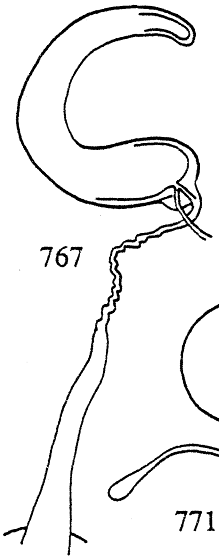
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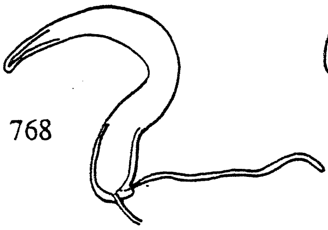
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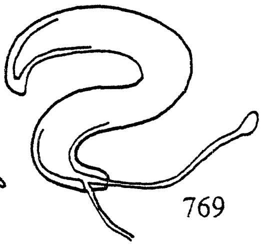
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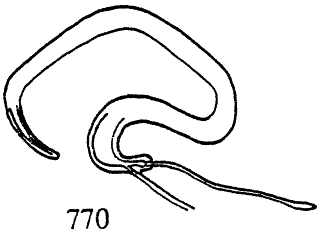
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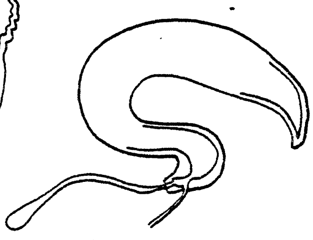
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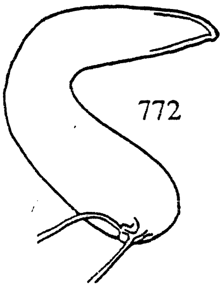
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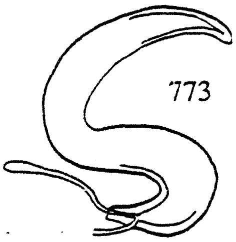
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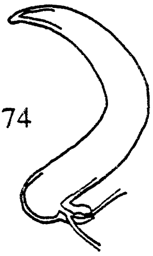
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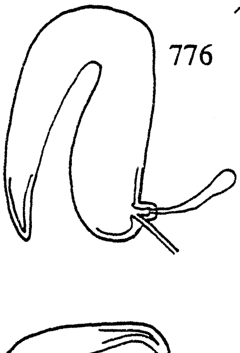
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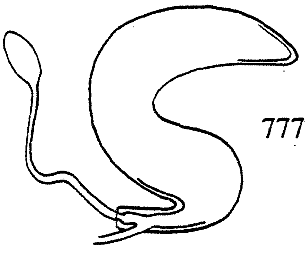
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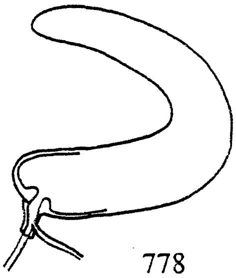
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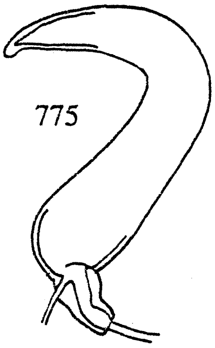
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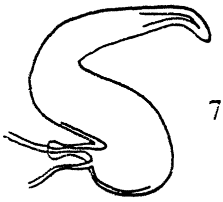
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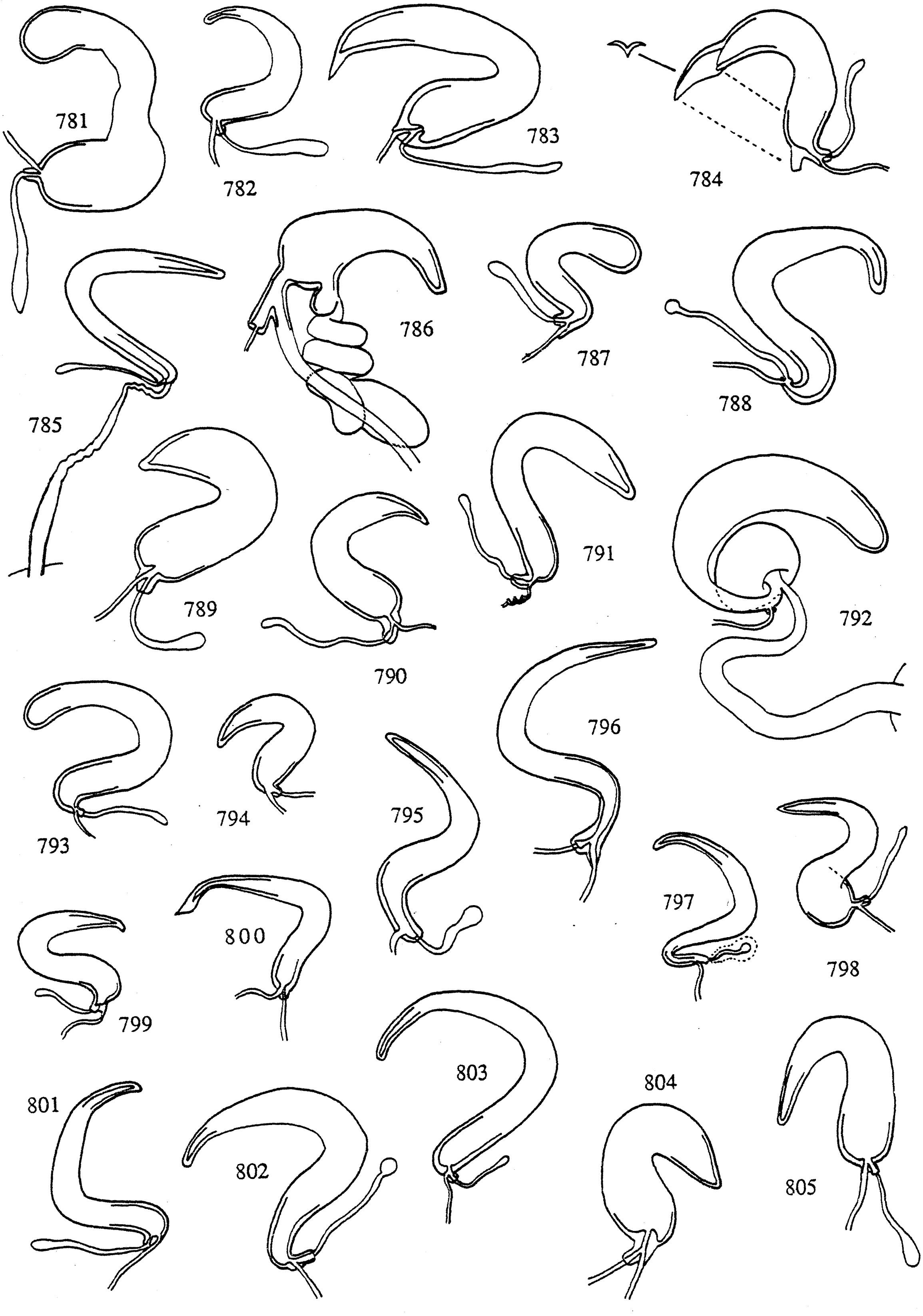
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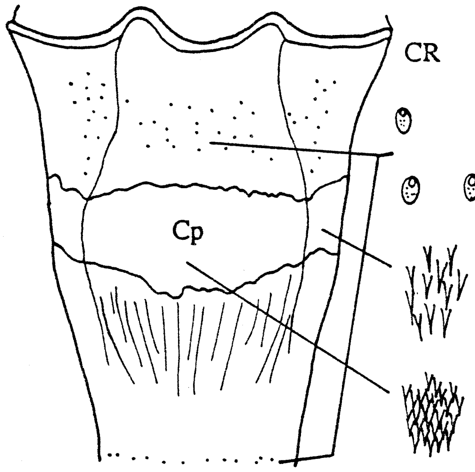

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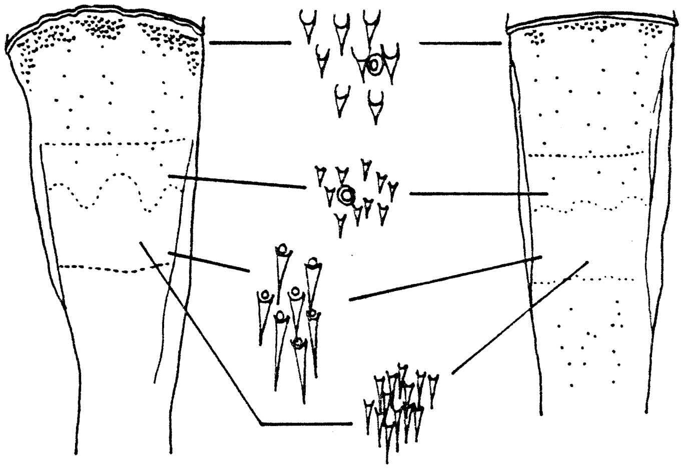

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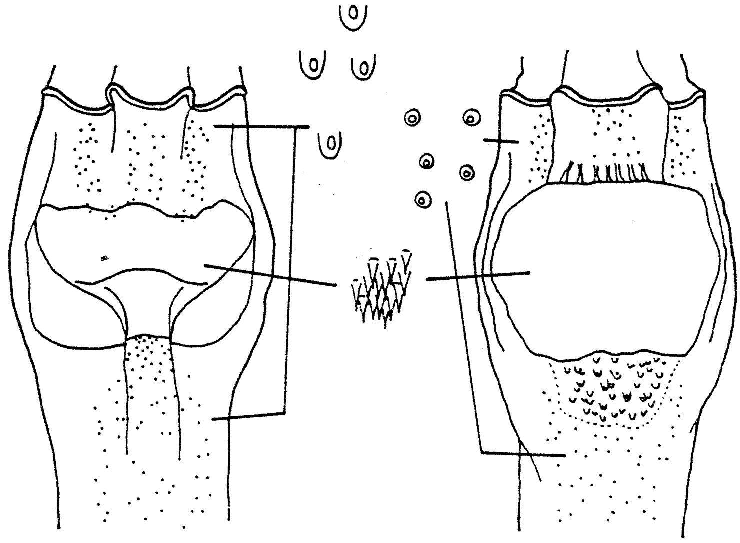

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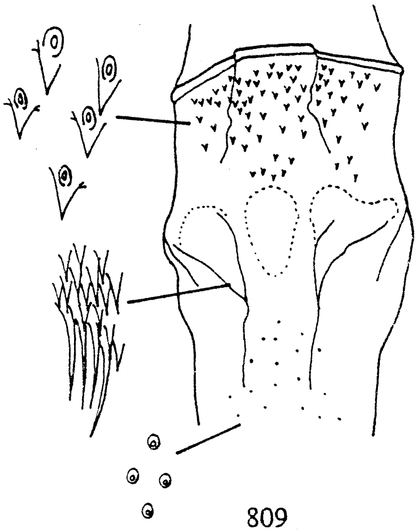

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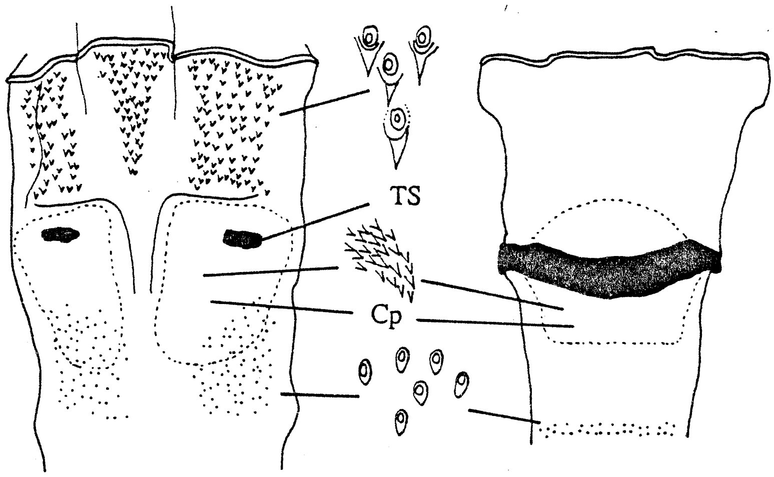

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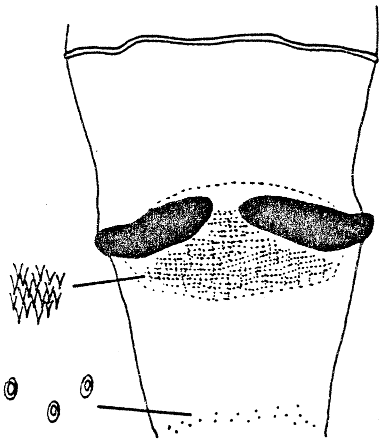

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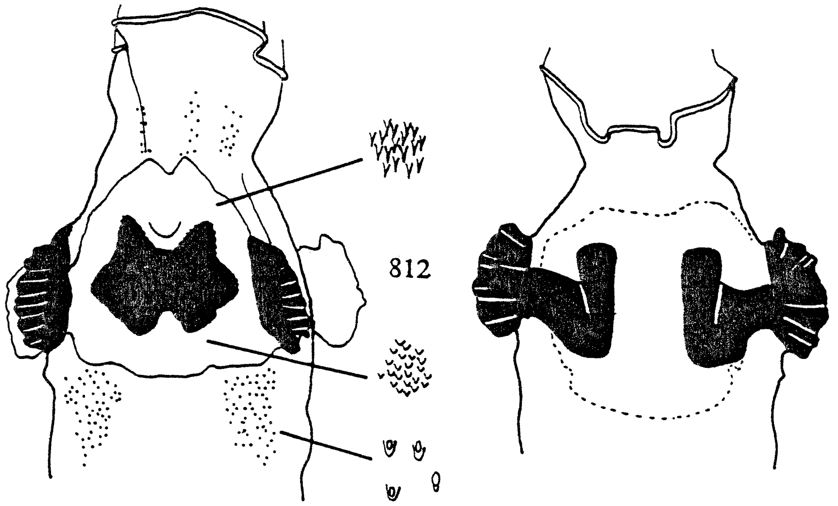

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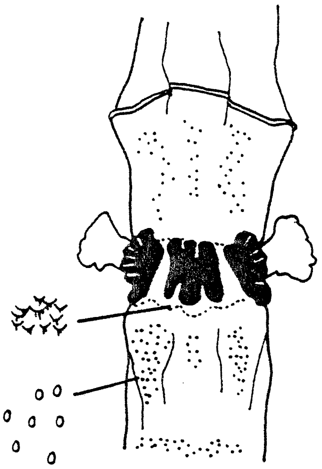

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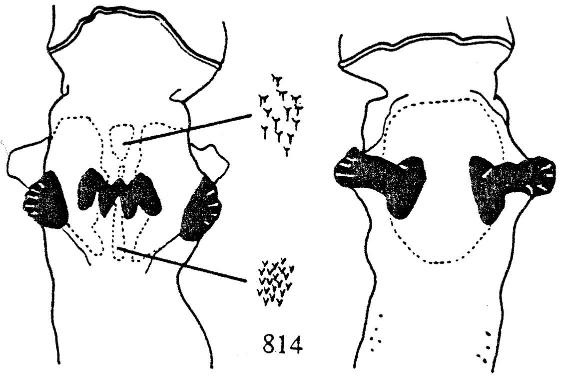

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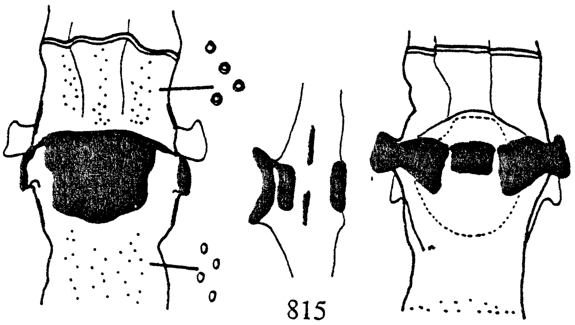

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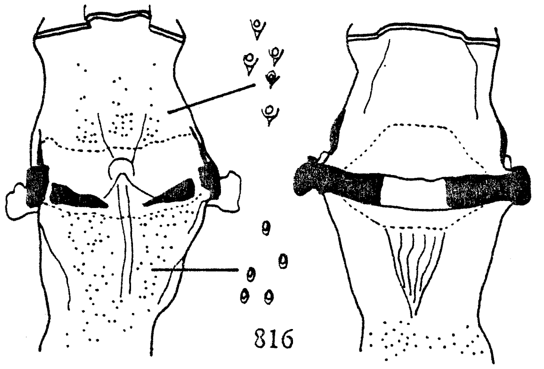

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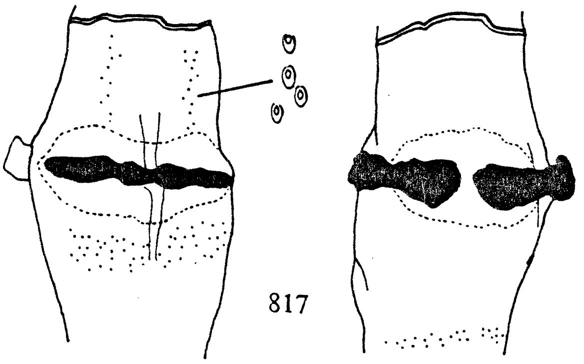

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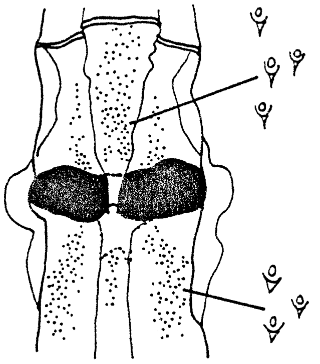

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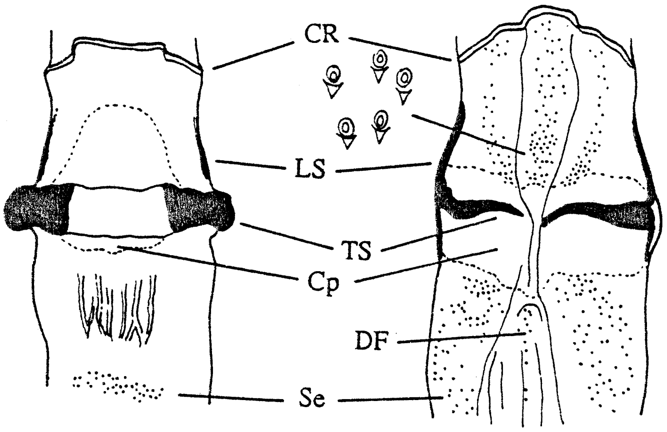

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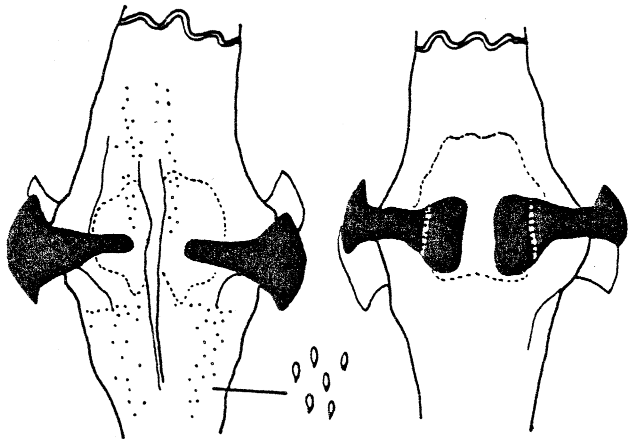

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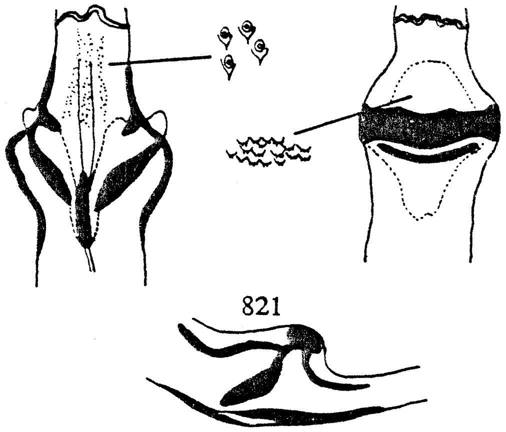

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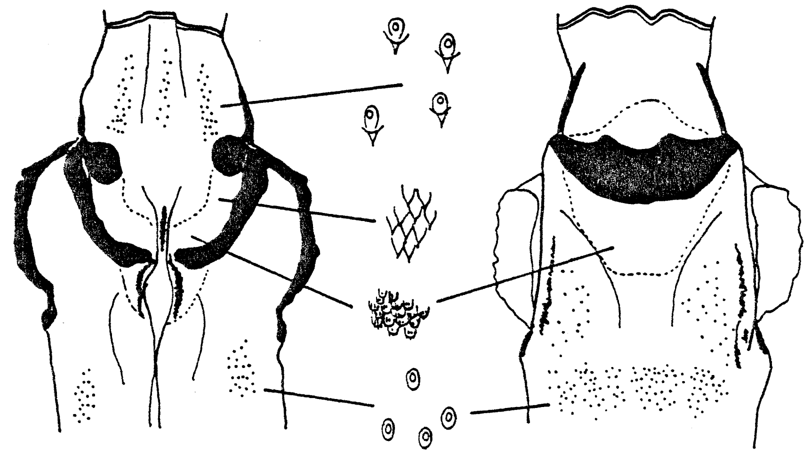

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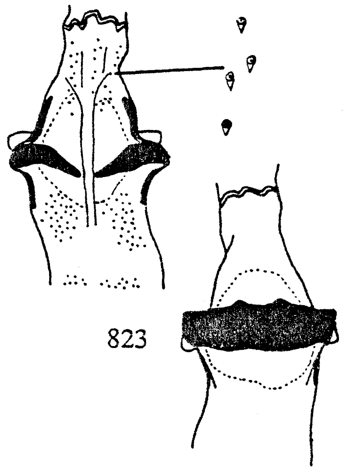

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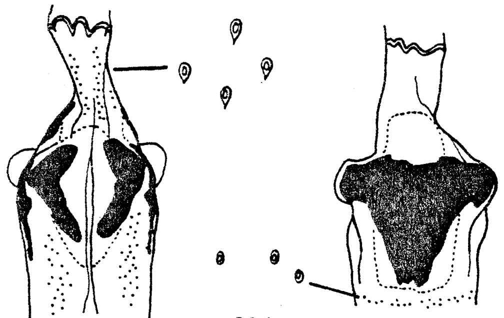

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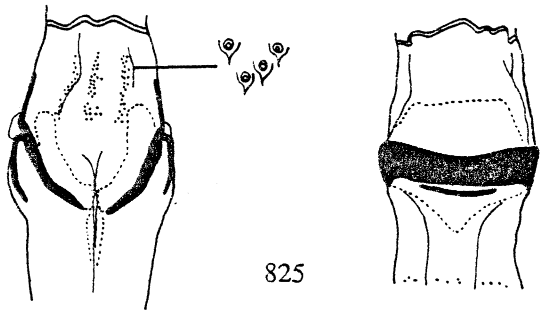

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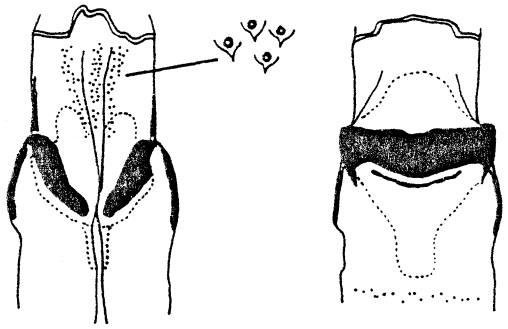

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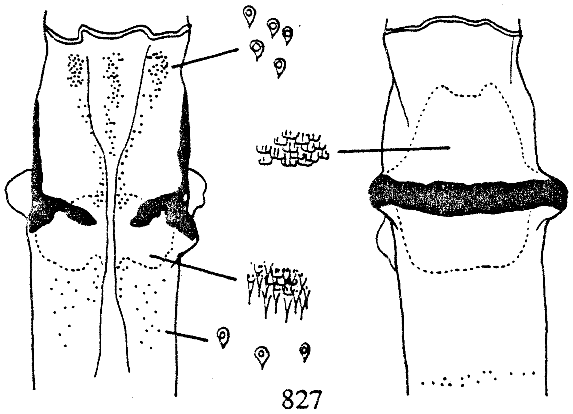

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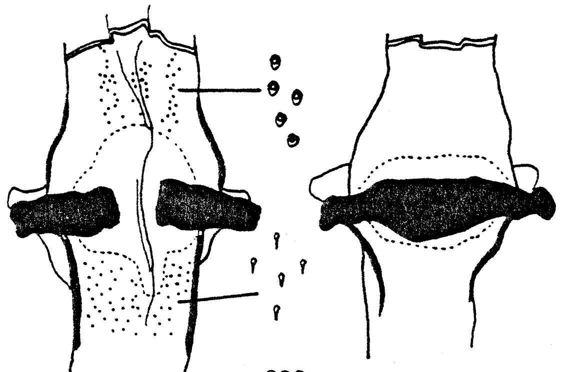

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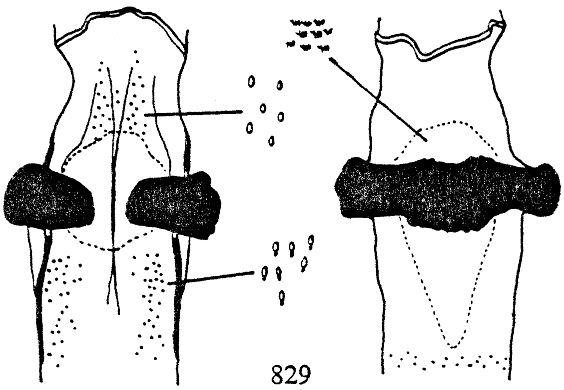

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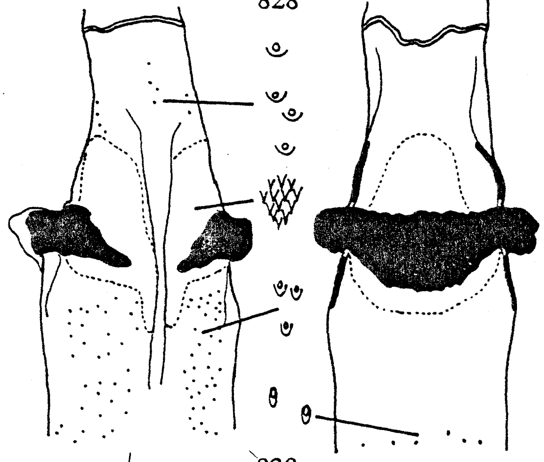

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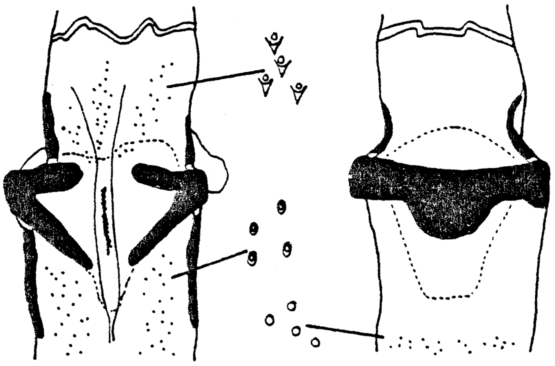

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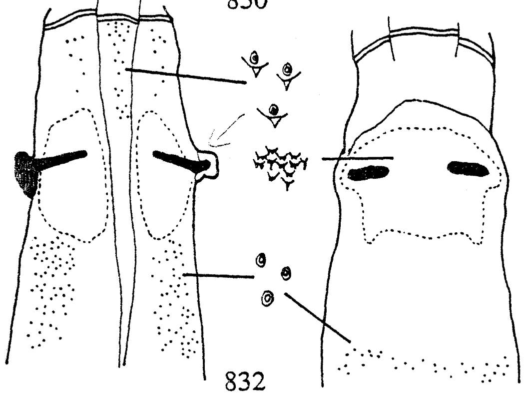

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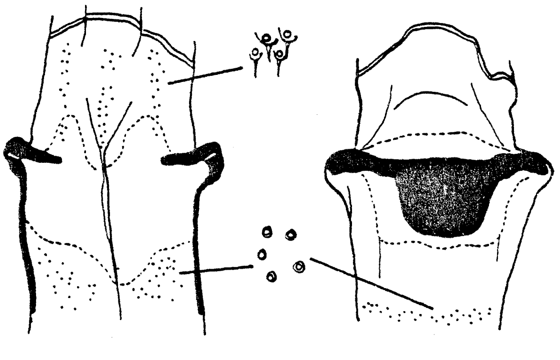

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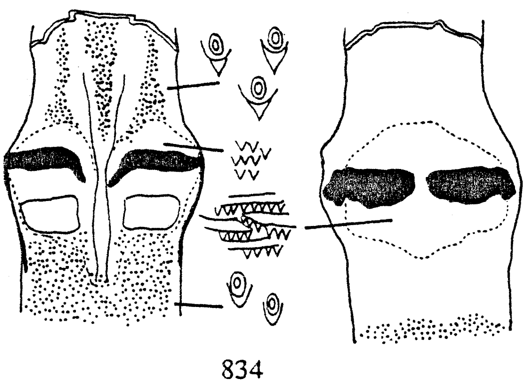

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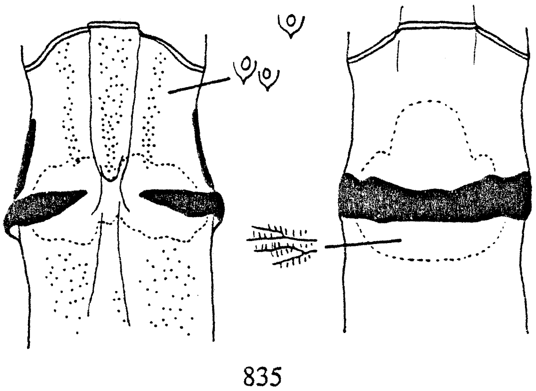

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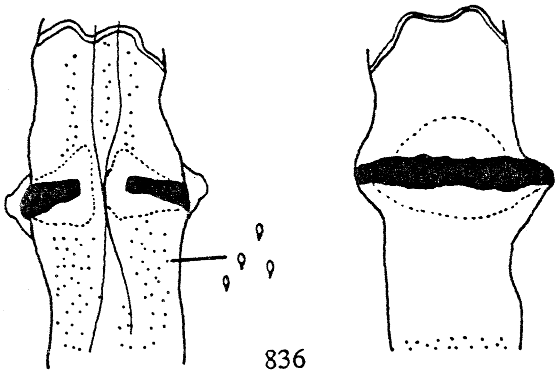
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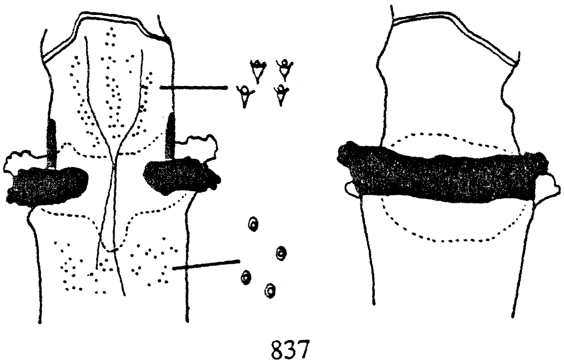
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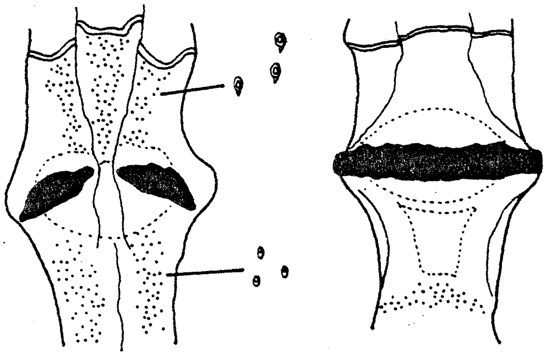
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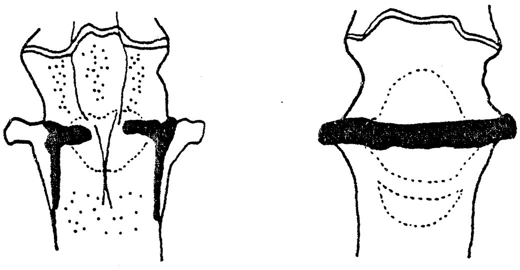
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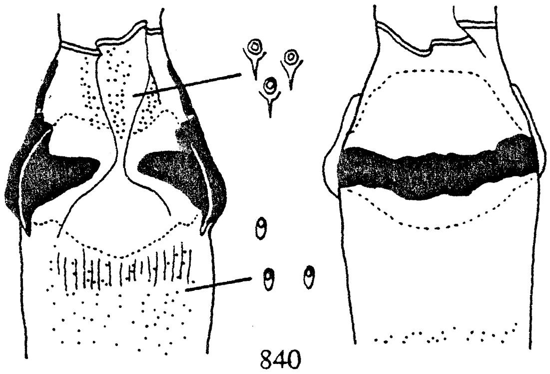
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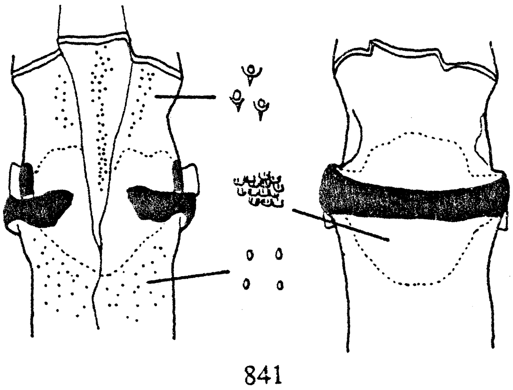
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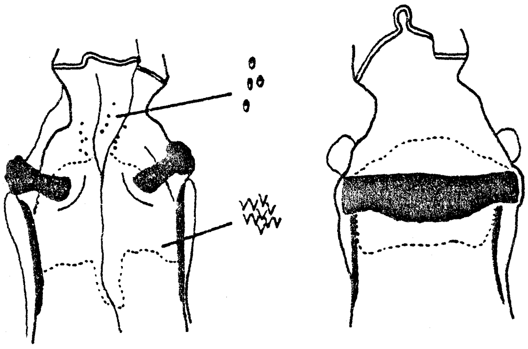
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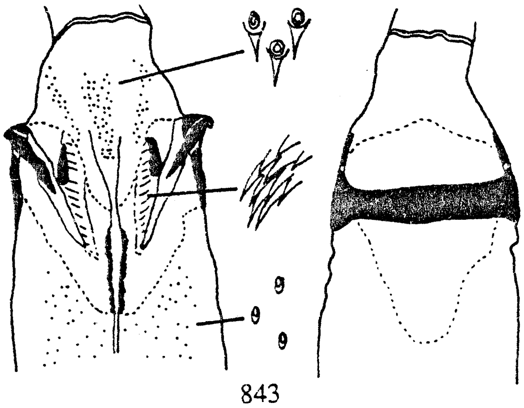
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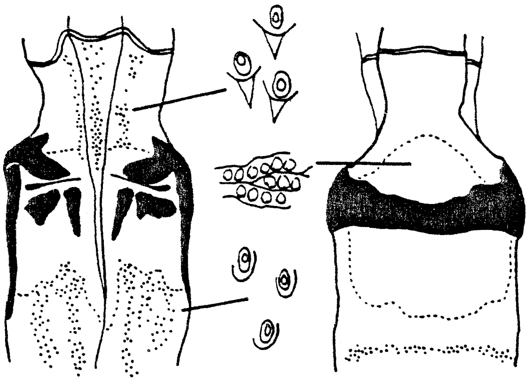
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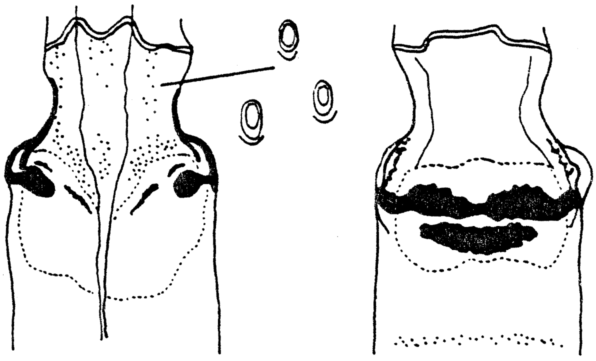
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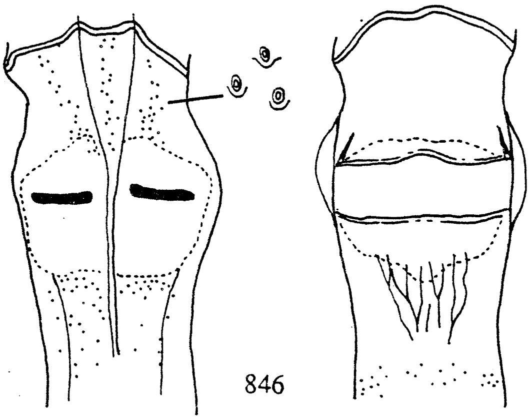
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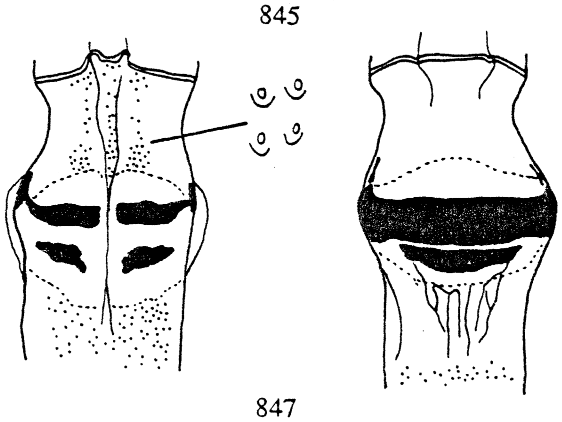
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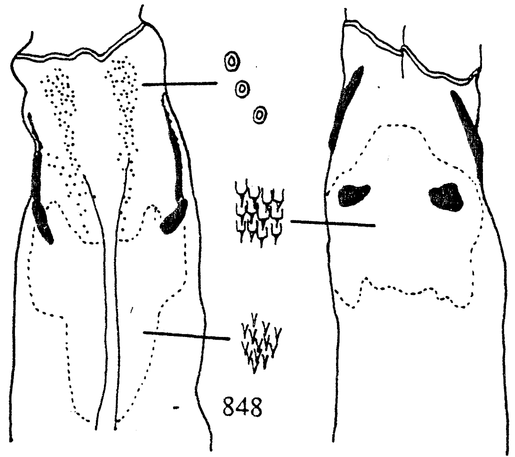
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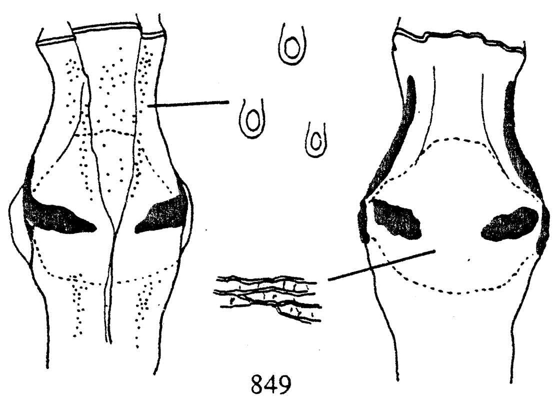
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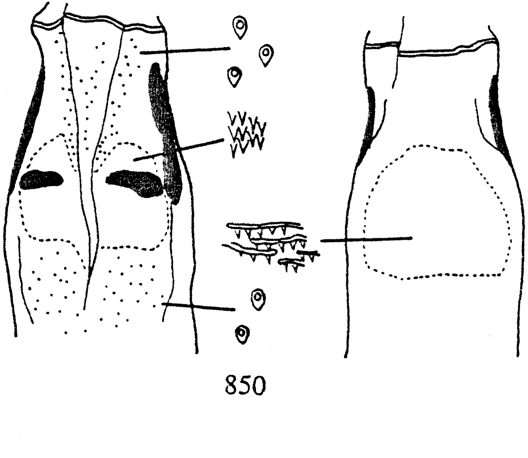
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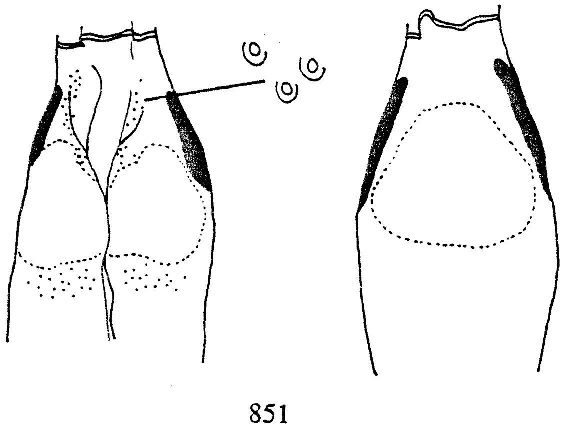
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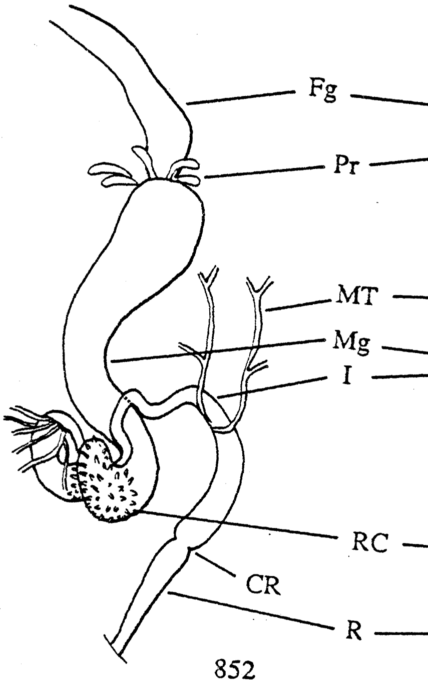

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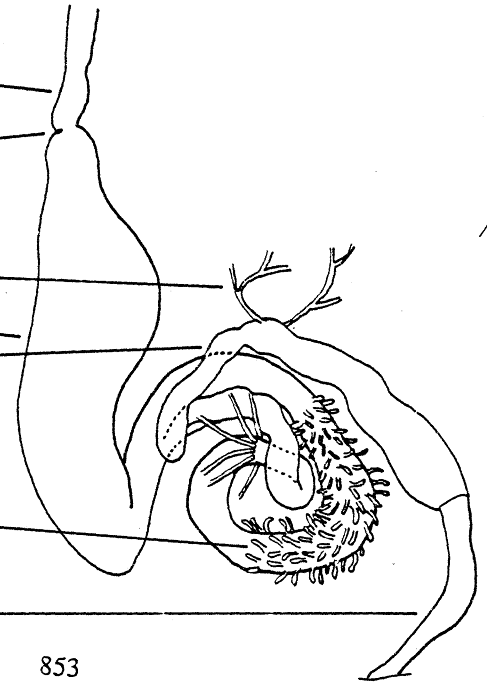

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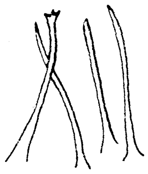

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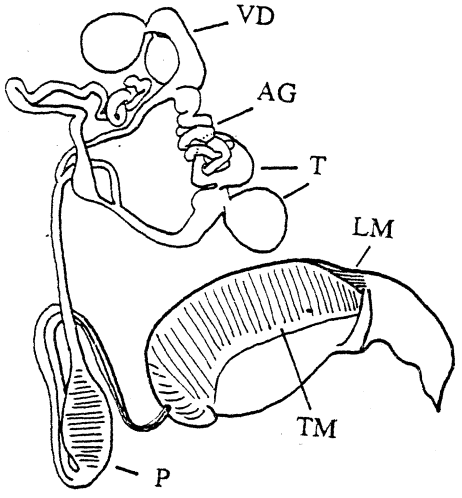

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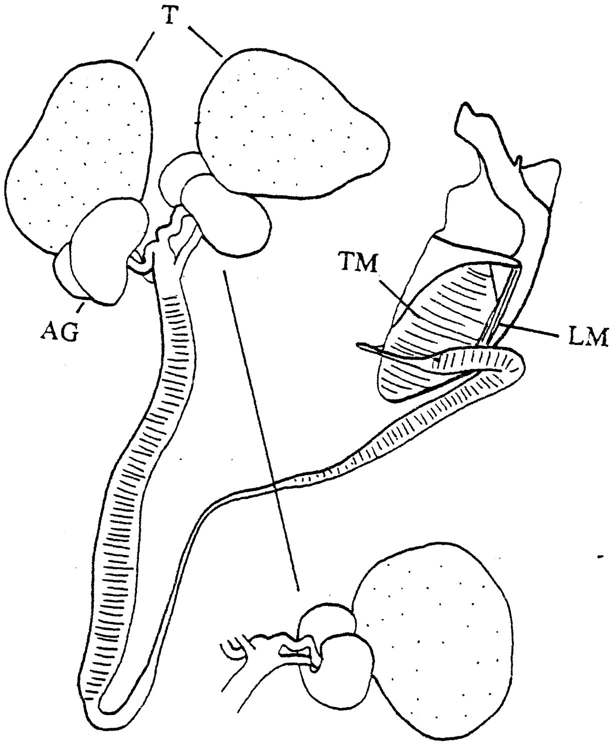

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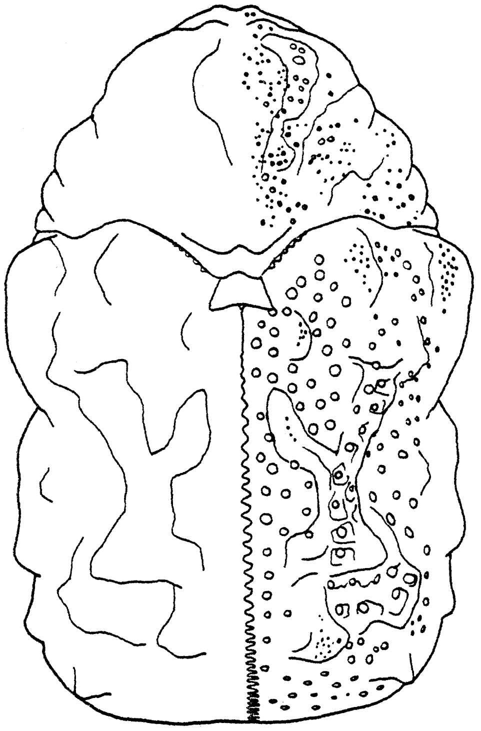
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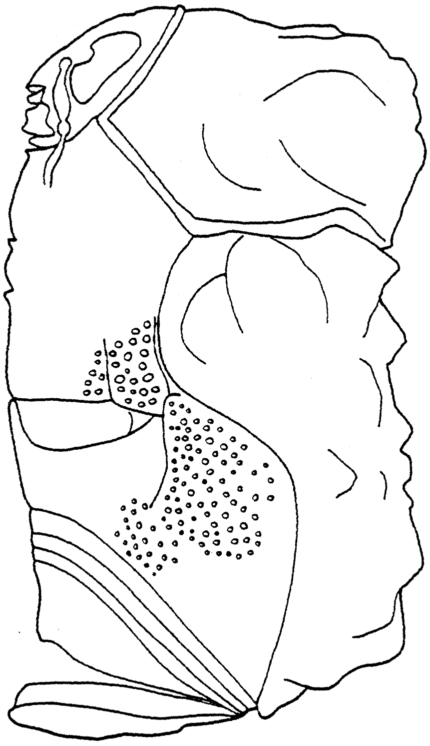
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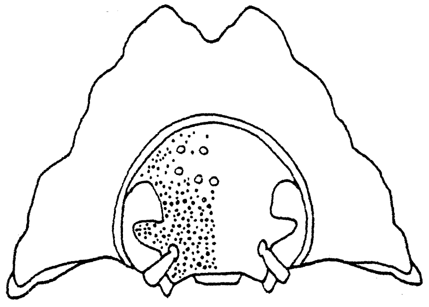
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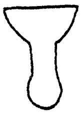
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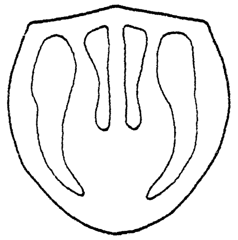
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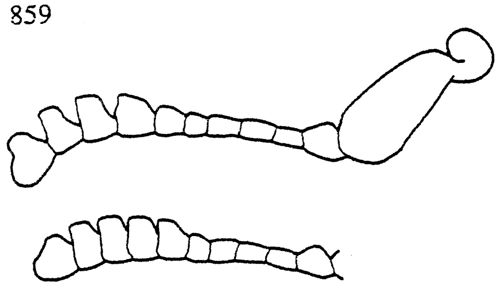
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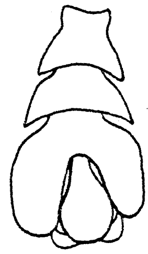
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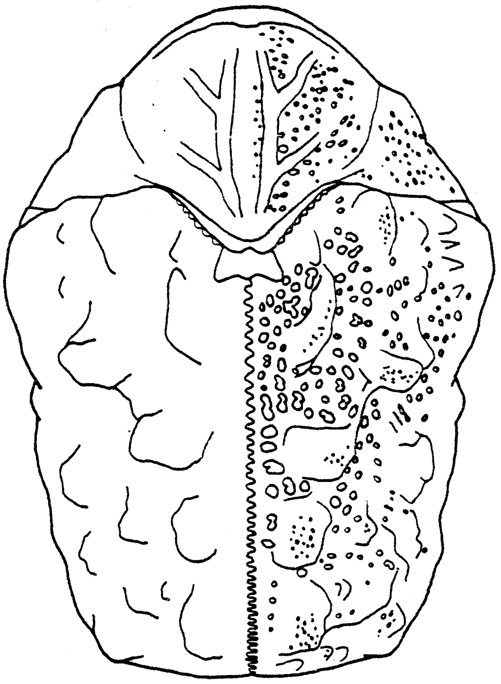

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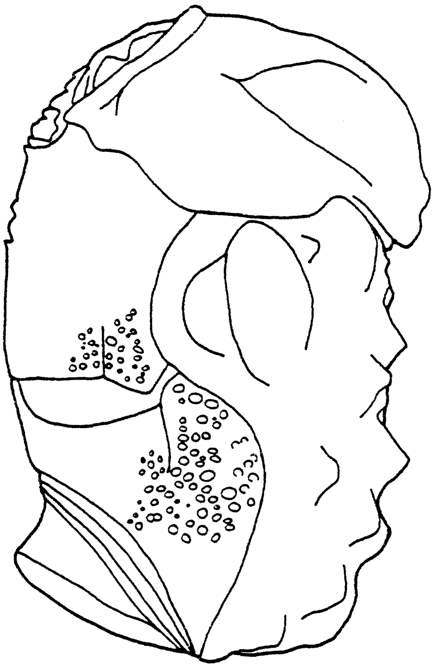

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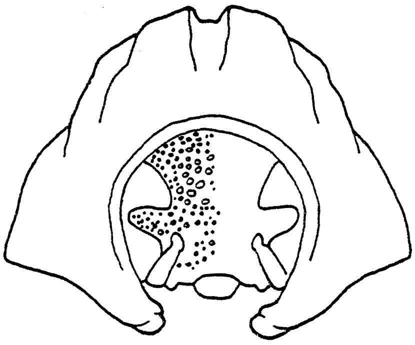

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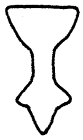

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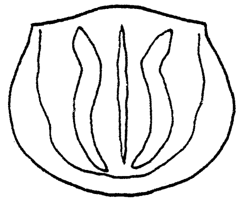

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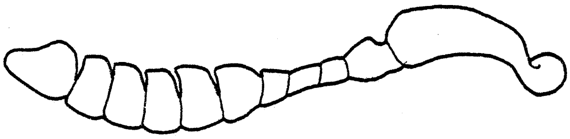

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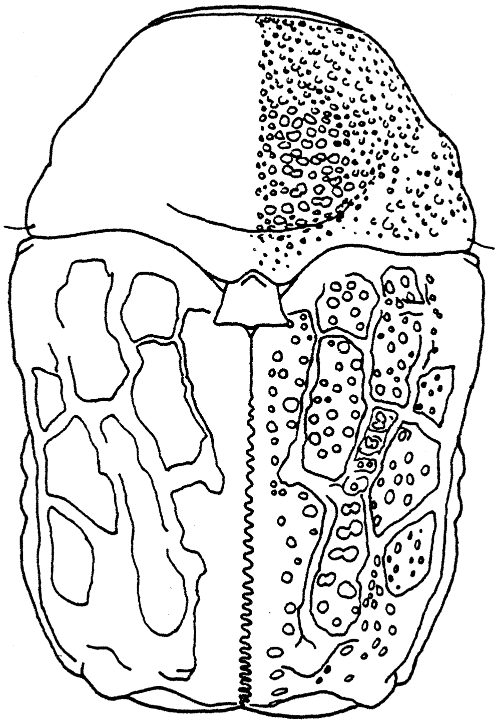

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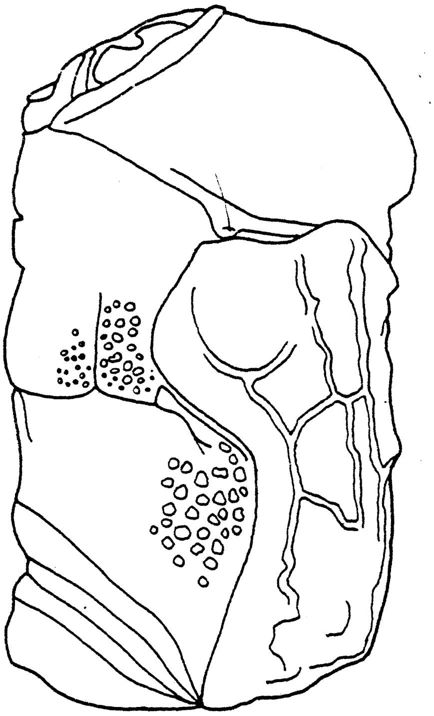

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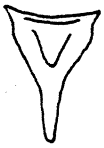

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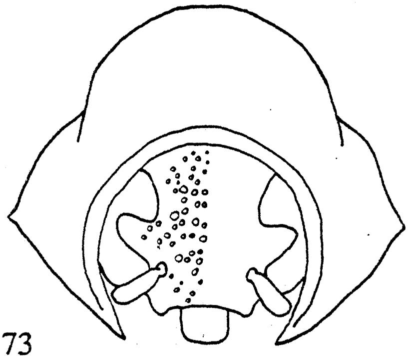

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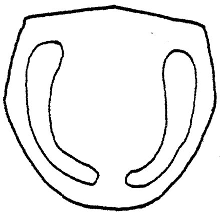

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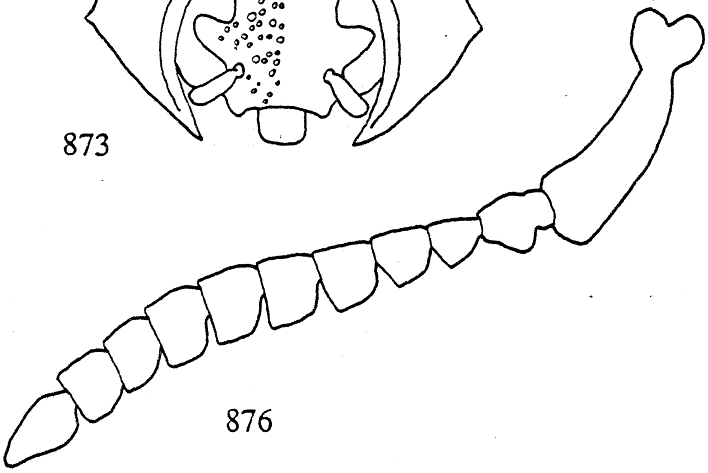

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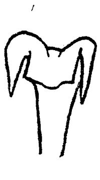

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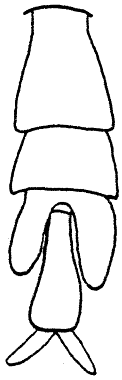

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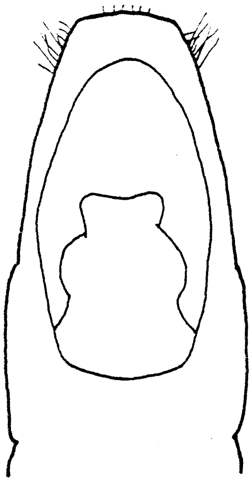

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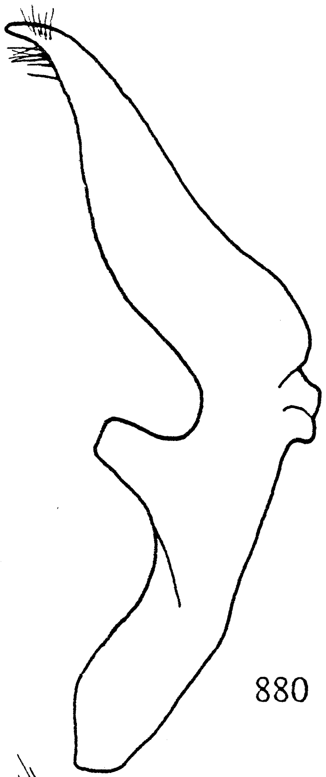

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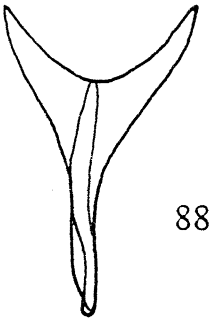

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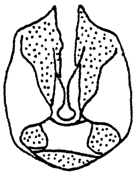

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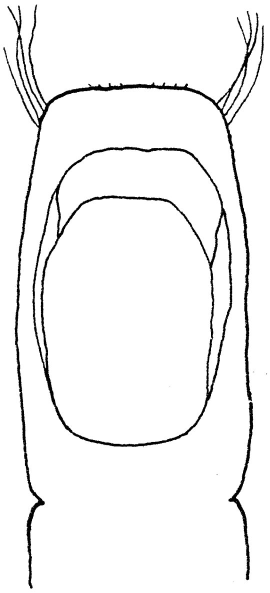

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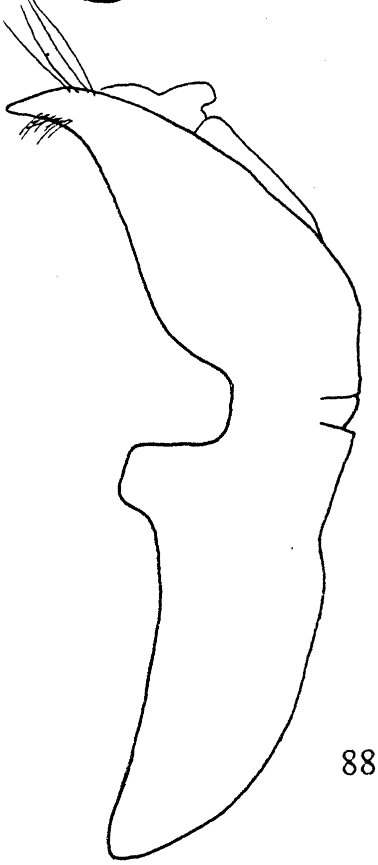

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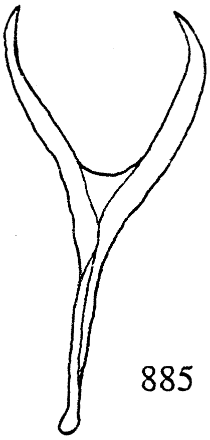

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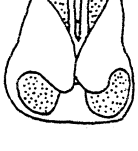

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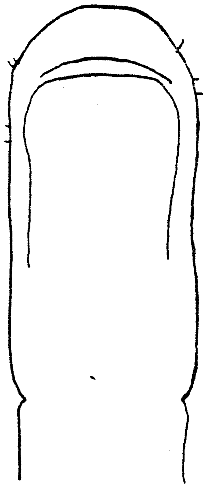

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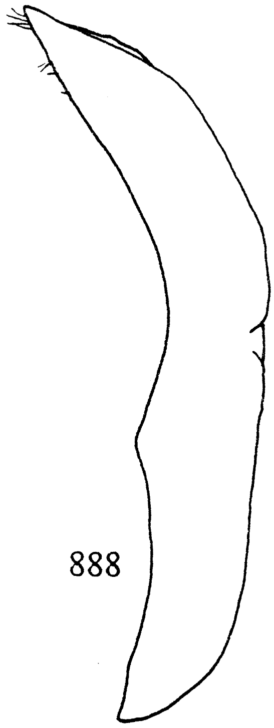

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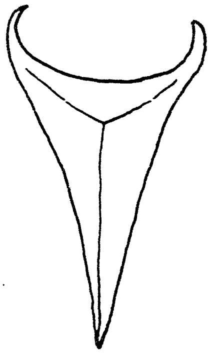

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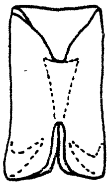

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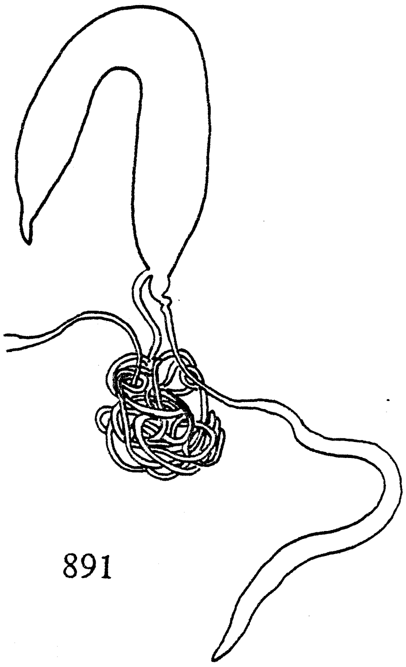

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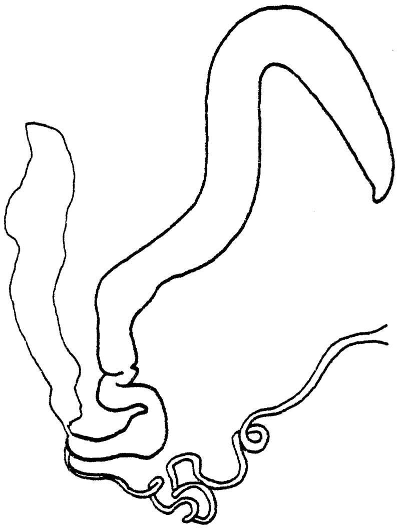

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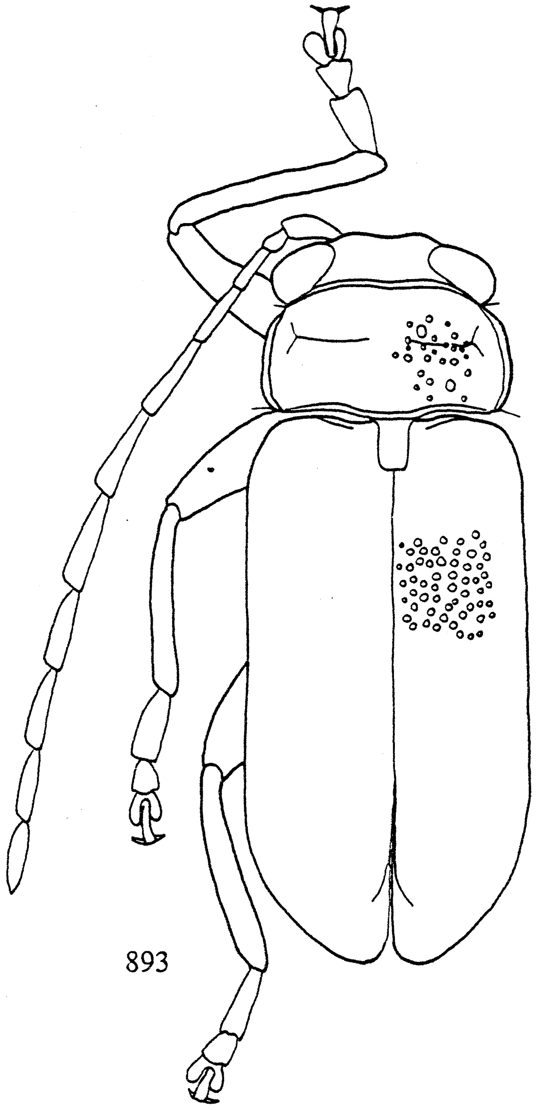

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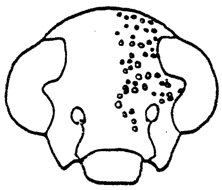

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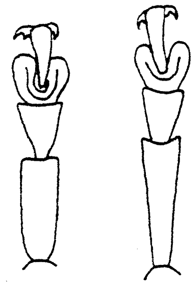

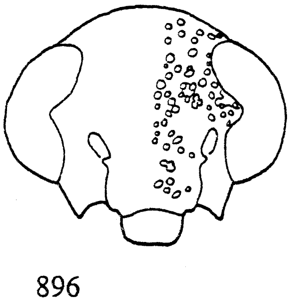

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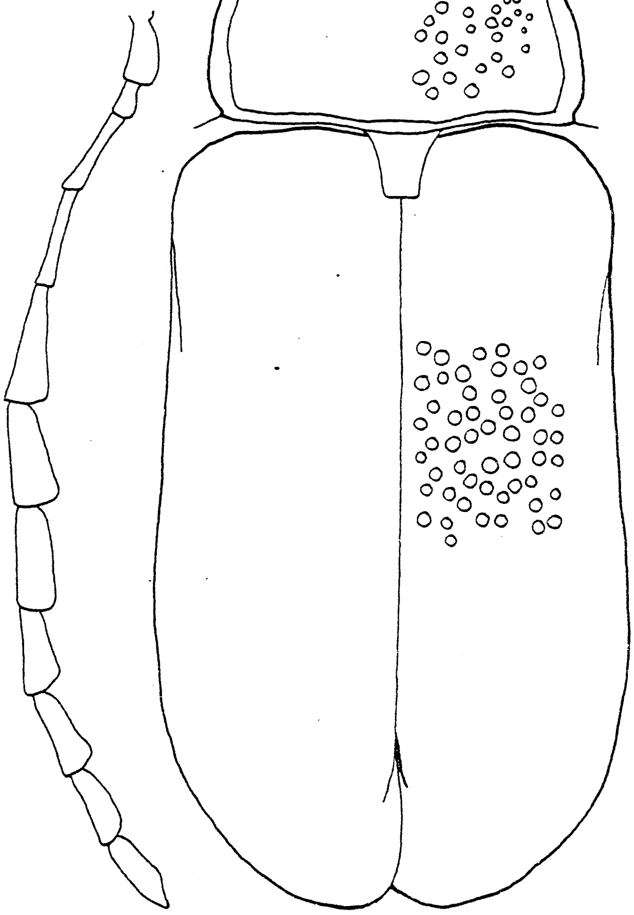

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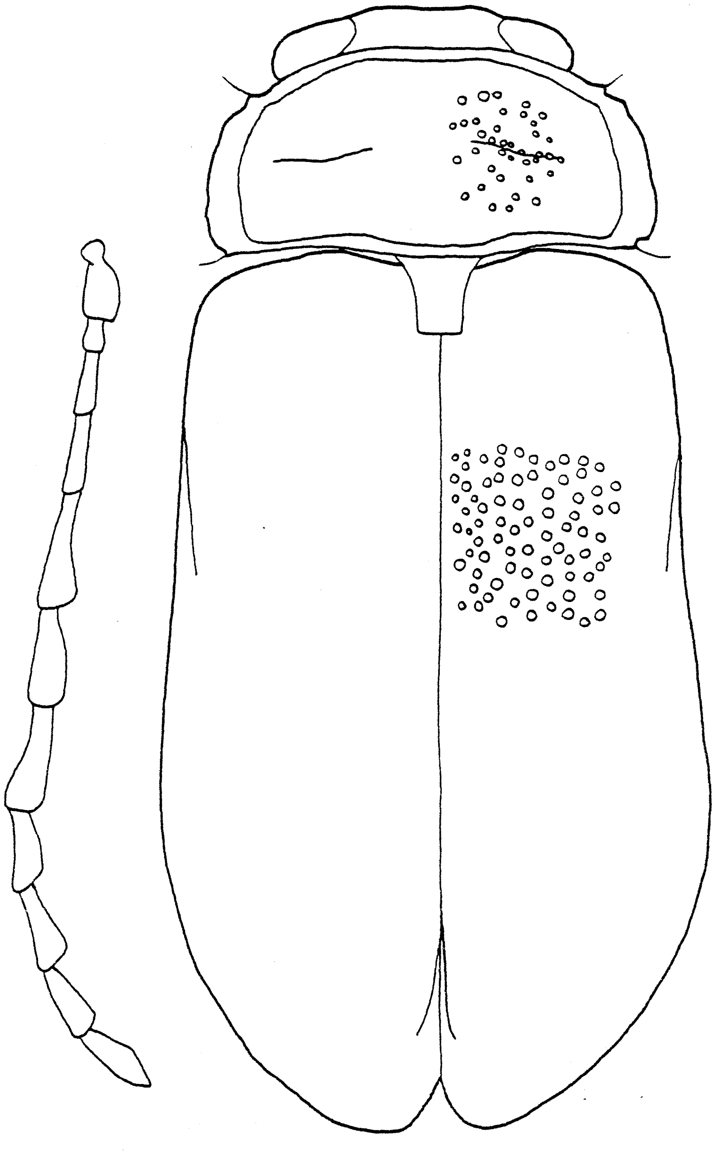

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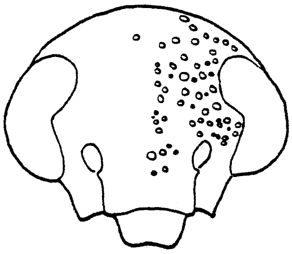

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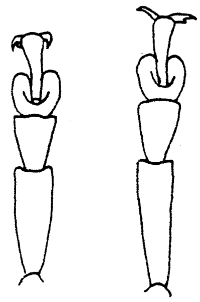

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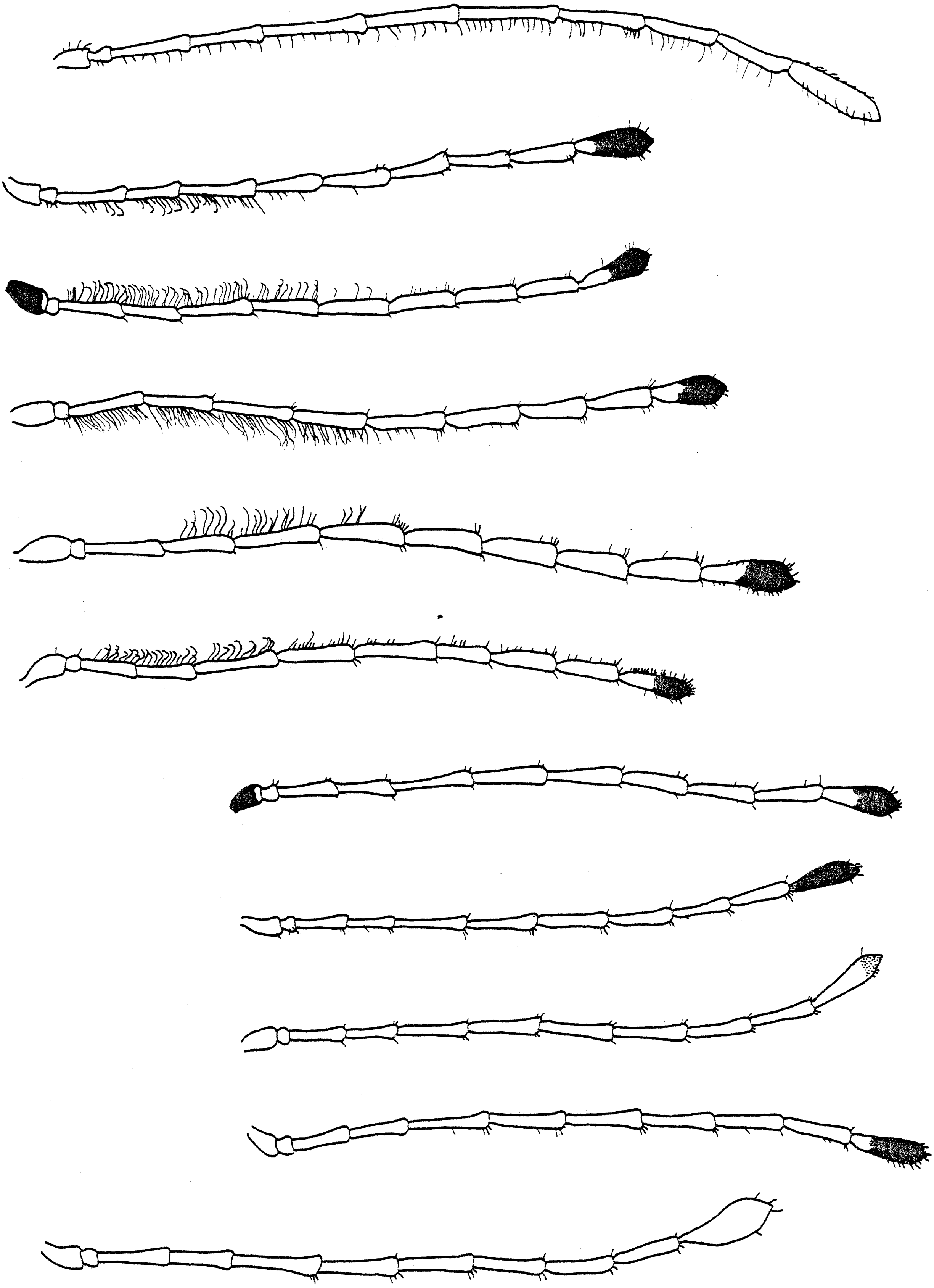

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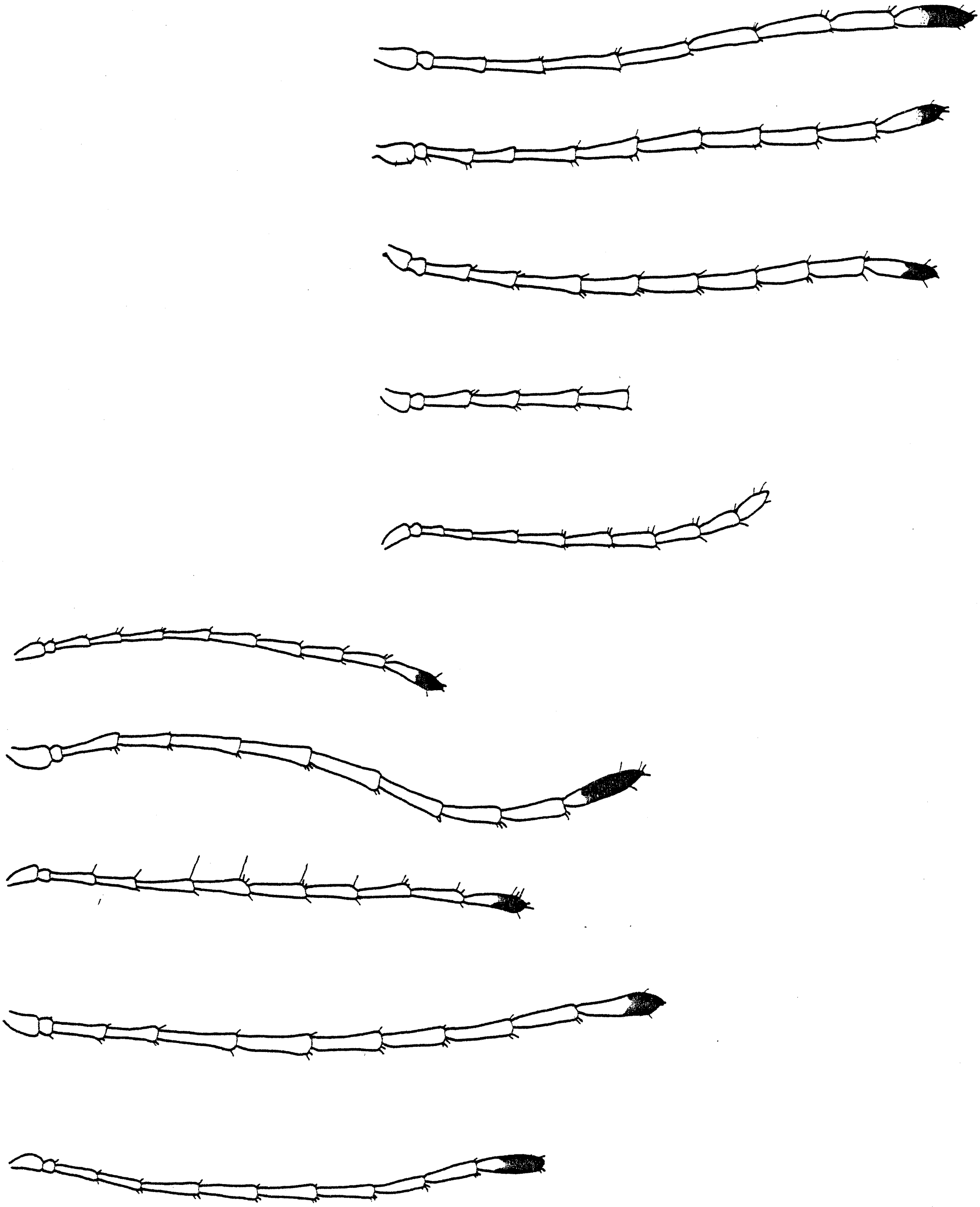

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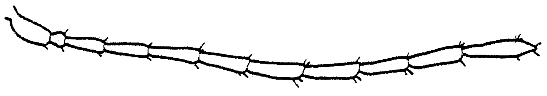

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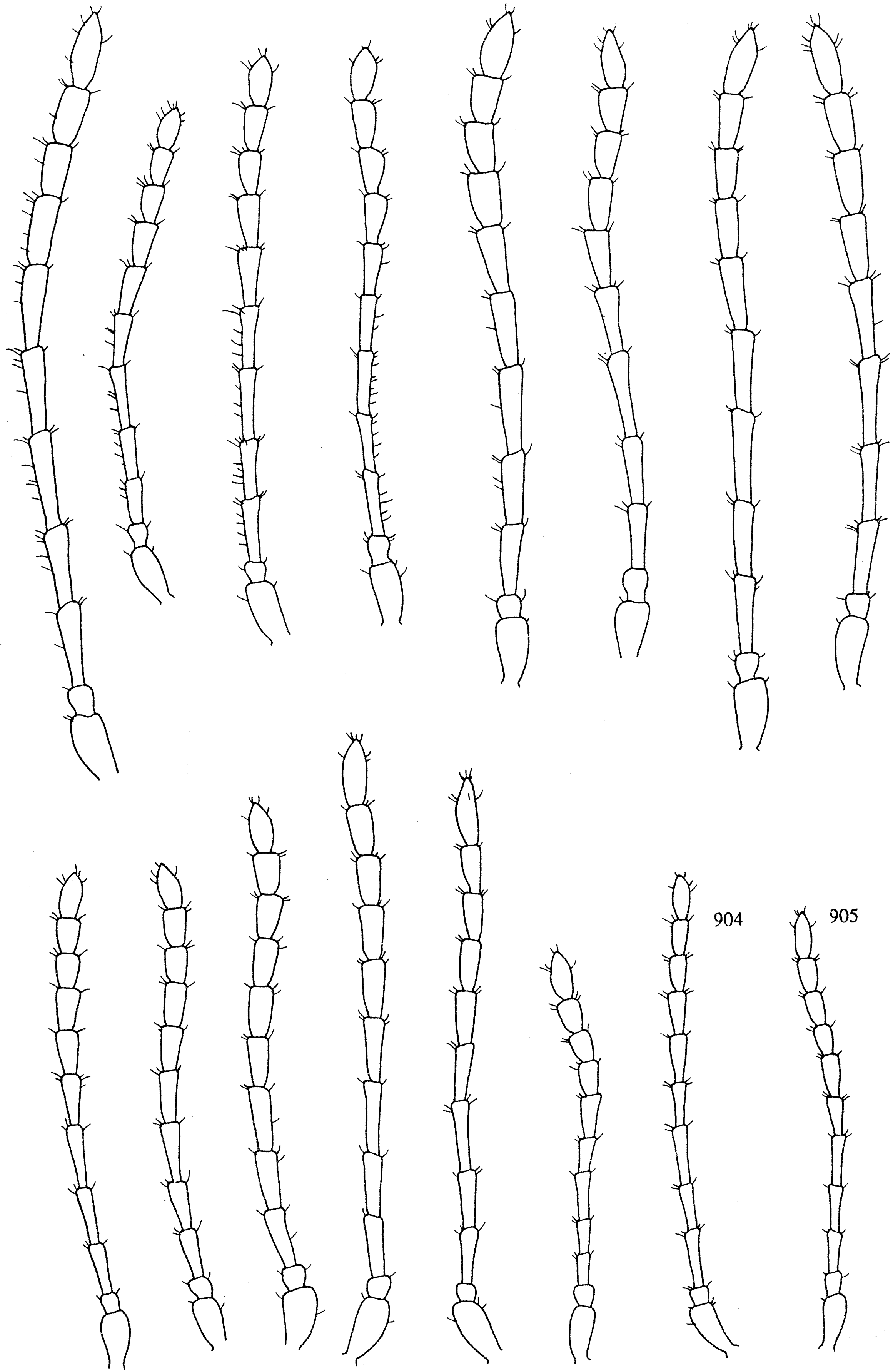
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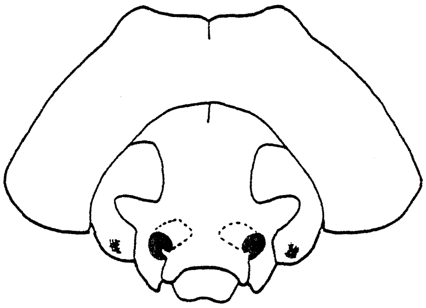

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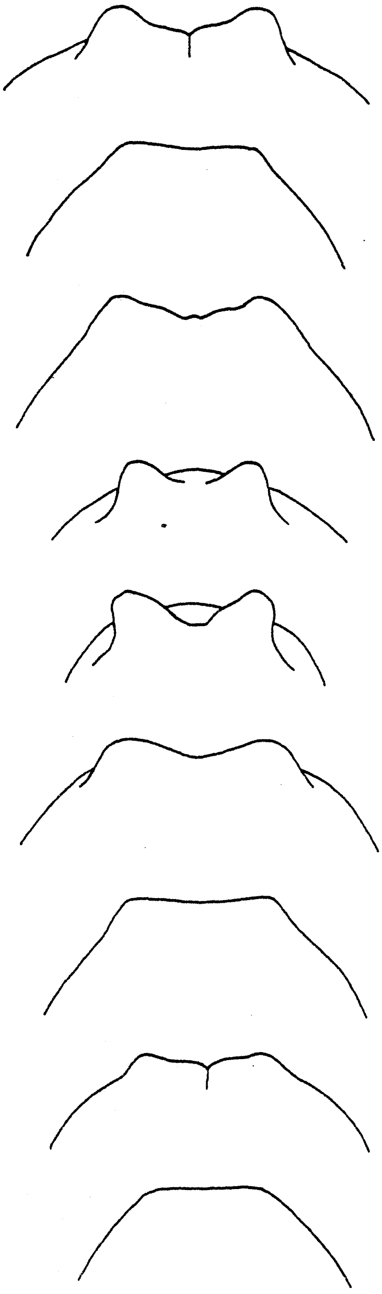

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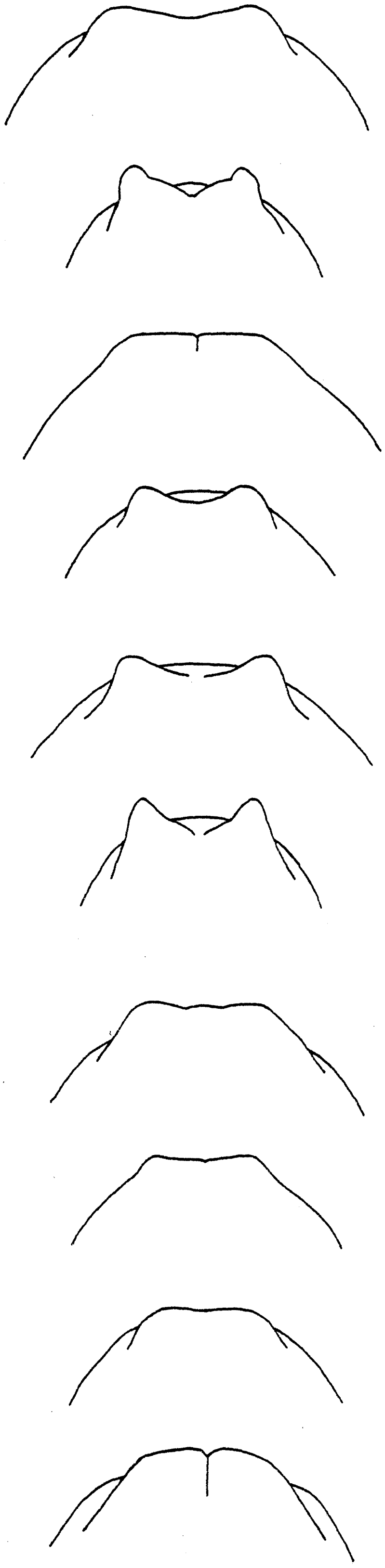

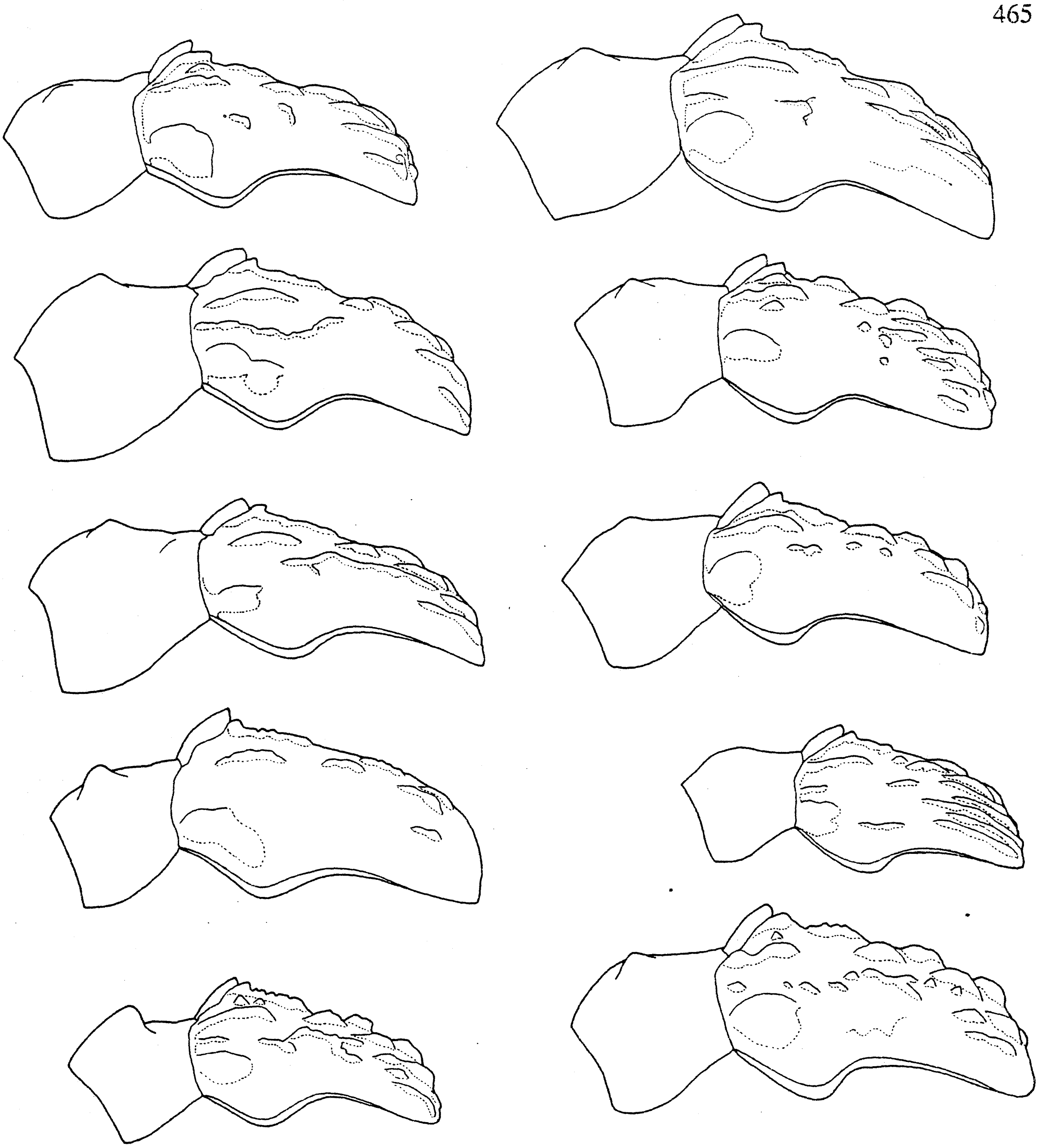

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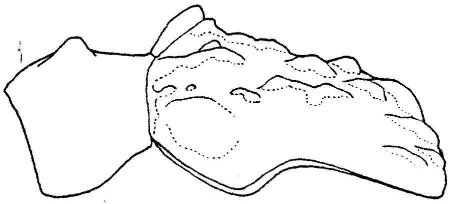

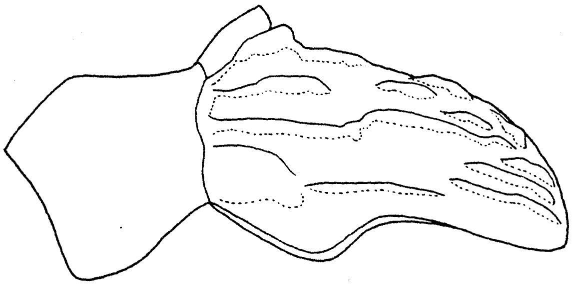

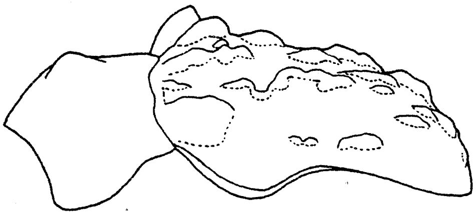

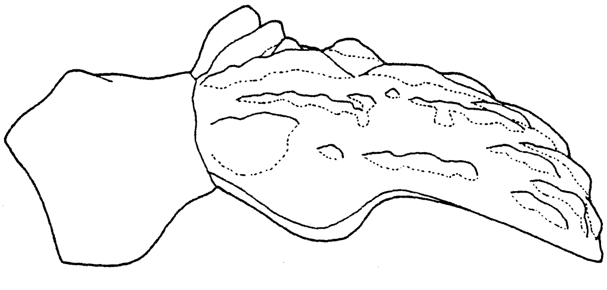

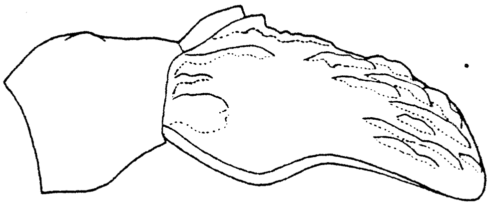

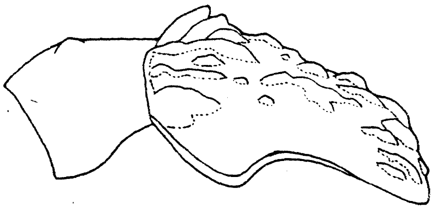

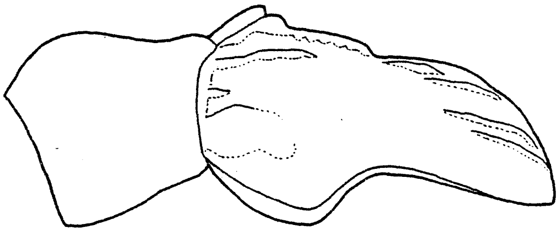

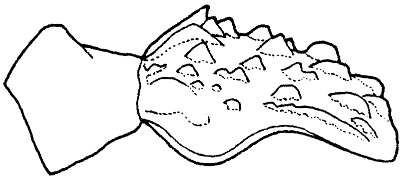

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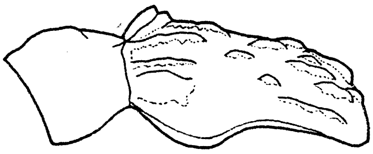

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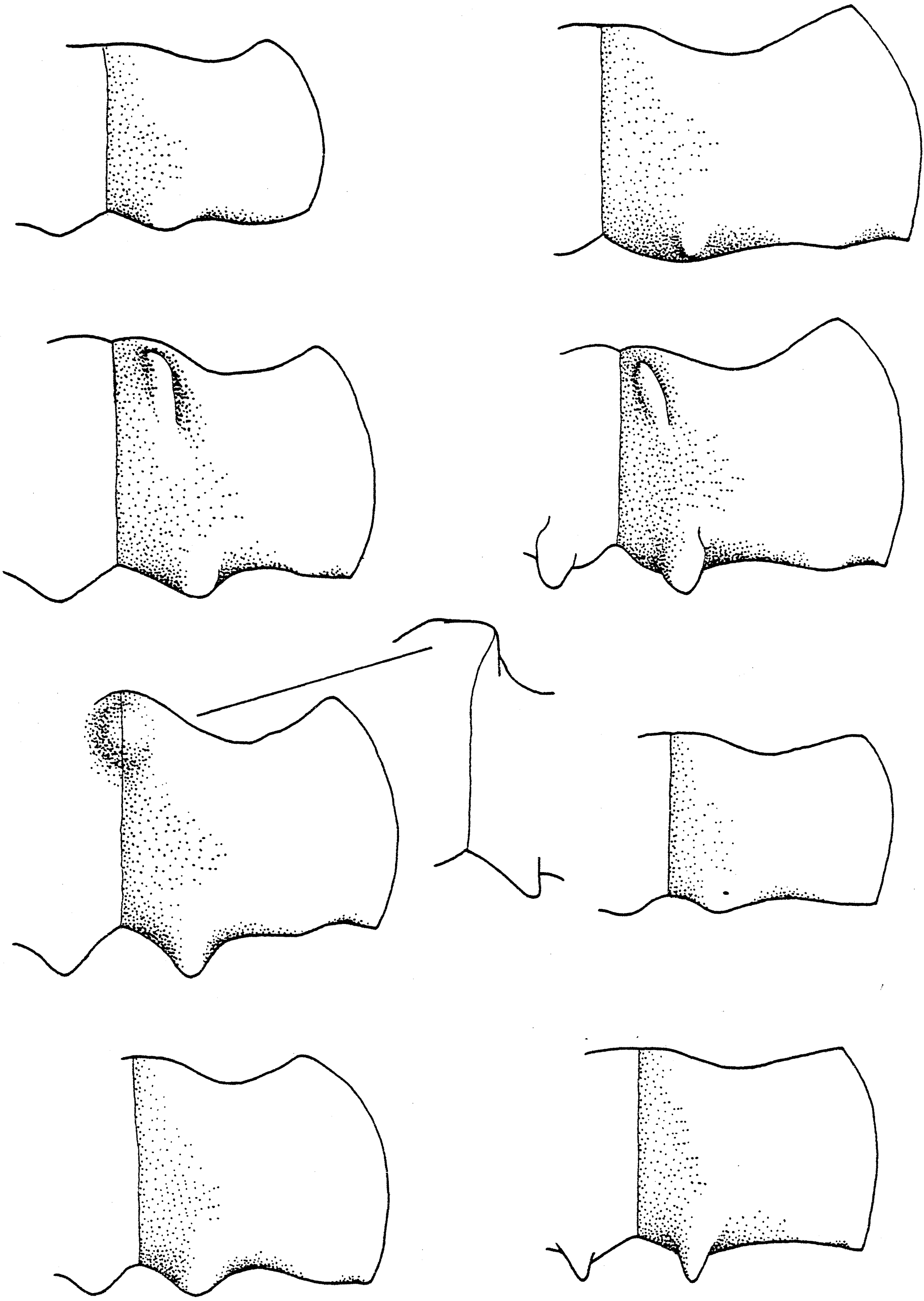

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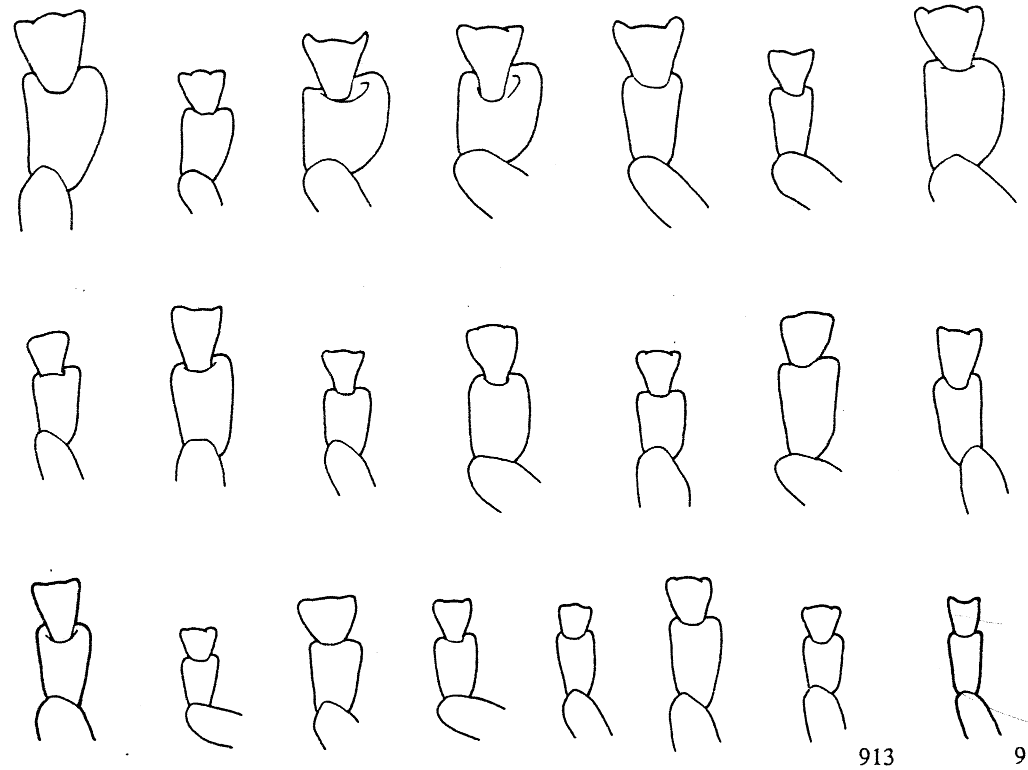

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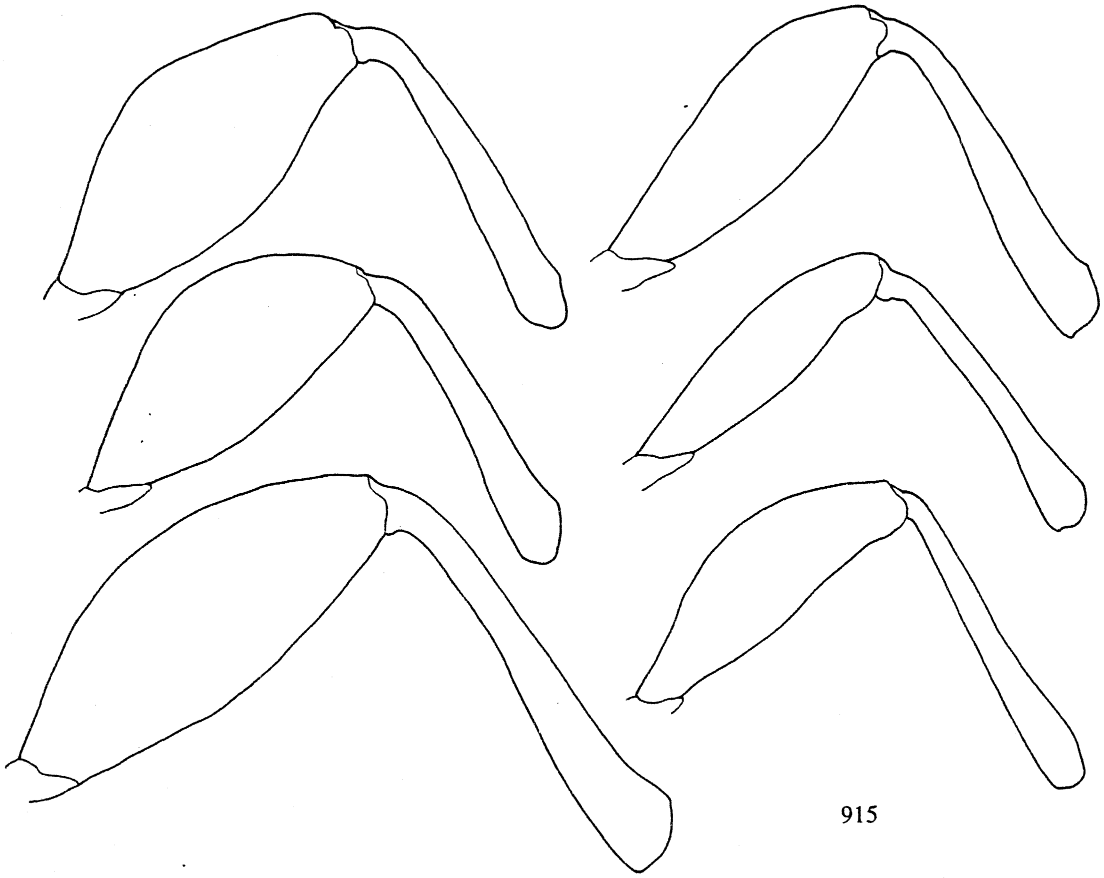

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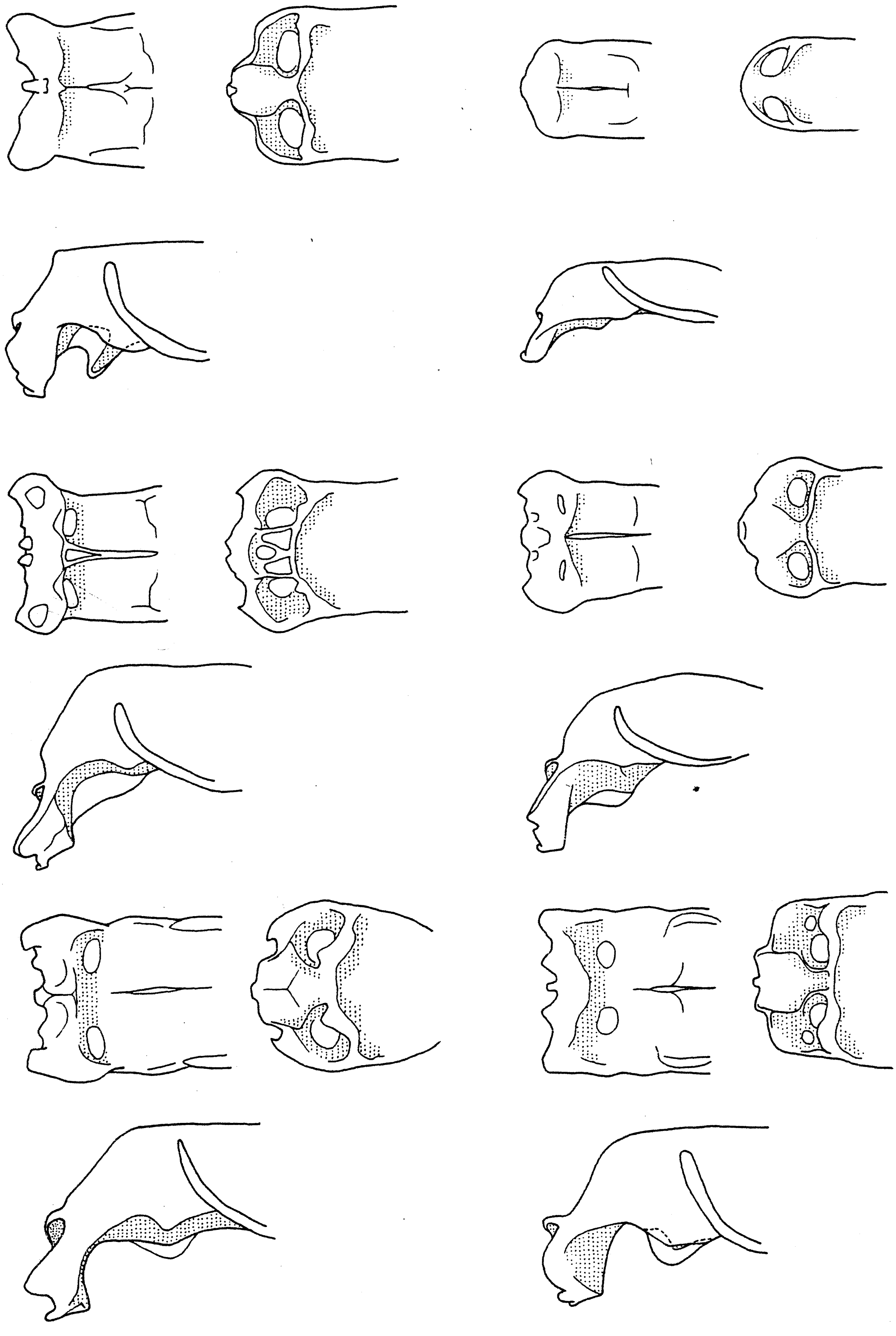

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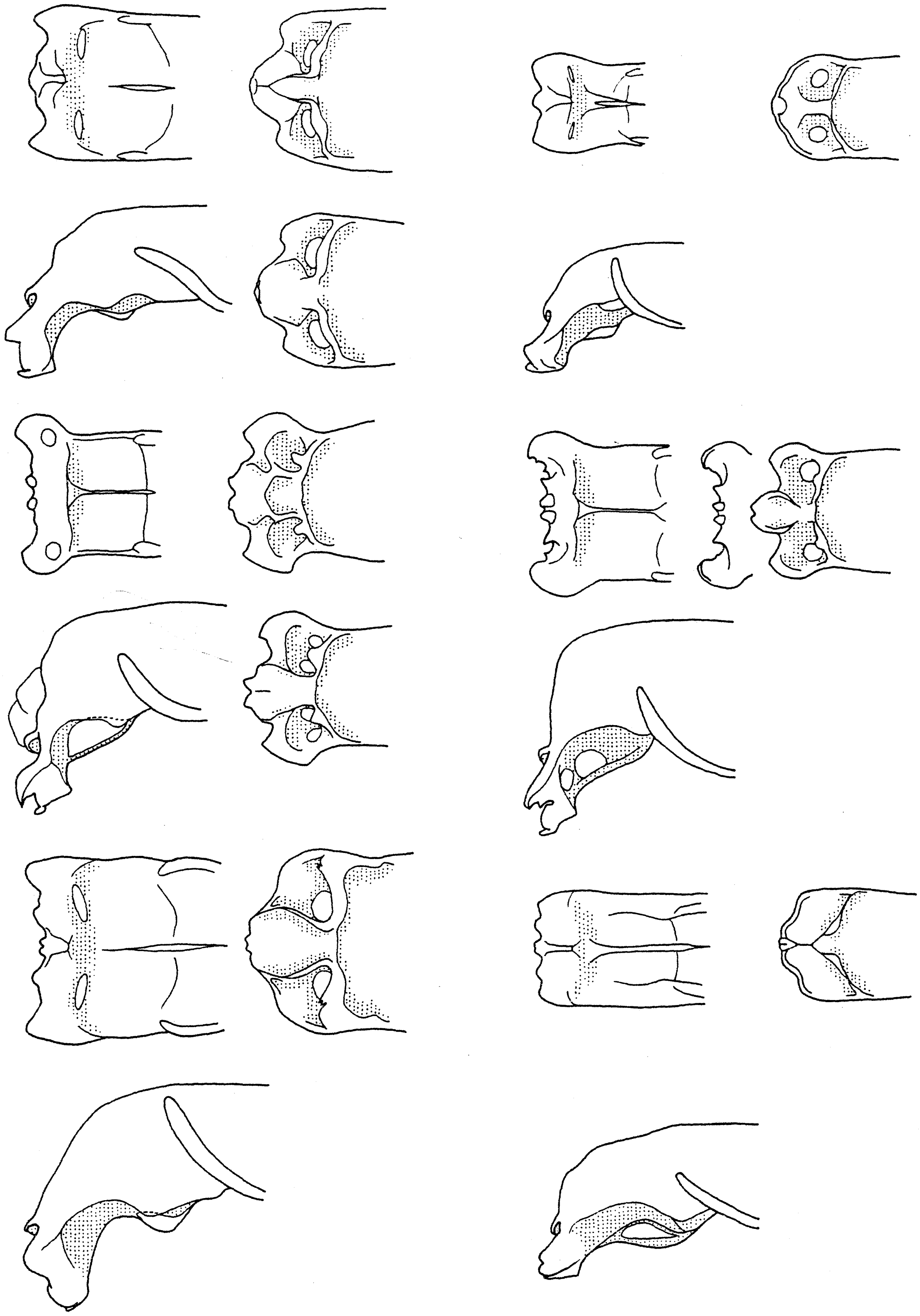

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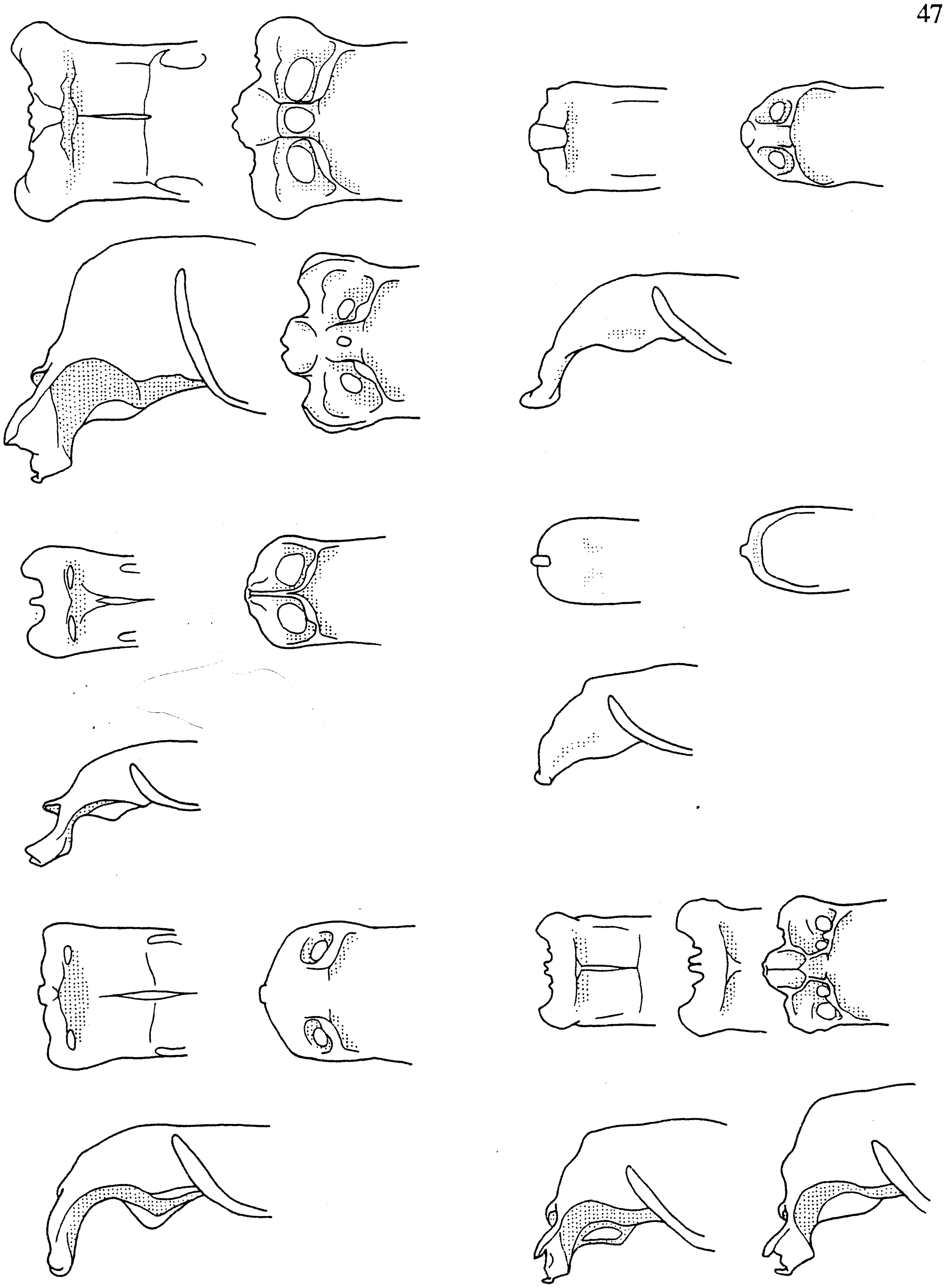

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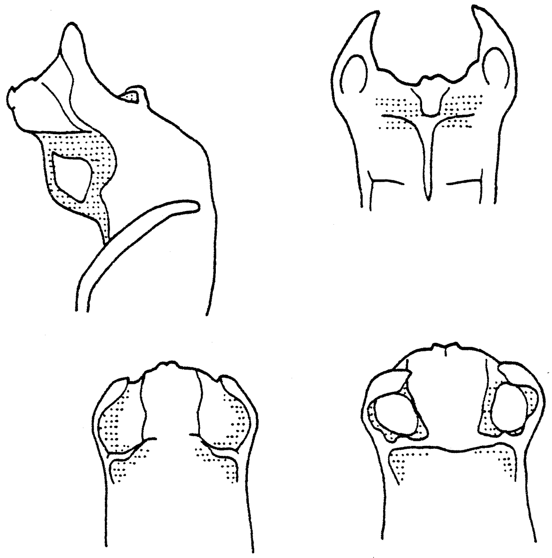

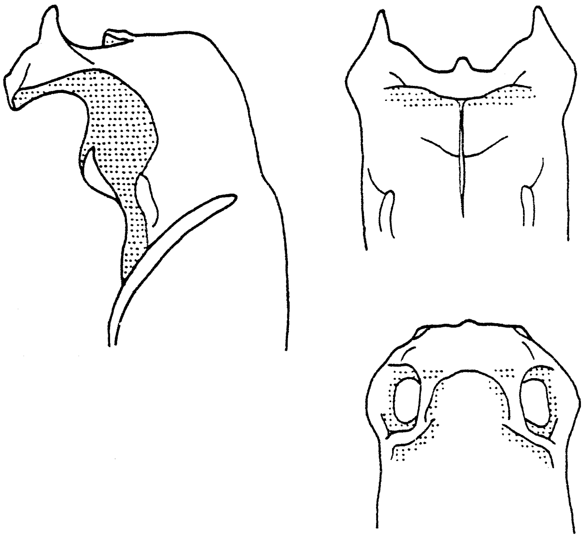

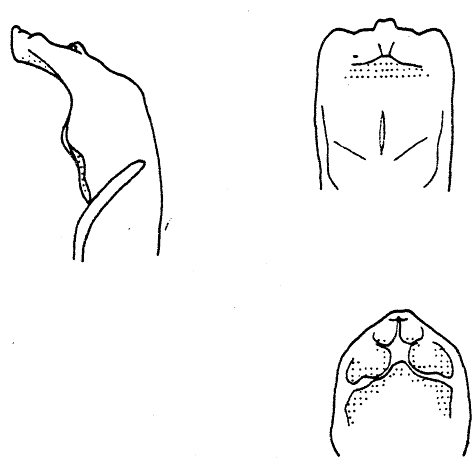

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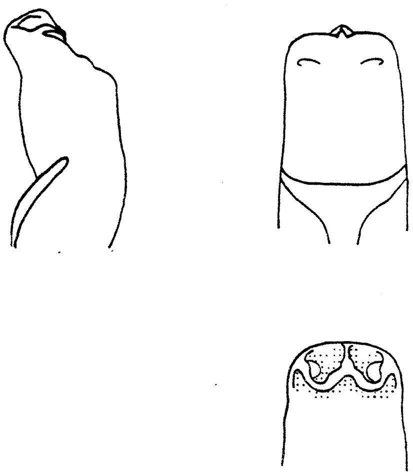

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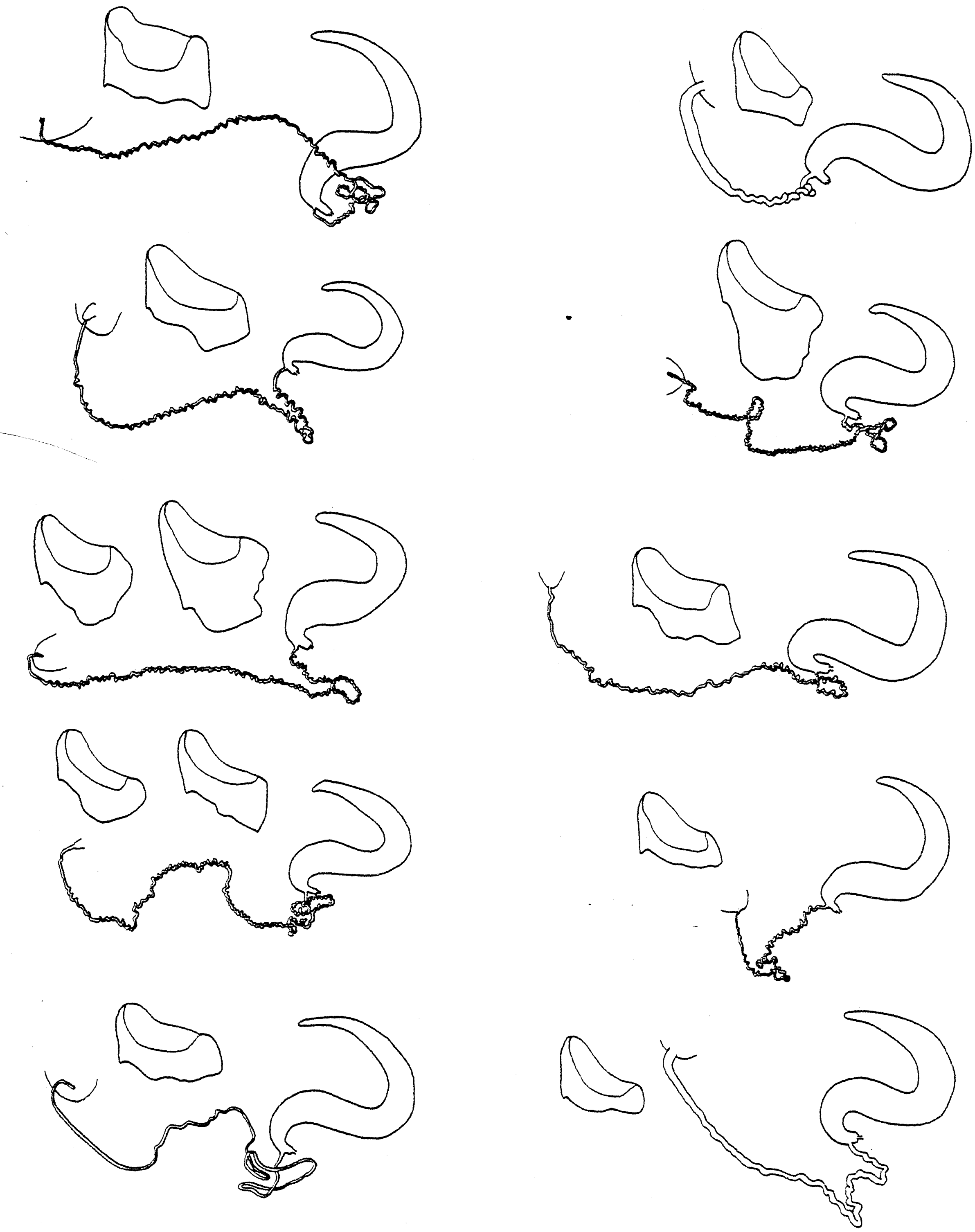

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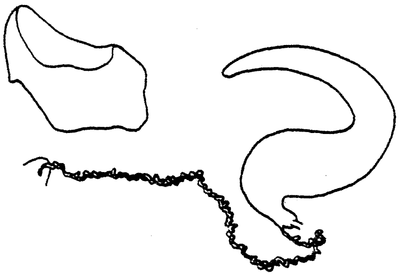
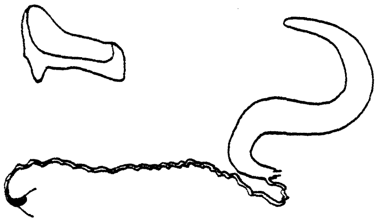
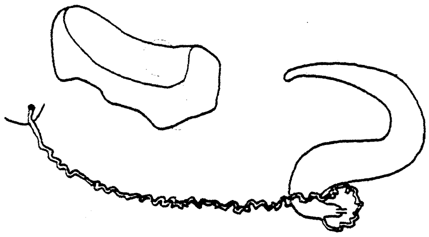
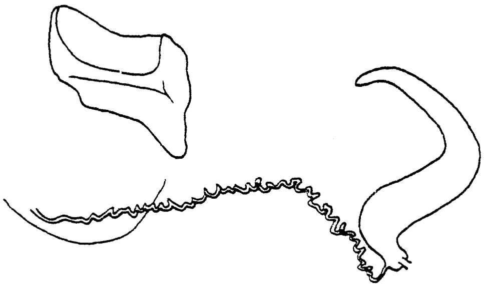
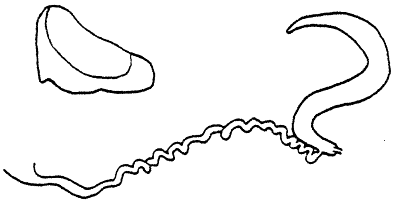


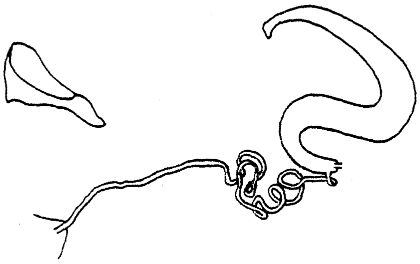




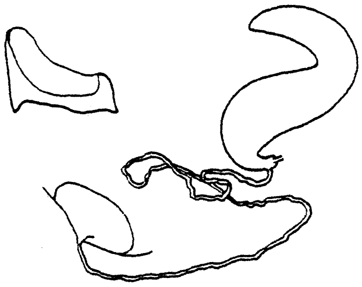


922





923



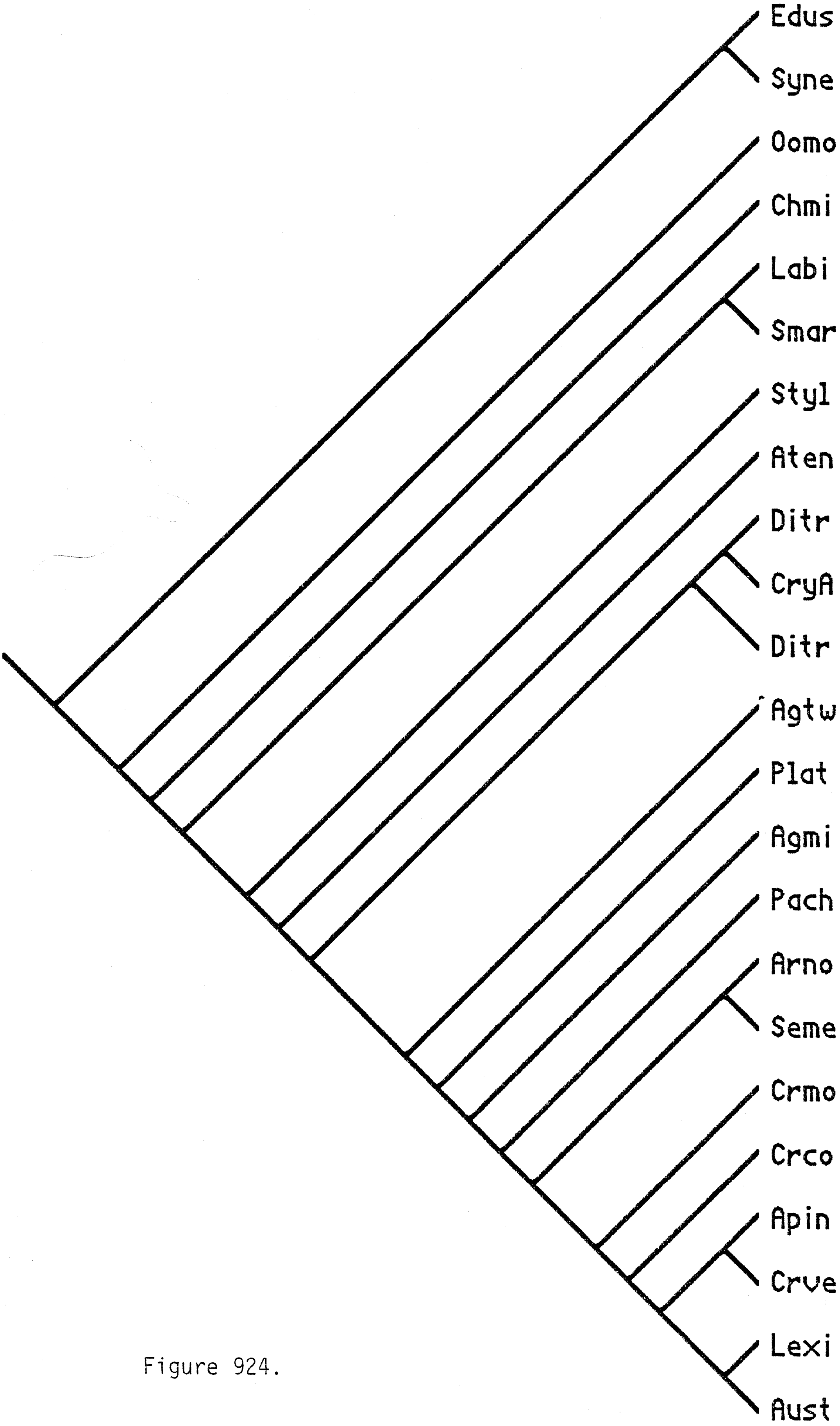

Edus
Syne
Oomo
Chmi
Labi
Smar
Styl
Aten
Ditr
CryA
Ditr
Agtw
Plat
Agmi
Pach
Arno
Seme
Crmo
Crco
Apin
Crve
Lexi
Aust

Figure 924.

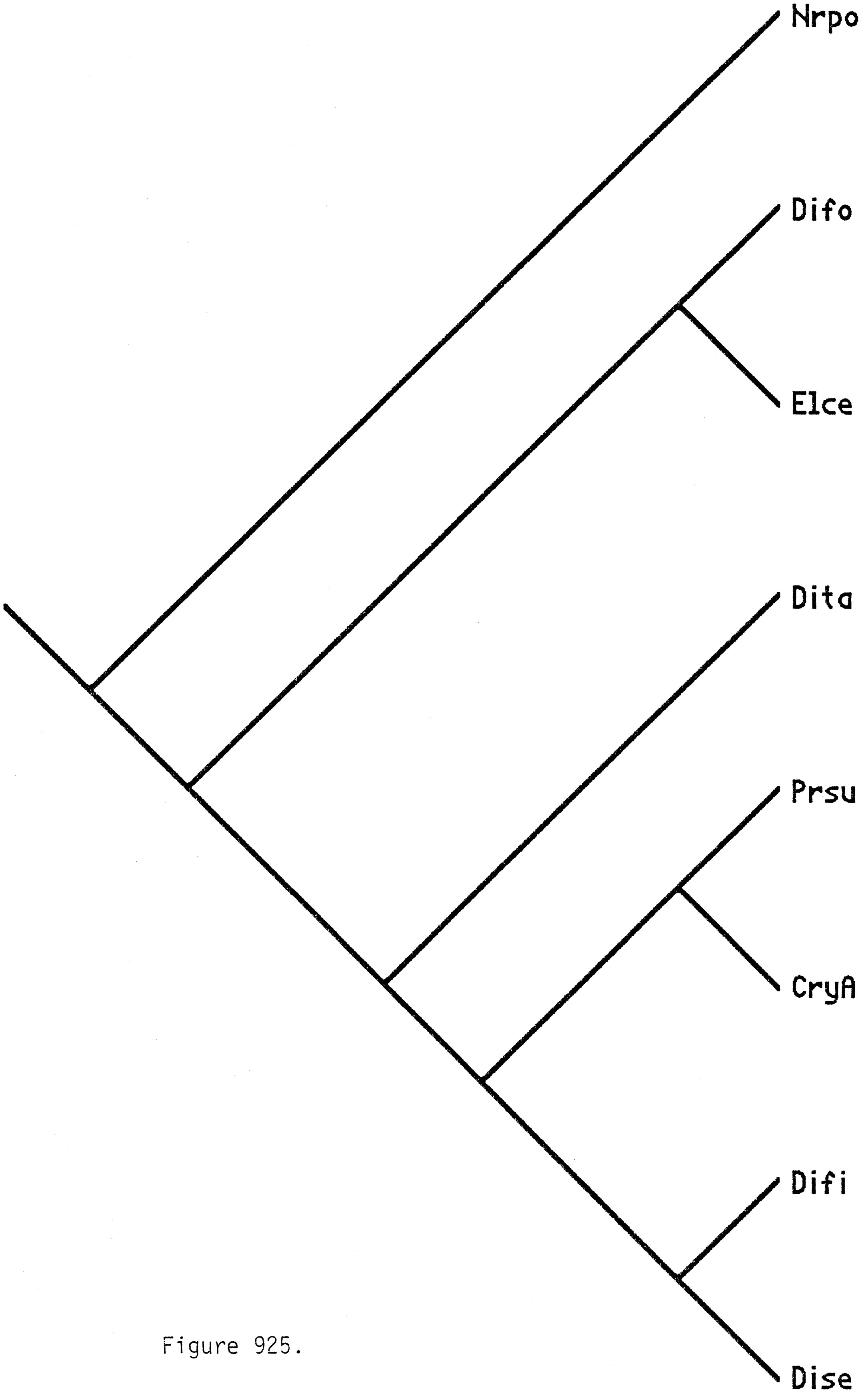


Figure 925.

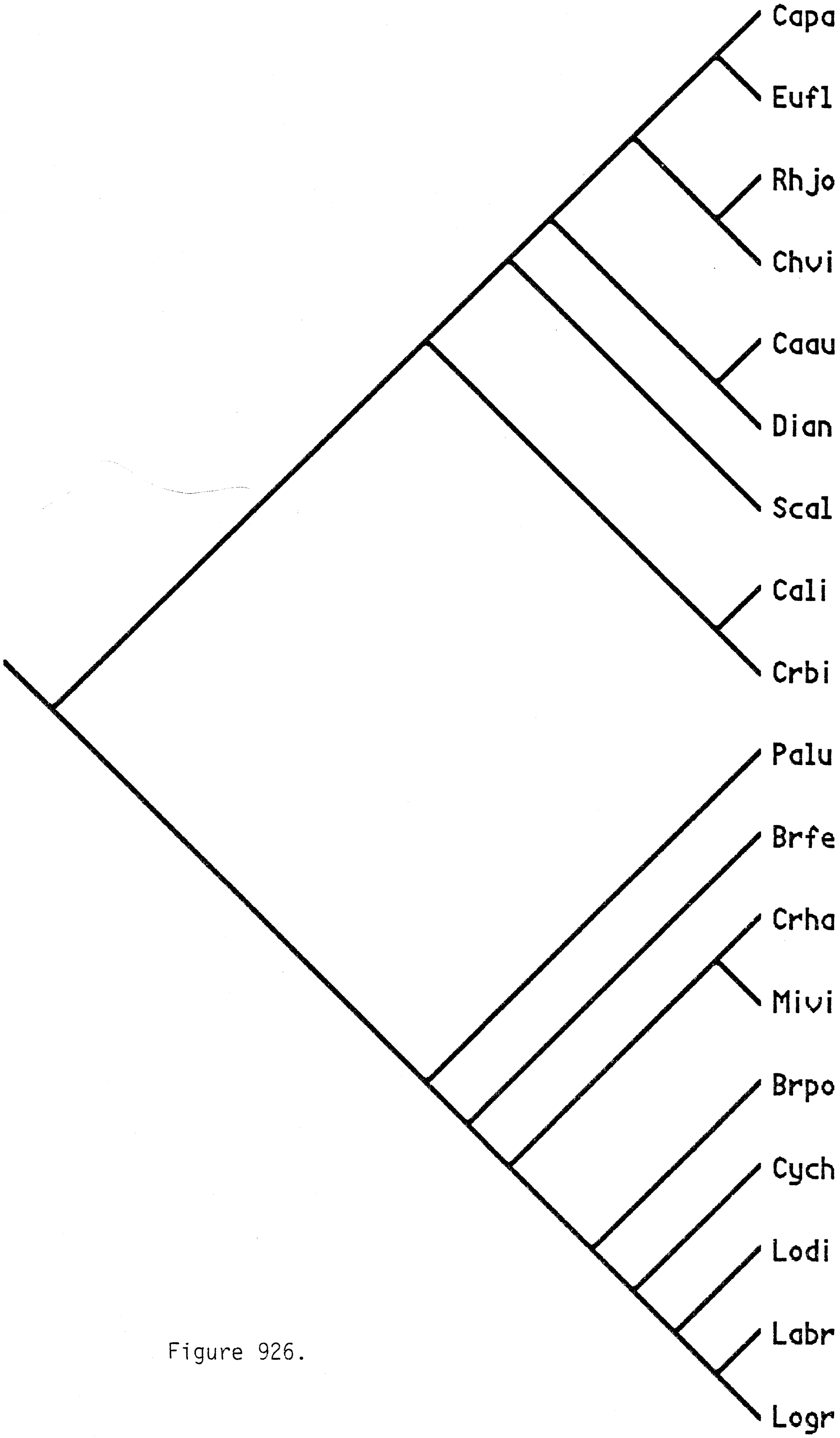

Capa
Eufl
Rhjo
Chvi
Caau
Dian
Scal
Cali
Crbi
Palu
Brfe
Crha
Mivi
Brpo
Cych
Lodi
Labr
Logr

Figure 926.

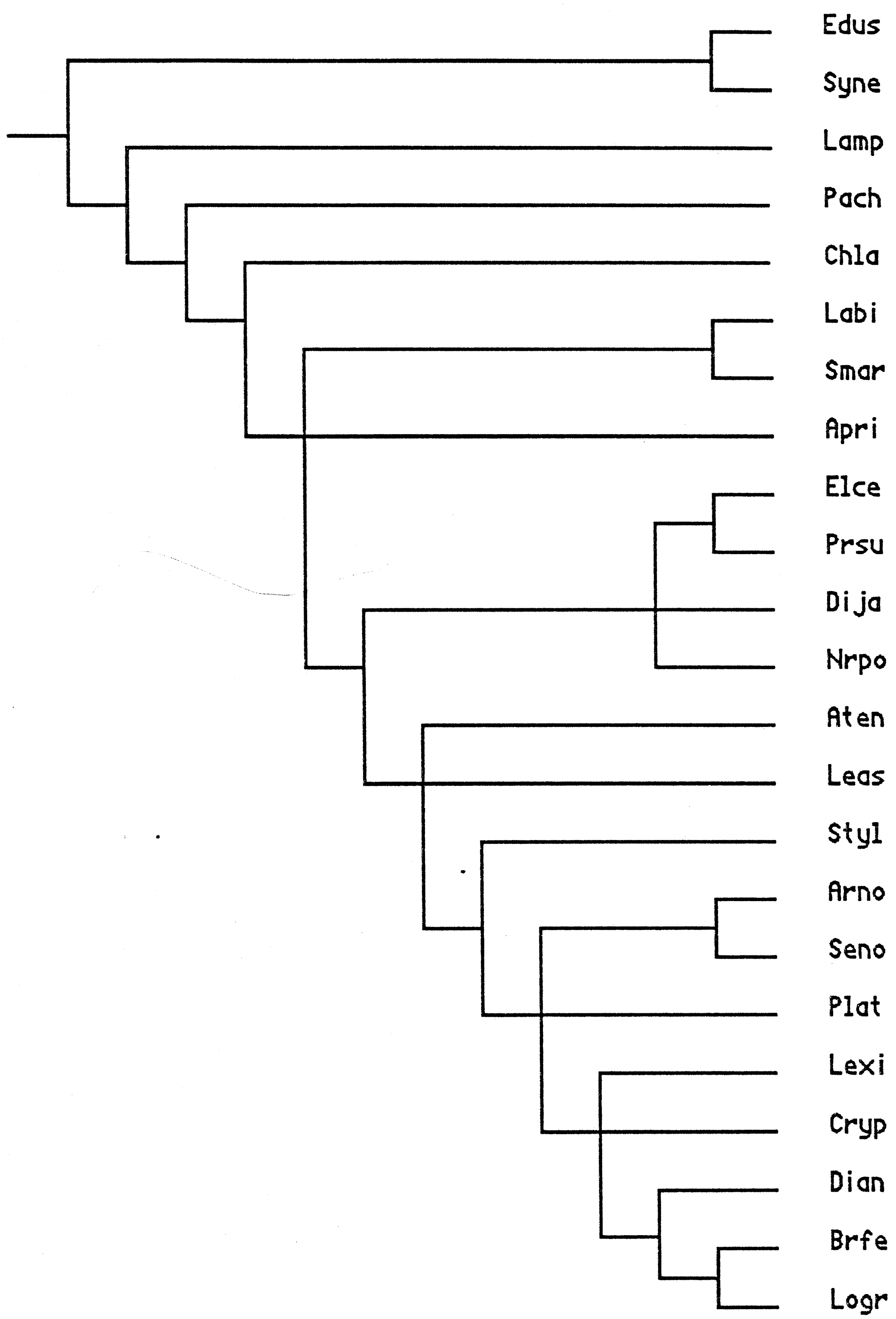

Edus
Syne
Lamp
Pach
Chla
Labi
Smar
Apri
Elce
Prsu
Dija
Nrpo
Aten
Leas
Styl
Arno
Seno
Plat
Lexi
Cryp
Dian
Brfe
Logr

Figure 927.

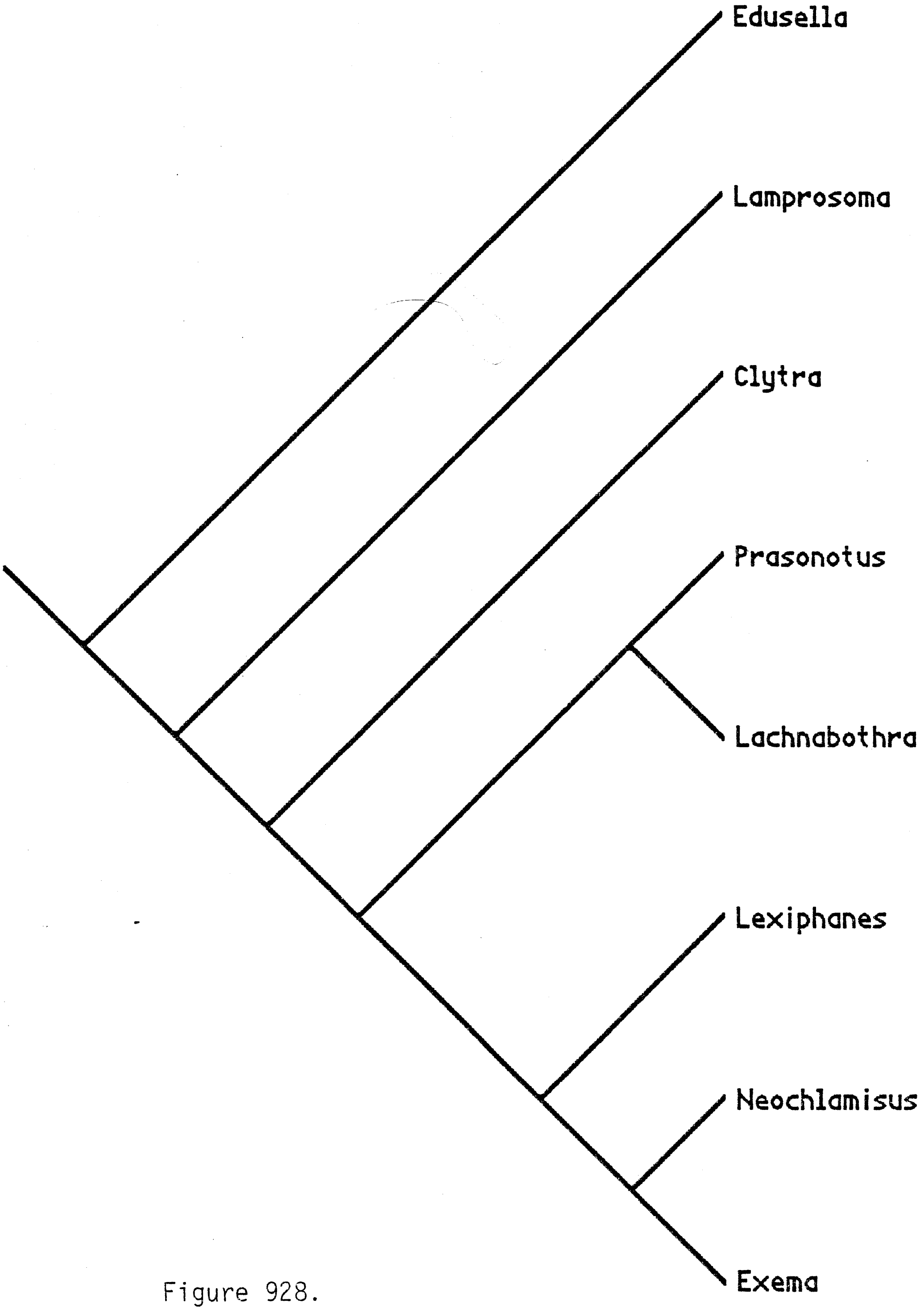

Edusella
Lamprosoma
Clytra
Prasonotus
Lachnabothra
Lexiphanes
Neochlamisus
Exema

Figure 928.

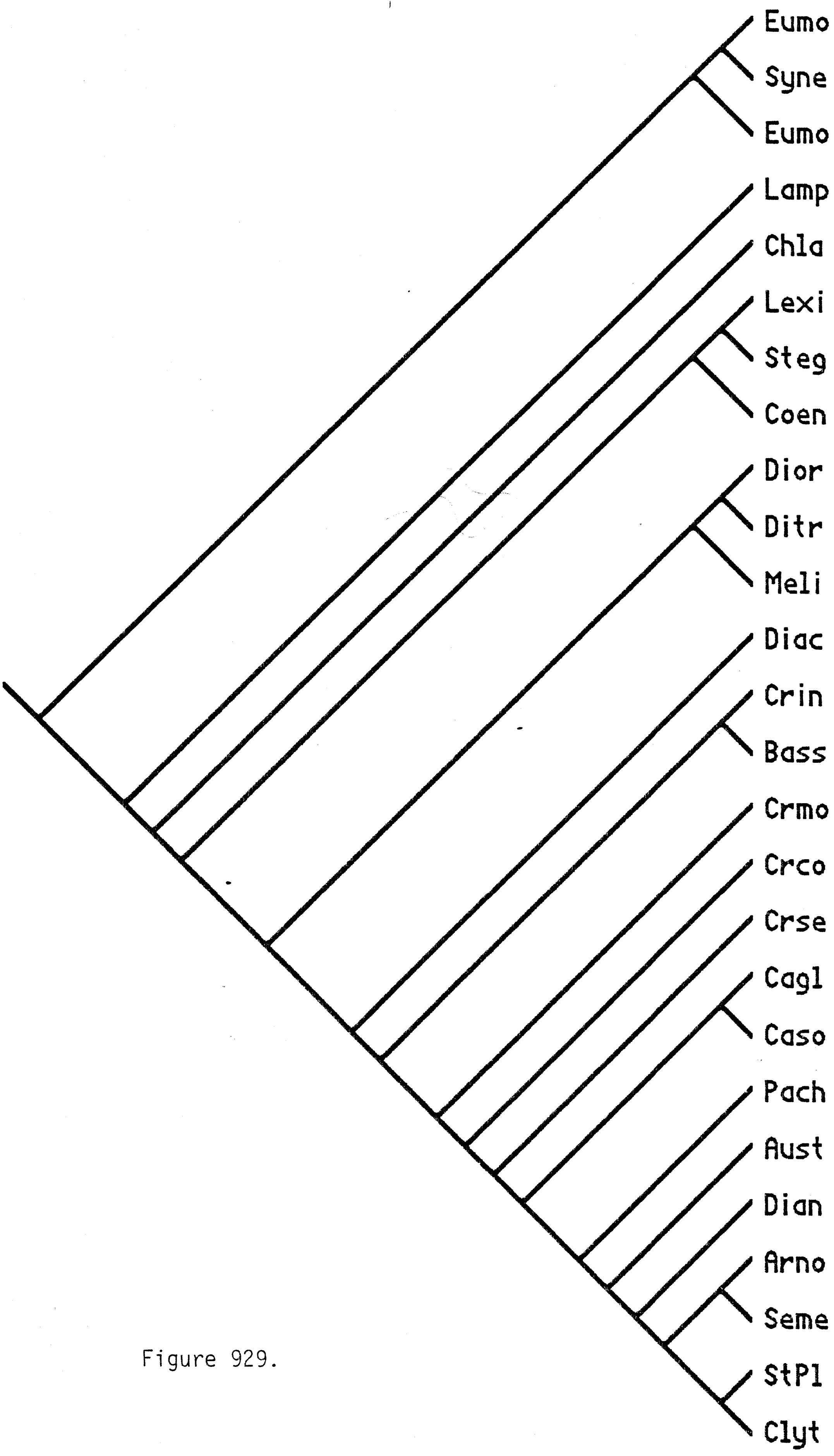

Eumo
Syne
Eumo
Lamp
Chla
Lexi
Steg
Coen
Dior
Ditr
Meli
Diac
Crin
Bass
Crmo
Crco
Crse
Cagl
Caso
Pach
Aust
Dian
Arno
Seme
StPl
Clyt

Figure 929.

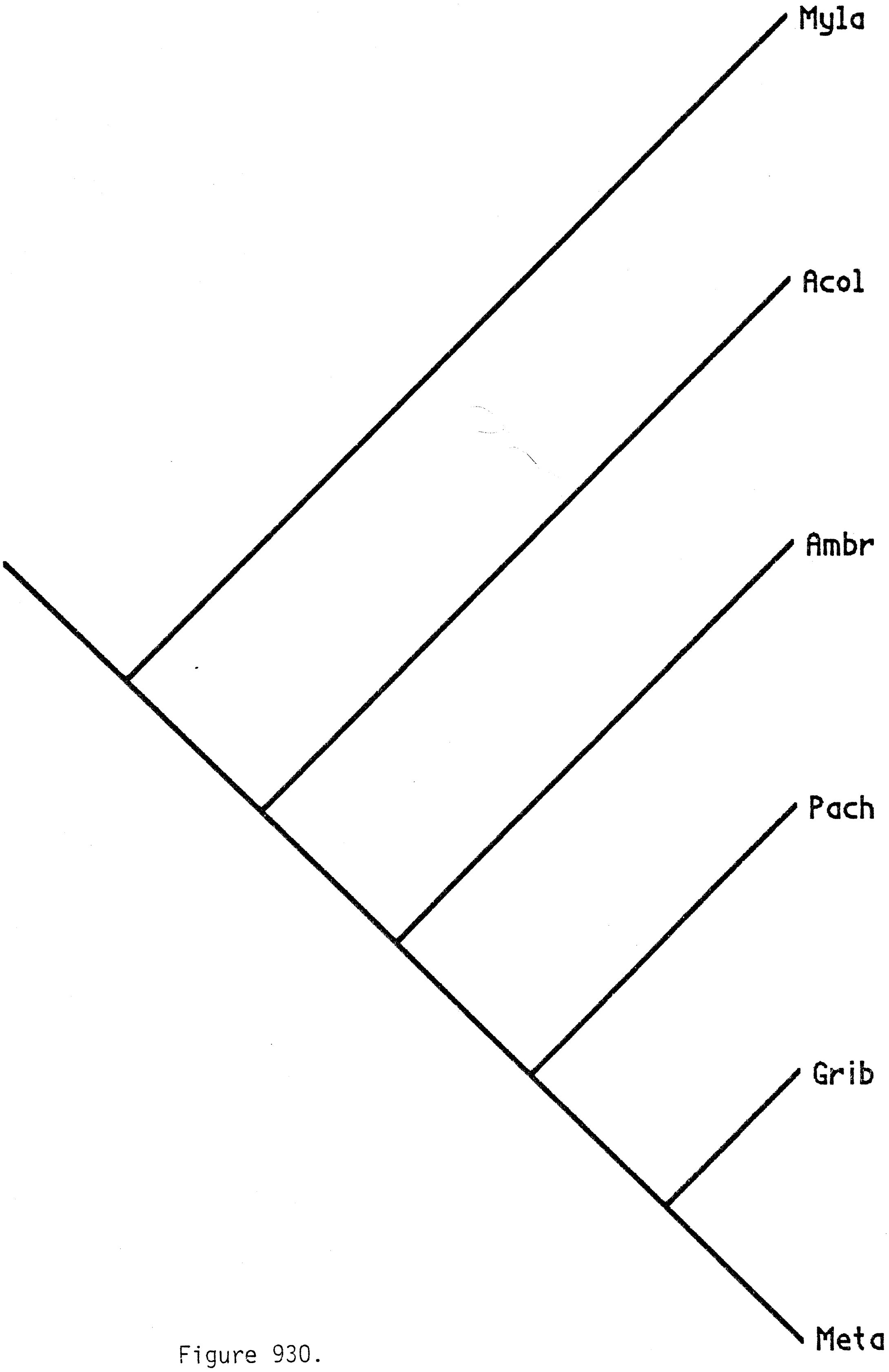


Figure 930.

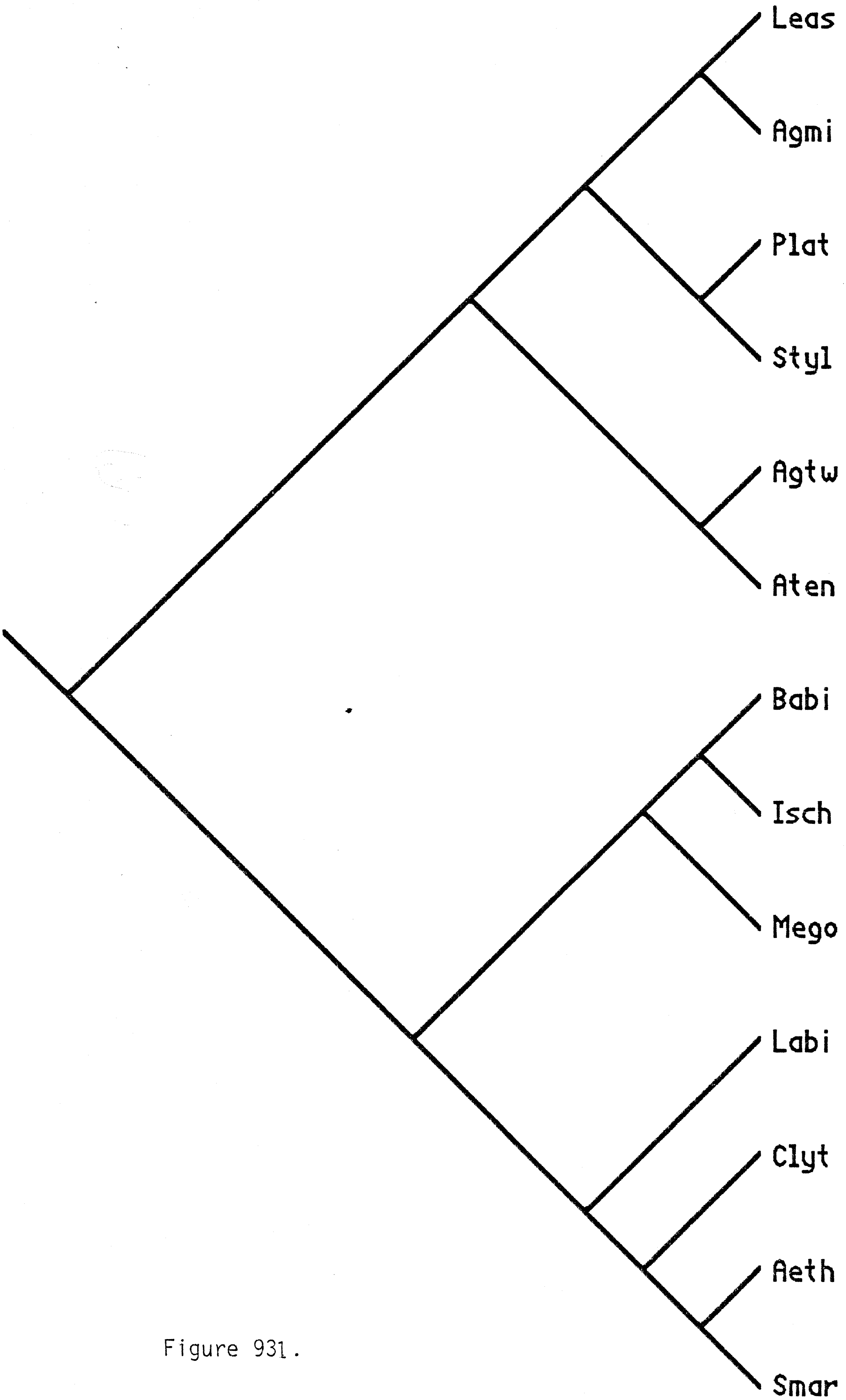

Leas
Agmi
Plat
Styl
Agtw
Aten
Babi
Isch
Mego
Labi
Clyt
Aeth
Smar

Figure 931.

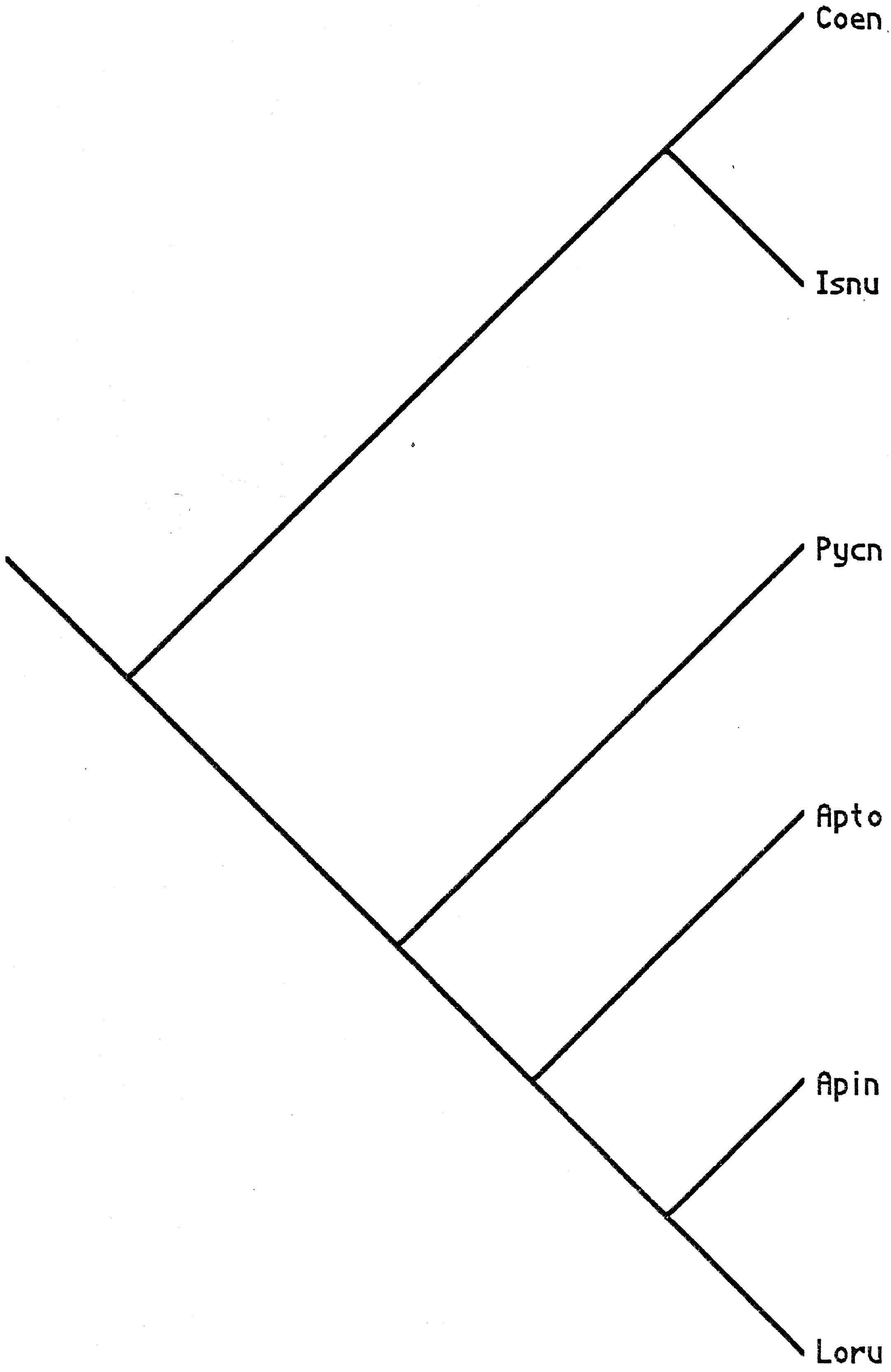


Figure 932.

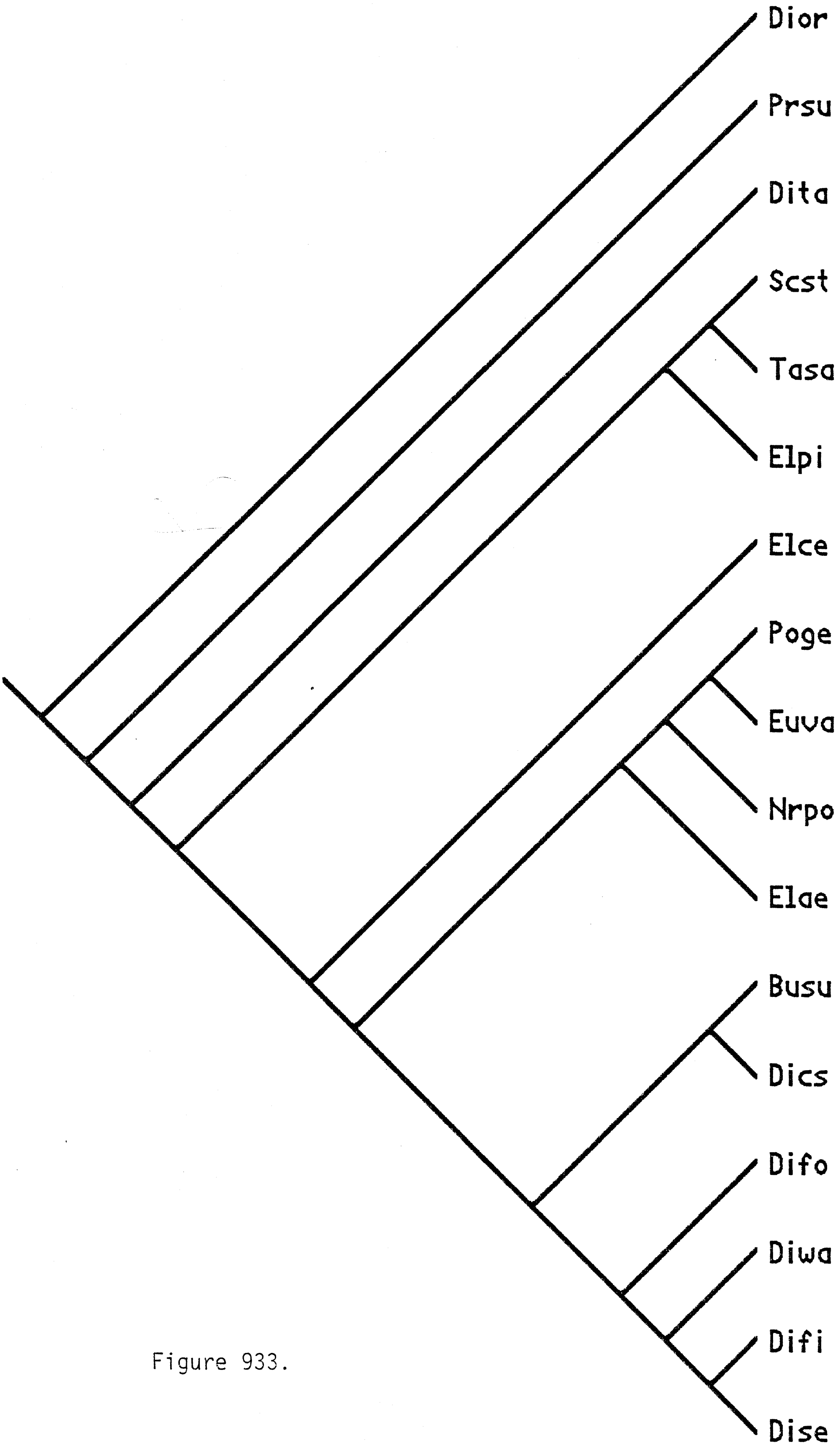

Dior
Prsu
Dita
Scst
Tasa
Elpi
Elce
Poge
Euva
Nrpo
Elae
Busu
Dics
Difo
Diwa
Difi
Dise

Figure 933.

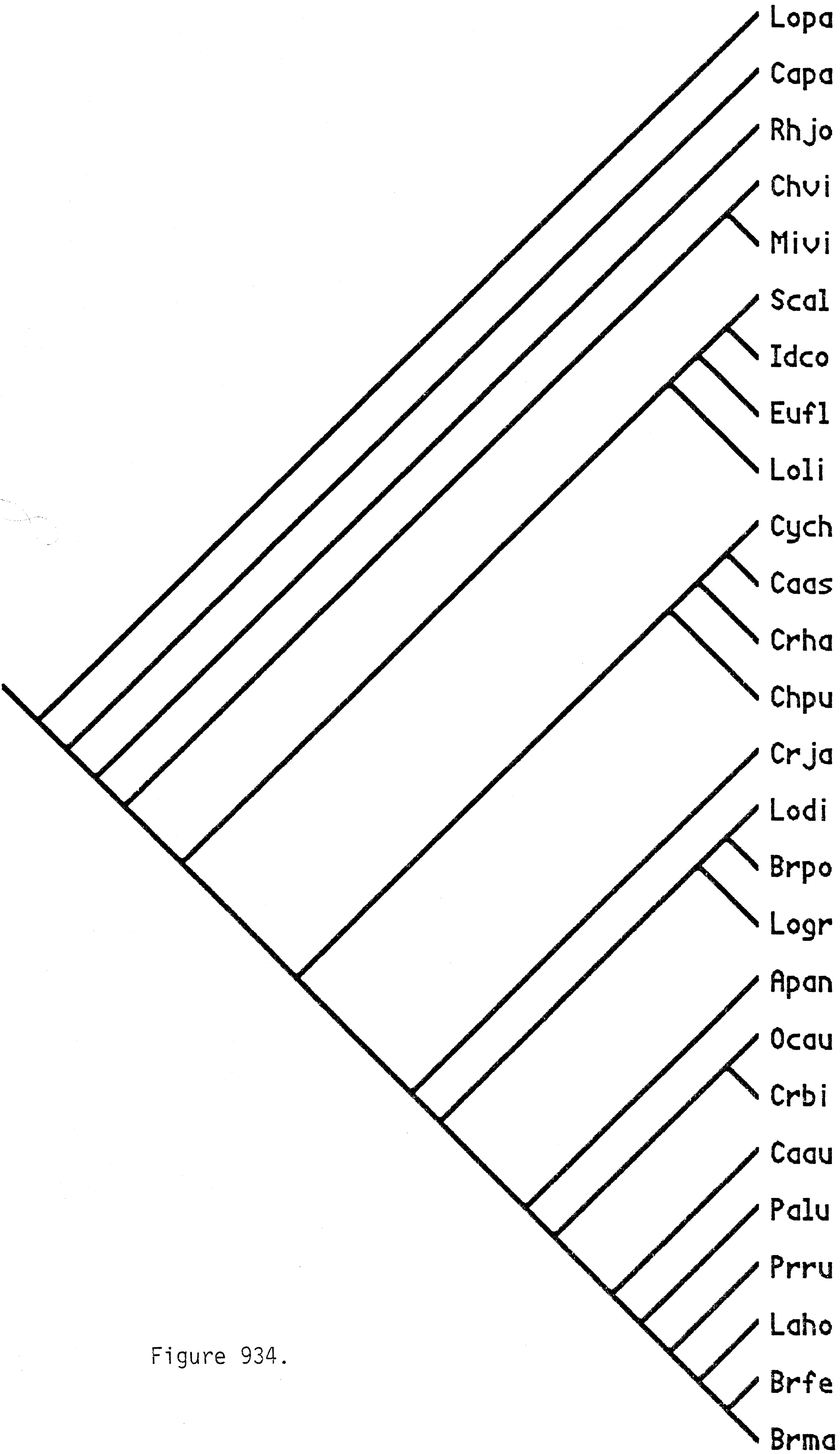

Lopa
Capa
Rhjo
Chvi
Mivi
Scal
Idco
Eufl
Loli
Cych
Caas
Crha
Chpu
Crja
Lodi
Brpo
Logr
Apan
Ocau
Crbi
Caau
Palu
Prru
Laho
Brfe
Brma

Figure 934.

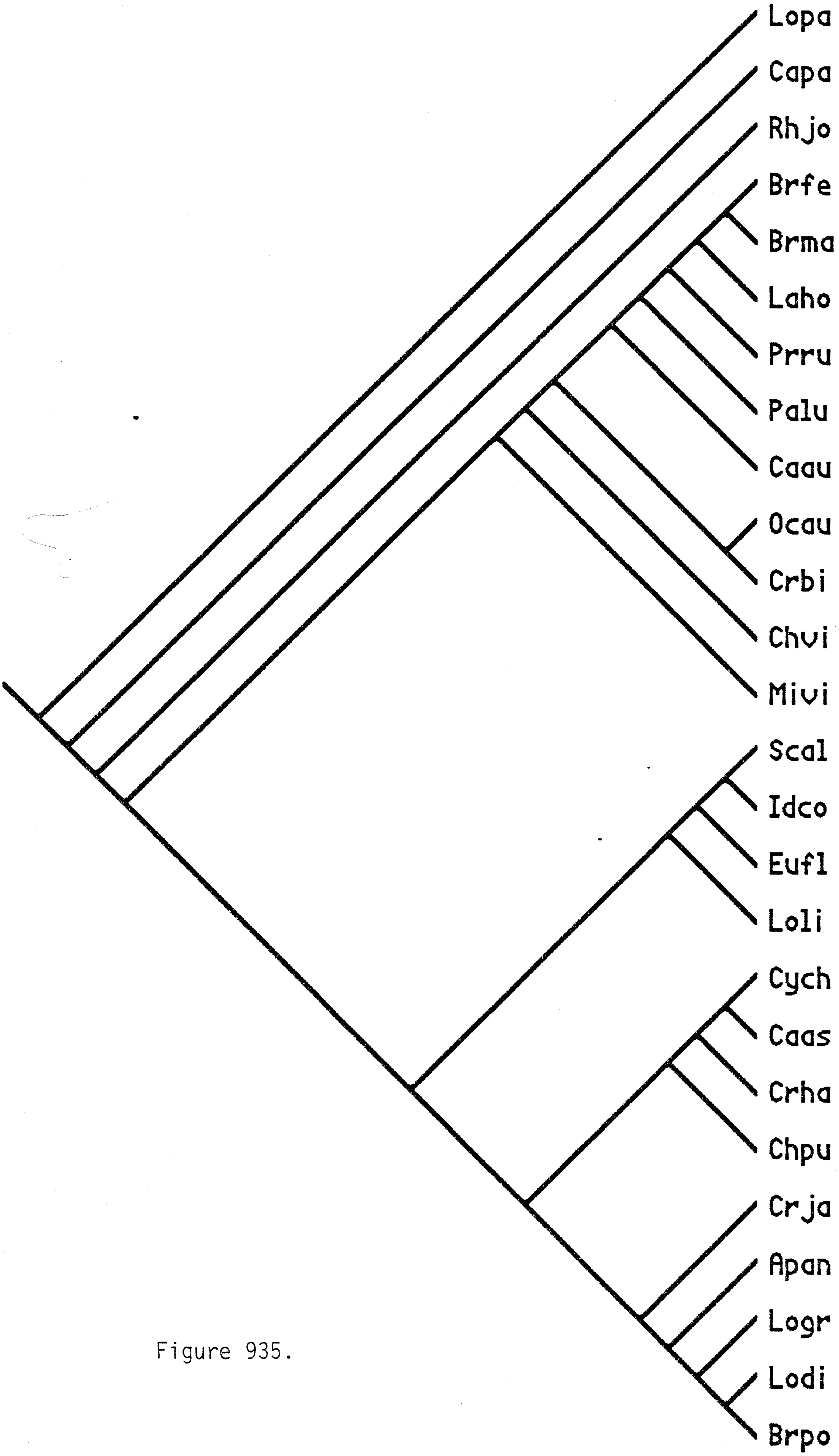

Lopa
Capa
Rhjo
Brfe
Brma
Laho
Prru
Palu
Caau
Ocau
Crbi
Chvi
Mivi
Scal
Idco
Eufl
Loli
Cych
Caas
Crha
Chpu
Crja
Apan
Logr
Lodi
Brpo

Figure 935.

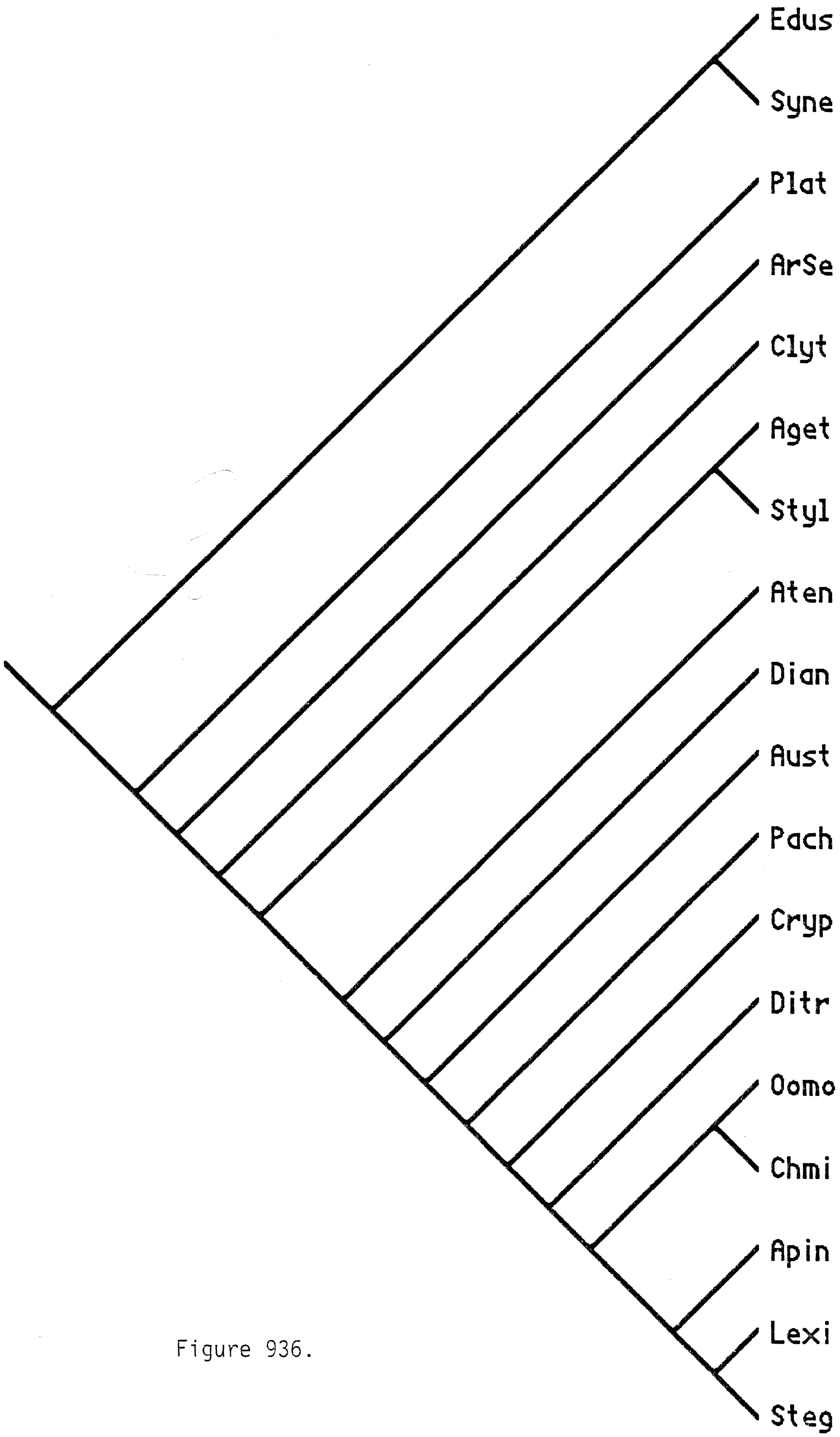

Edus
Syne
Plat
ArSe
Clyt
Aget
Styl
Aten
Dian
Aust
Pach
Cryp
Ditr
Oomo
Chmi
Apin
Lexi
Steg

Figure 936.

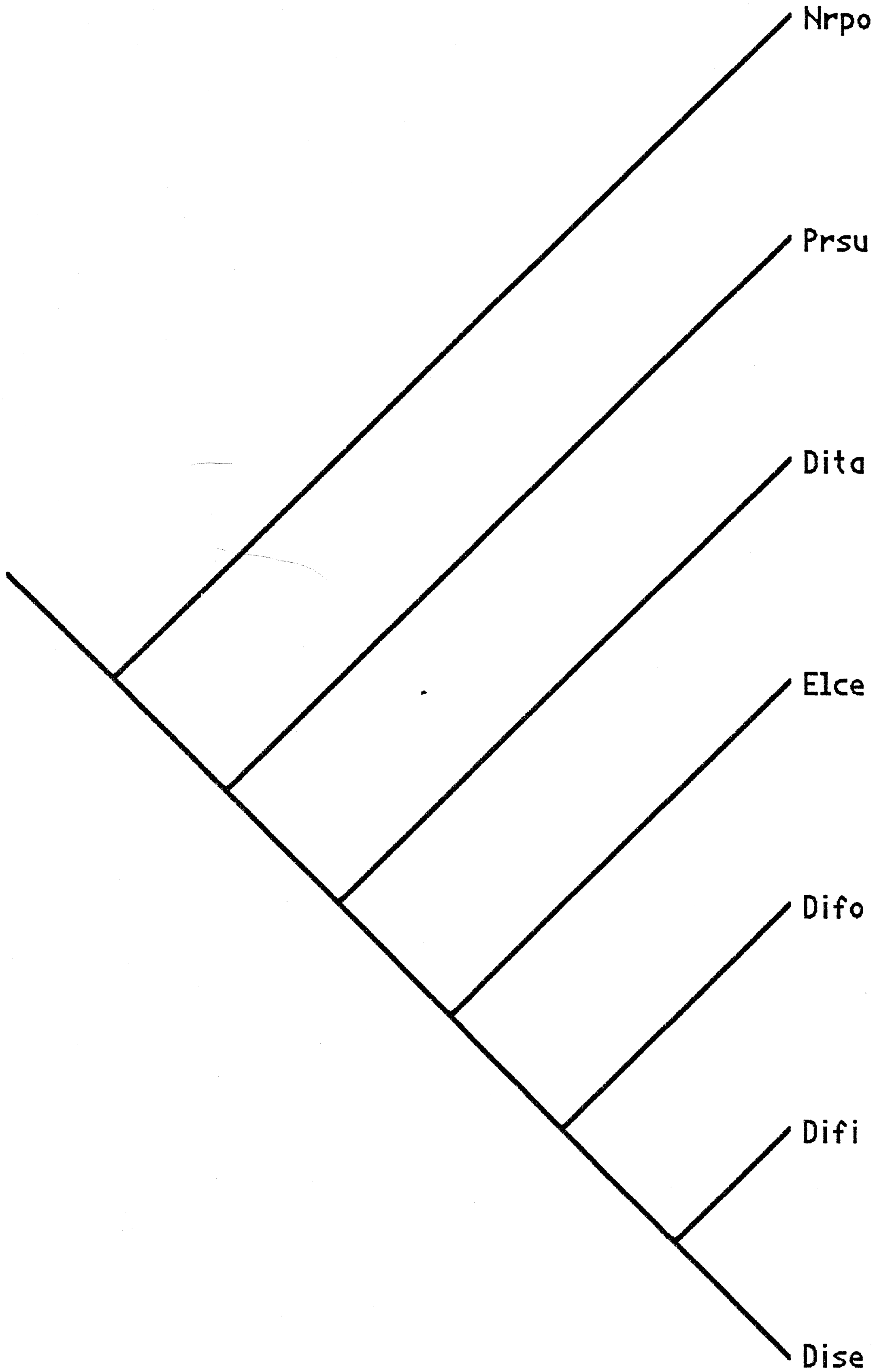


Figure 937.

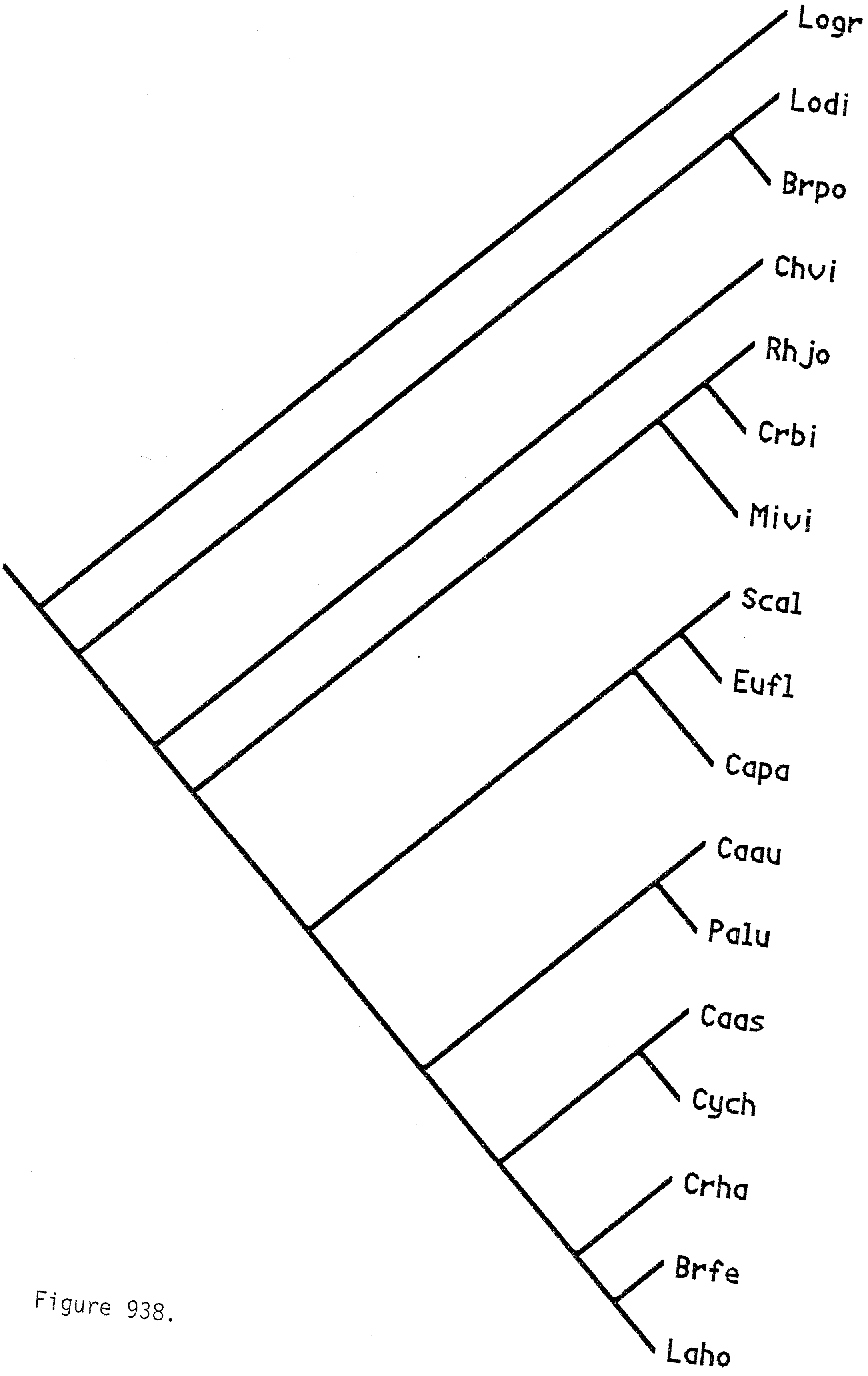

Logr
Lodi
Brpo
Chvi
Rhjo
Crbi
Mivi
Scal
Eufl
Capa
Caau
Palu
Caas
Cych
Crha
Brfe
Laho

Figure 938.

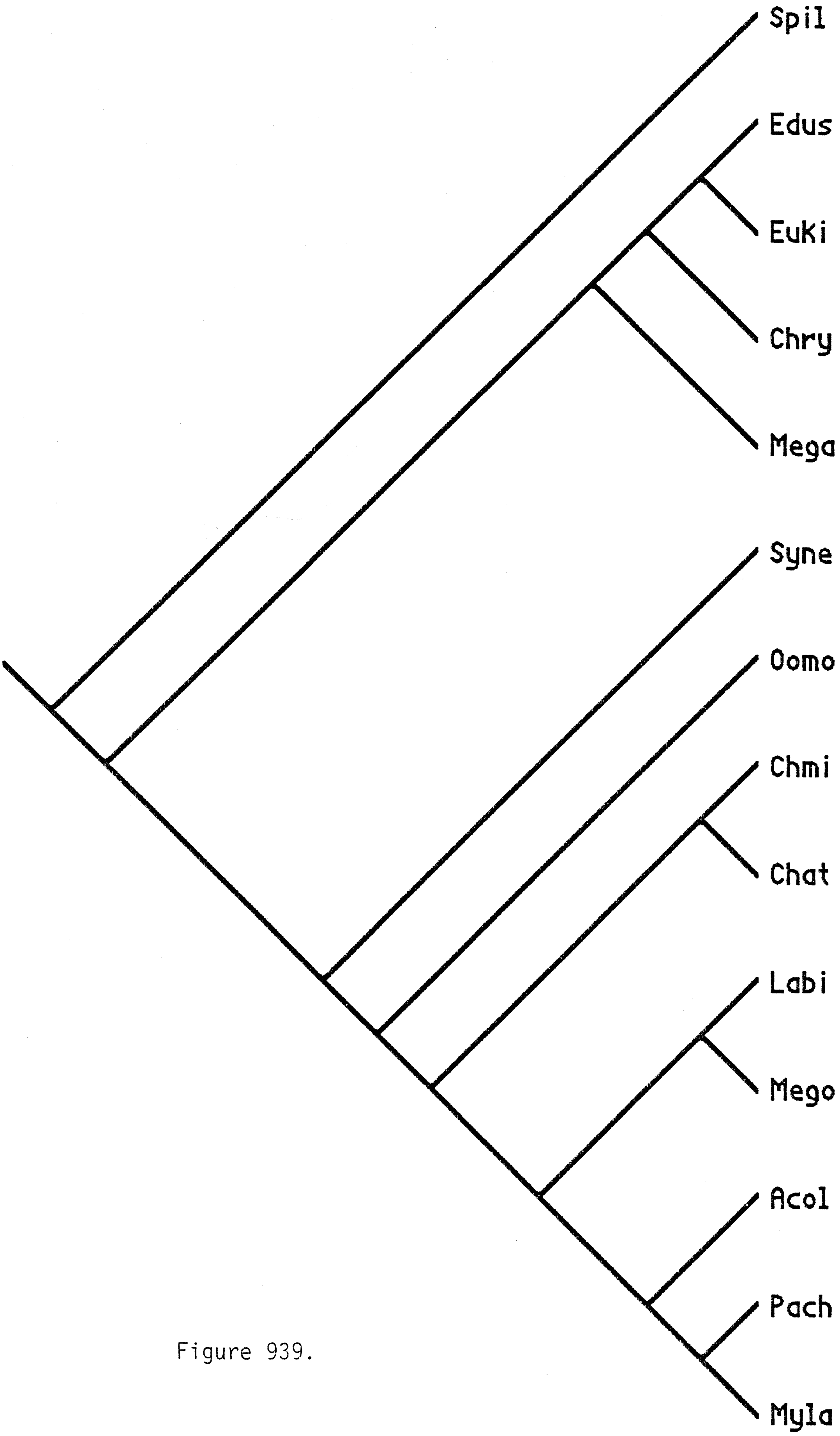

Spil
Edus
Euki
Chry
Mega
Syne
Oomo
Chmi
Chat
Labi
Mego
Acol
Pach
Myla

Figure 939.

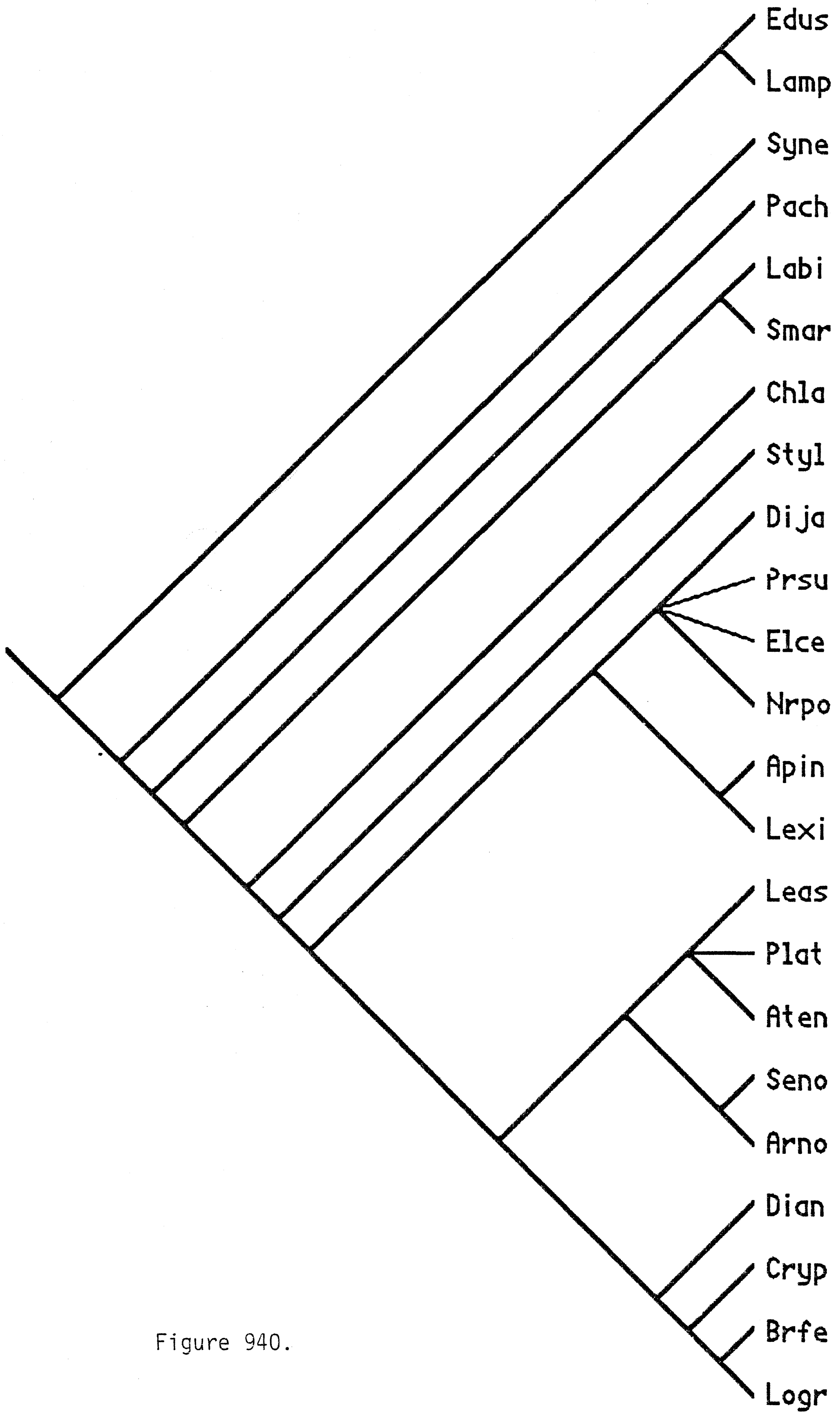

Edus
Lamp
Syne
Pach
Labi
Smar
Chla
Styl
Dija
Prsu
Elce
Nrpo
Apin
Lexi
Leas
Plat
Aten
Seno
Arno
Dian
Cryp
Brfe
Logr

Figure 940.

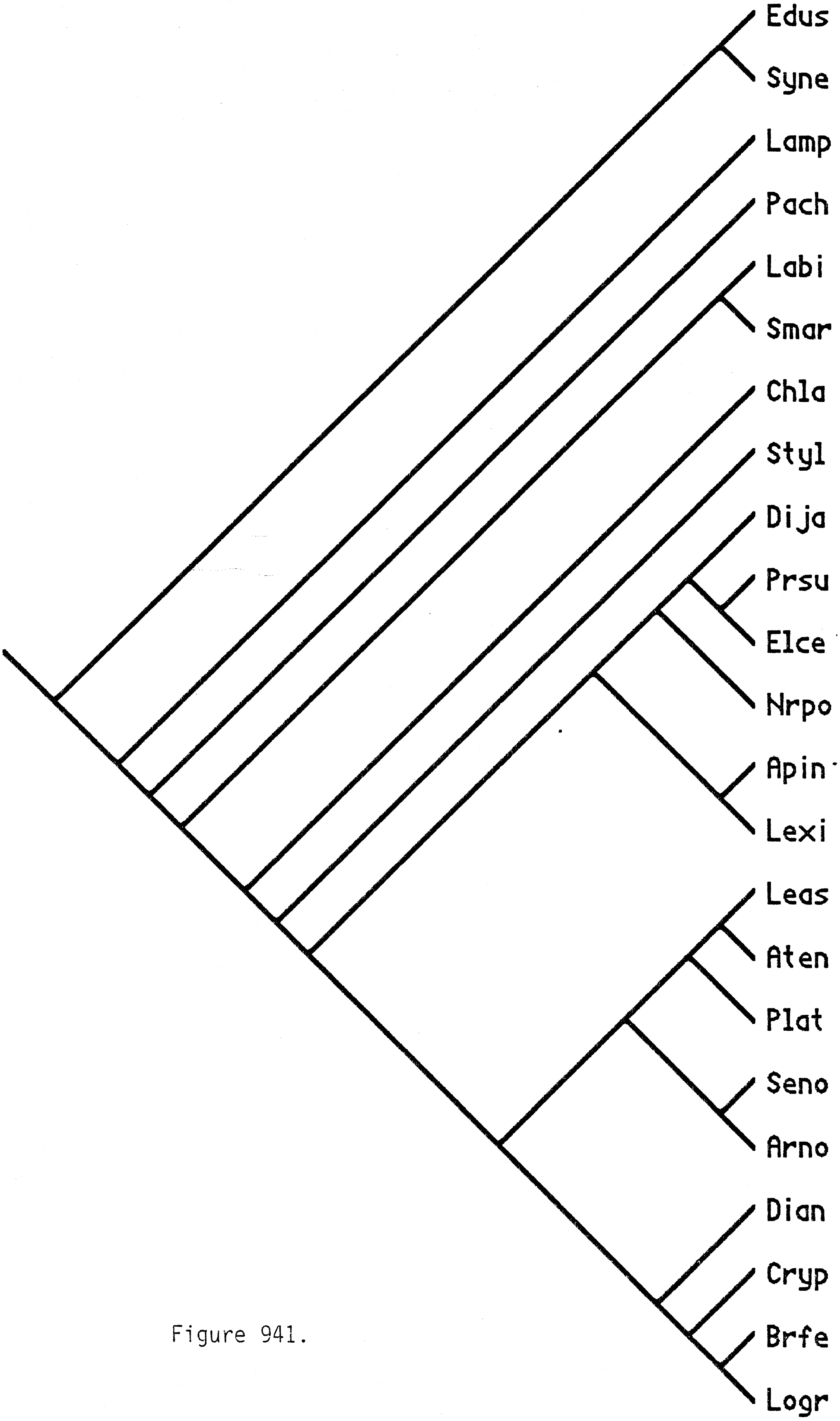

Edus
Syne
Lamp
Pach
Labi
Smar
Chla
Styl
Dija
Prsu
Elce
Nrpo
Apin
Lexi
Leas
Aten
Plat
Seno
Arno
Dian
Cryp
Brfe
Logr

Figure 941.

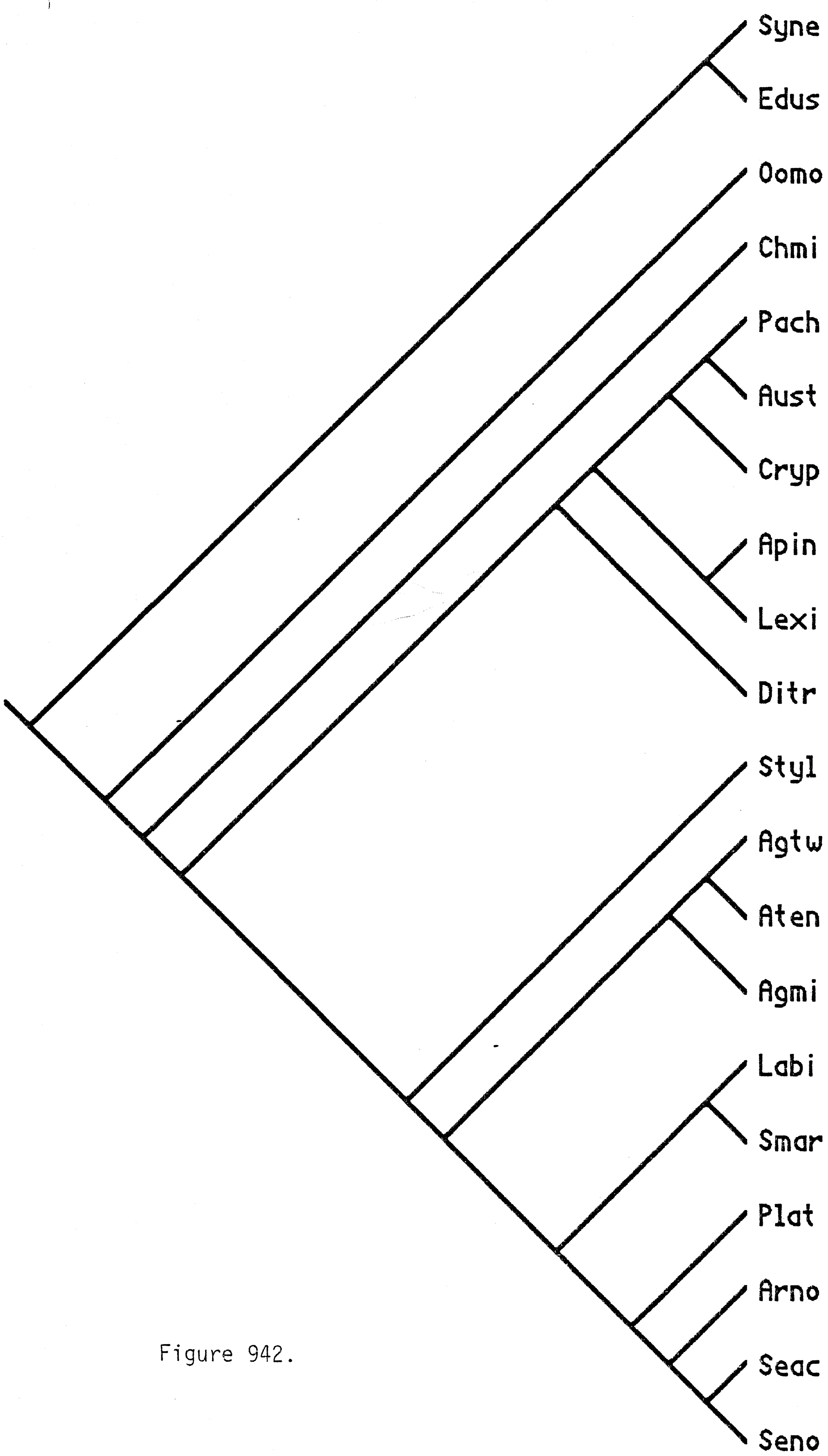

Syne
Edus
Oomo
Chmi
Pach
Aust
Cryp
Apin
Lexi
Ditr
Styl
Agtw
Aten
Agmi
Labi
Smar
Plat
Arno
Seac
Seno

Figure 942.

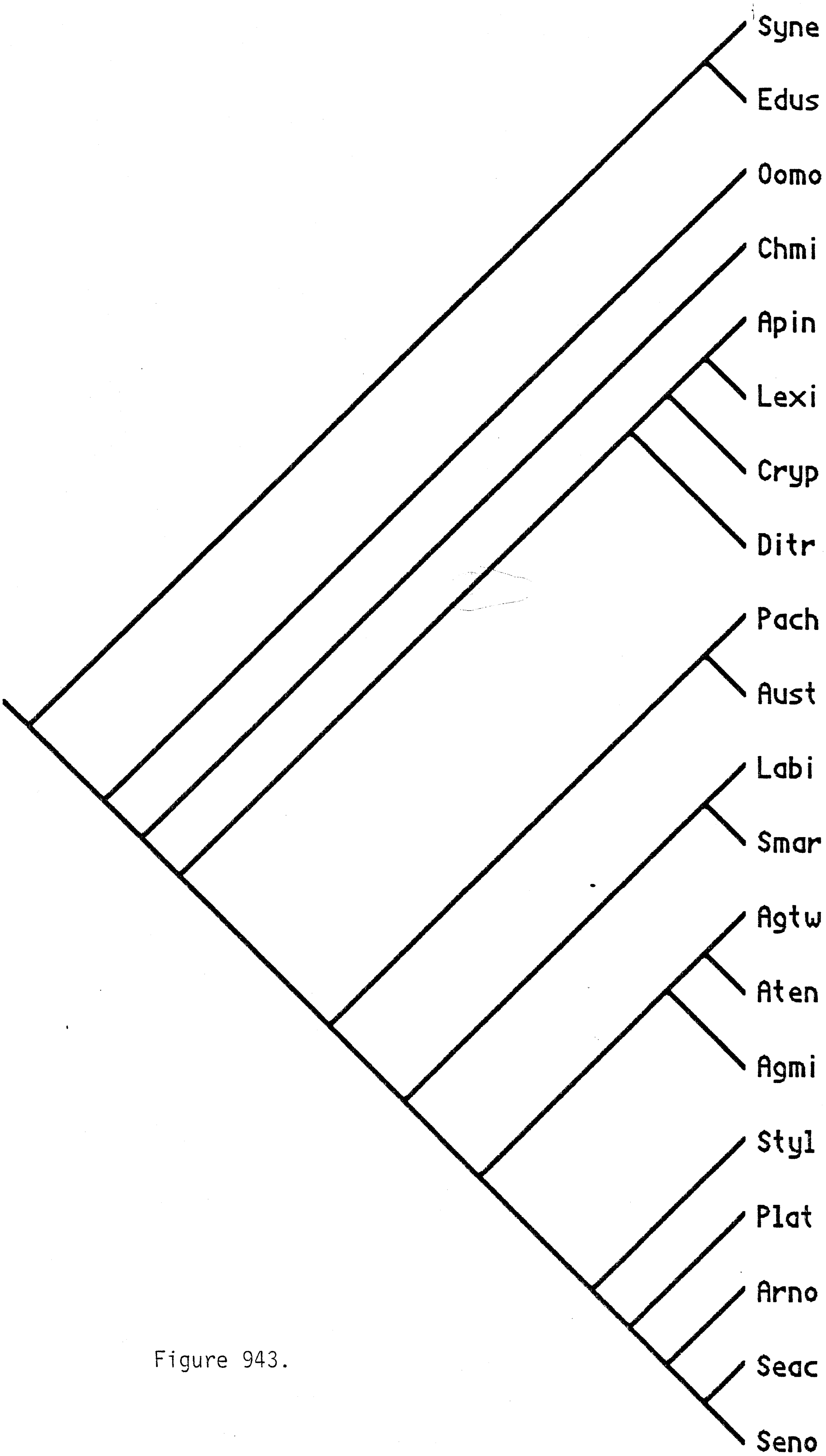

Syne
Edus
Oomo
Chmi
Apin
Lexi
Cryp
Ditr
Pach
Aust
Labi
Smar
Agtw
Aten
Agmi
Styl
Plat
Arno
Seac
Seno

Figure 943.

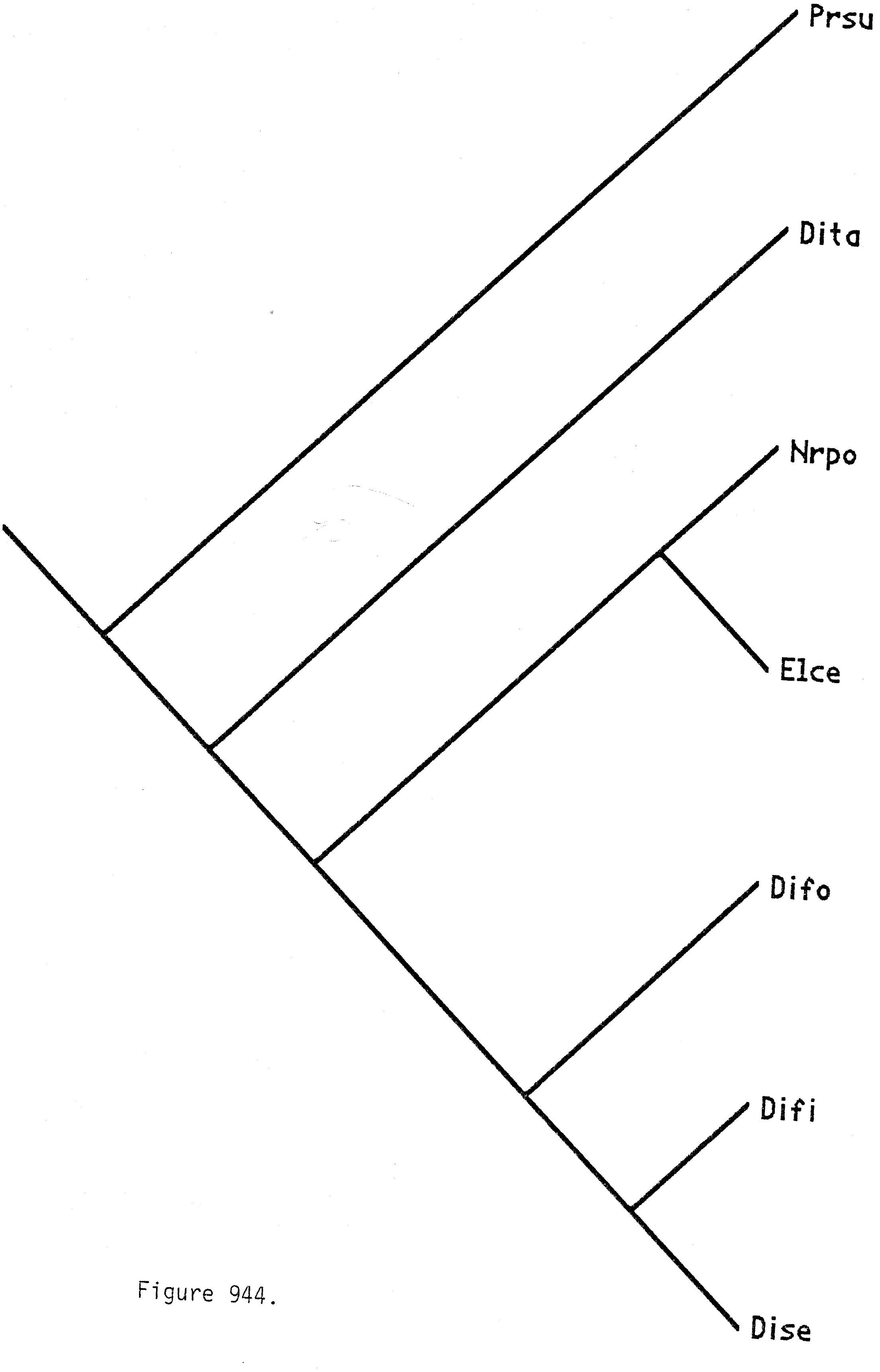


Figure 944.

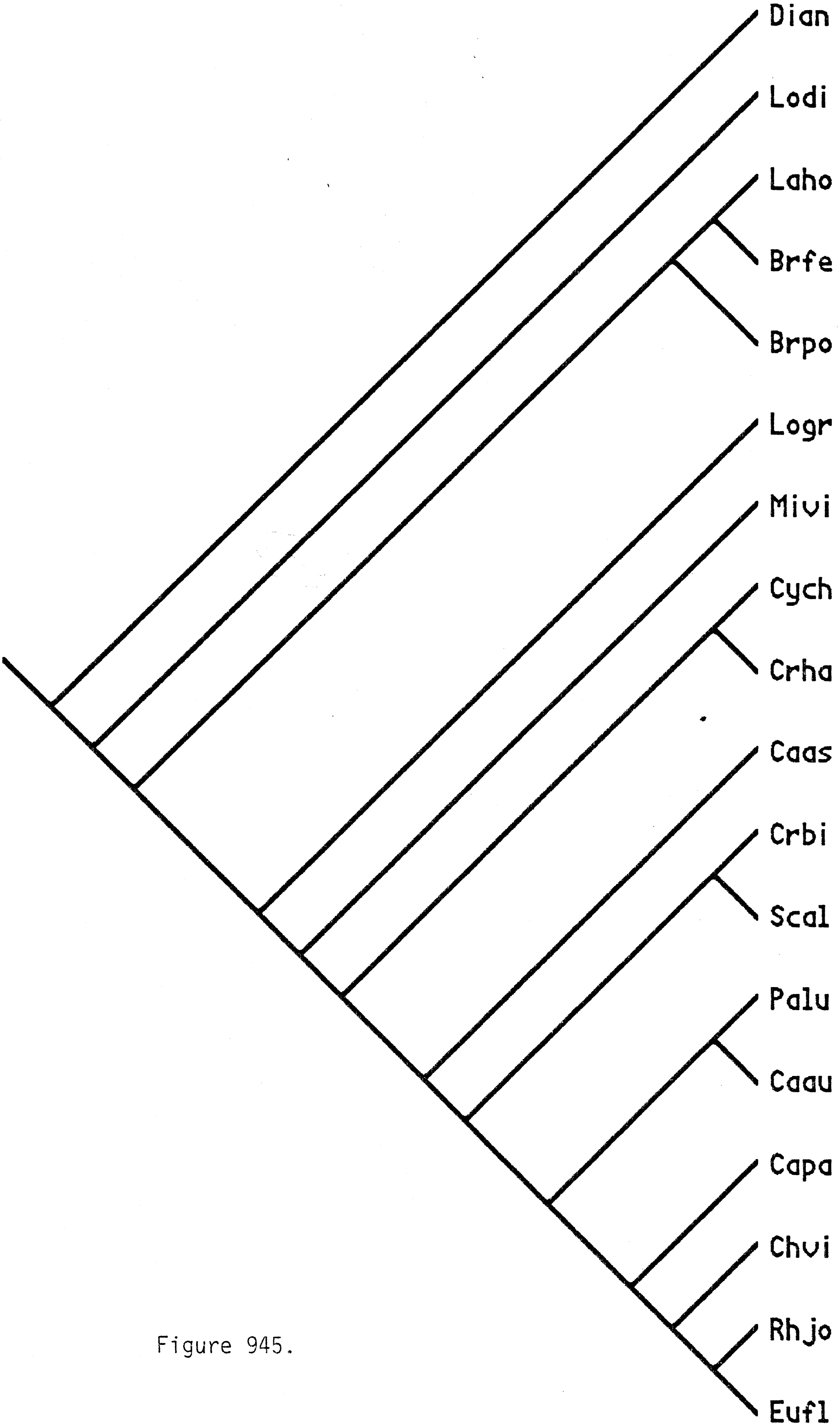

Dian
Lodi
Laho
Brfe
Brpo
Logr
Mivi
Cych
Crha
Caas
Crbi
Scal
Palu
Caau
Capa
Chvi
Rhjo
Eufl

Figure 945.

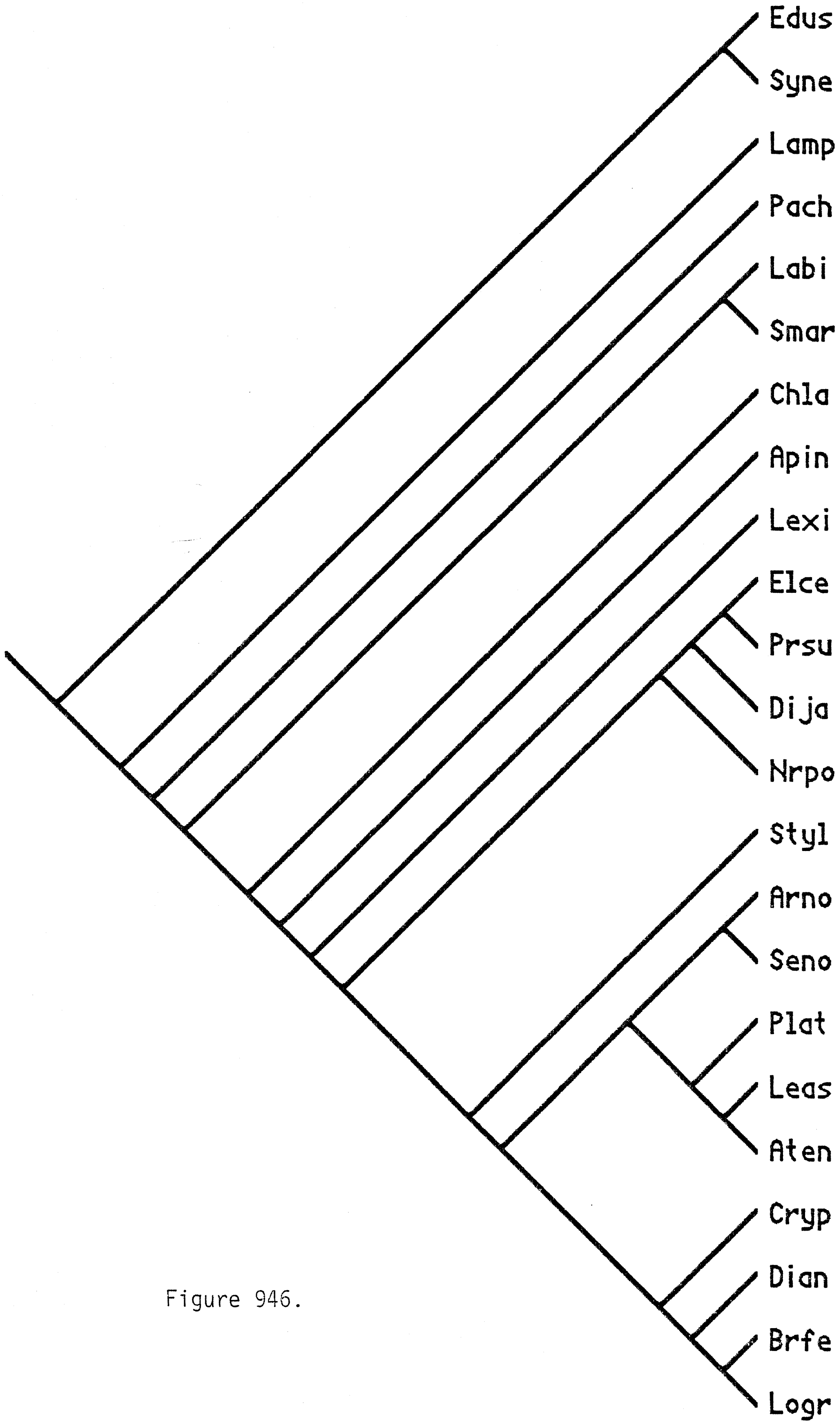

Edus
Syne
Lamp
Pach
Labi
Smar
Chla
Apin
Lexi
Elce
Prsu
Dija
Nrpo
Styl
Arno
Seno
Plat
Leas
Aten
Cryp
Dian
Brfe
Logr

Figure 946.

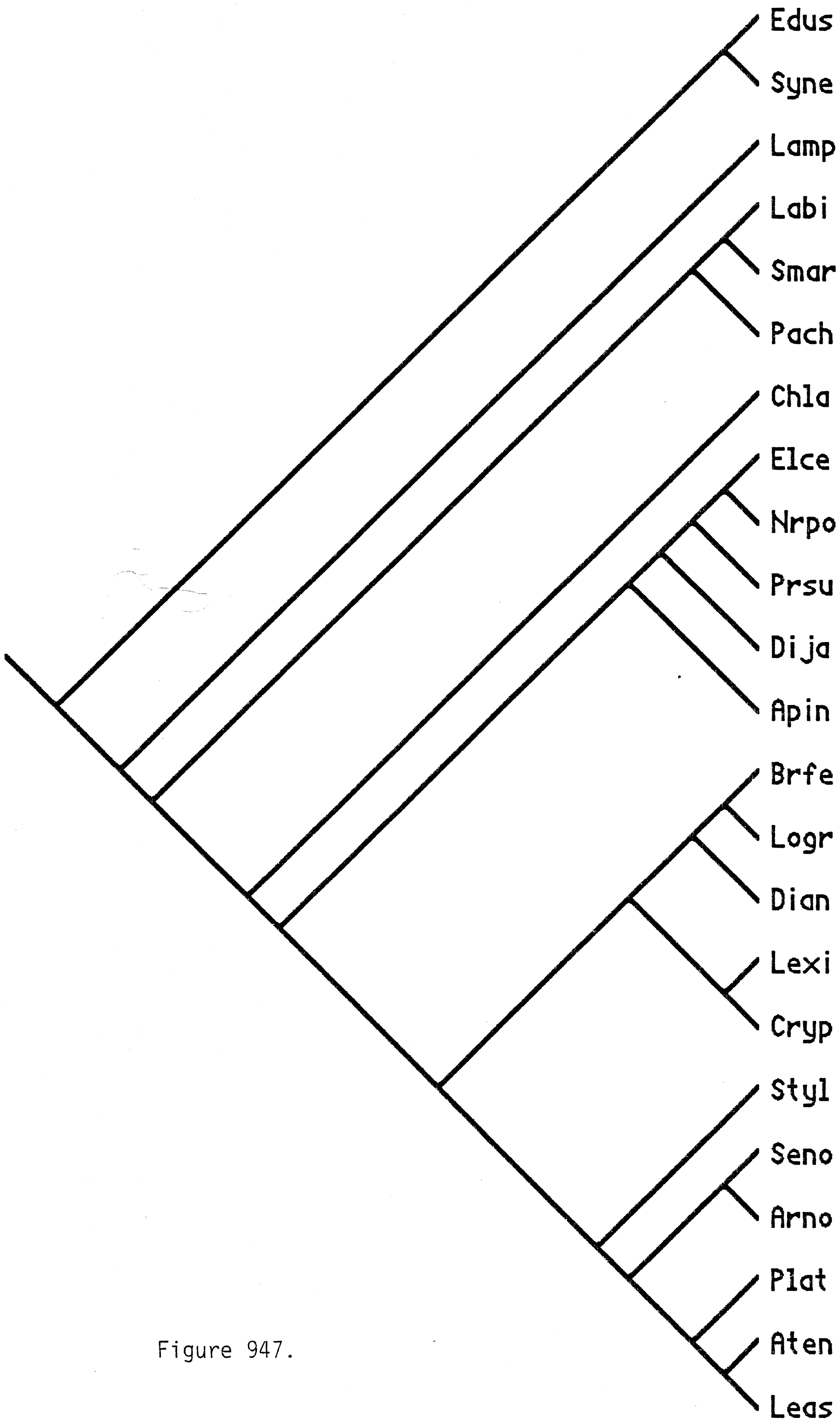

Edus
Syne
Lamp
Labi
Smar
Pach
Chla
Elce
Nrpo
Prsu
Dija
Apin
Brfe
Logr
Dian
Lexi
Cryp
Styl
Seno
Arno
Plat
Aten
Leas

Figure 947.

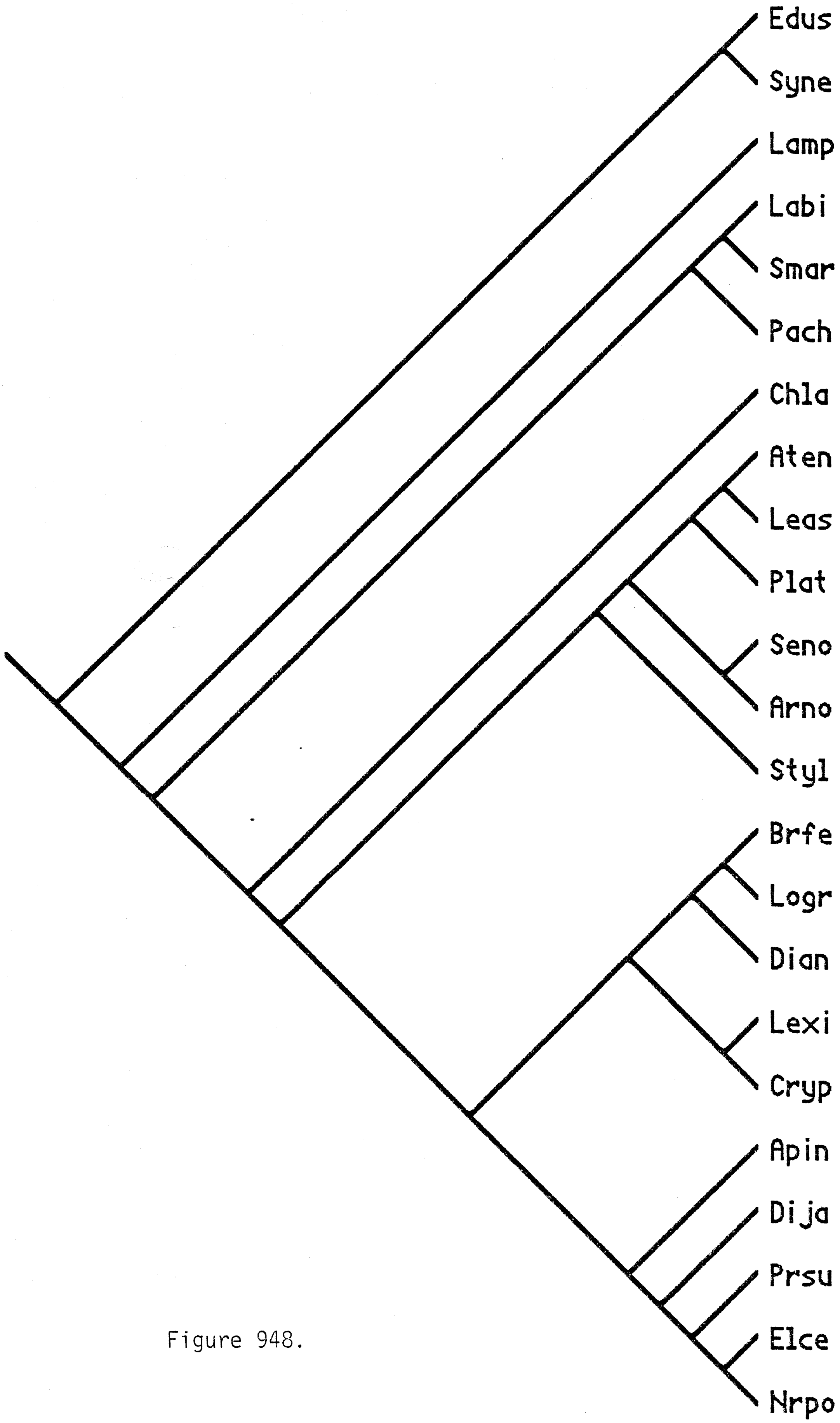

Edus
Syne
Lamp
Labi
Smar
Pach
Chla
Aten
Leas
Plat
Seno
Arno
Styl
Brfe
Logr
Dian
Lexi
Cryp
Apin
Dija
Prsu
Elce
Nrpo

Figure 948.

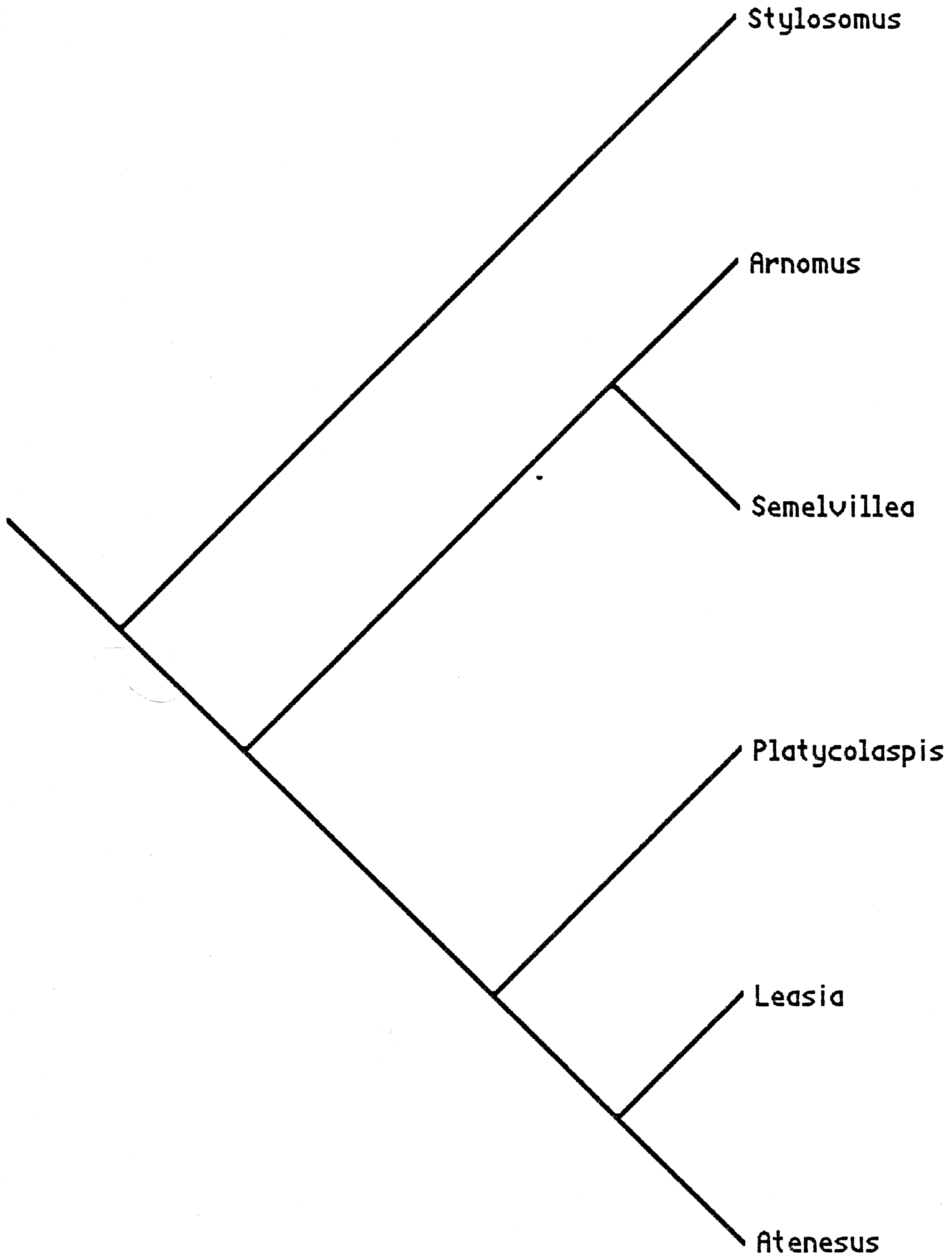

Stylosomus
Arnomus
Semelvillea
Platycolaspis
Leasia
Atenesus

Figure 949.

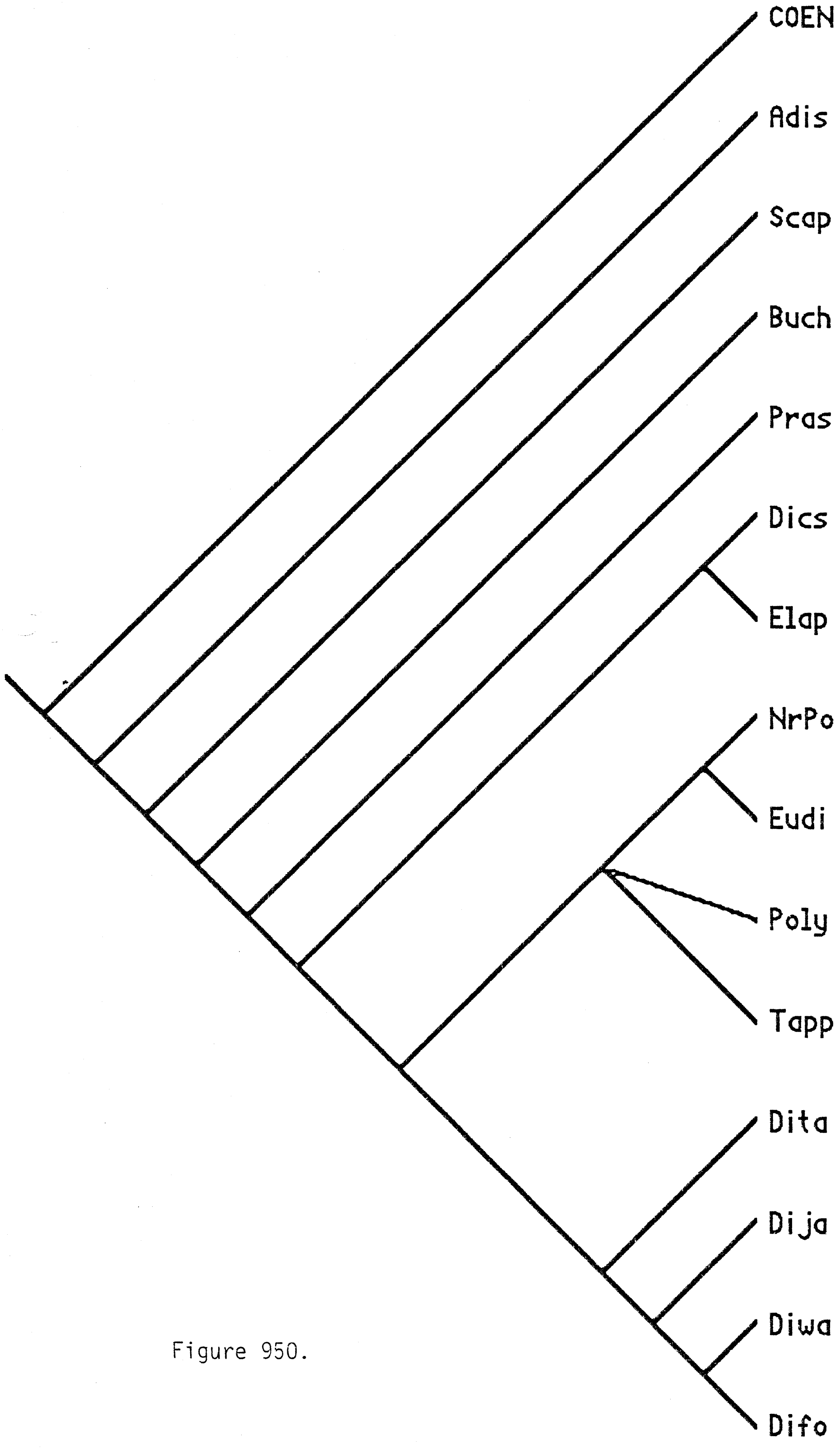

COEN
Adis
Scap
Buch
Pras
Dics
Elap
NrPo
Eudi
Poly
Tapp
Dita
Dija
Diwa
Difo

Figure 950.

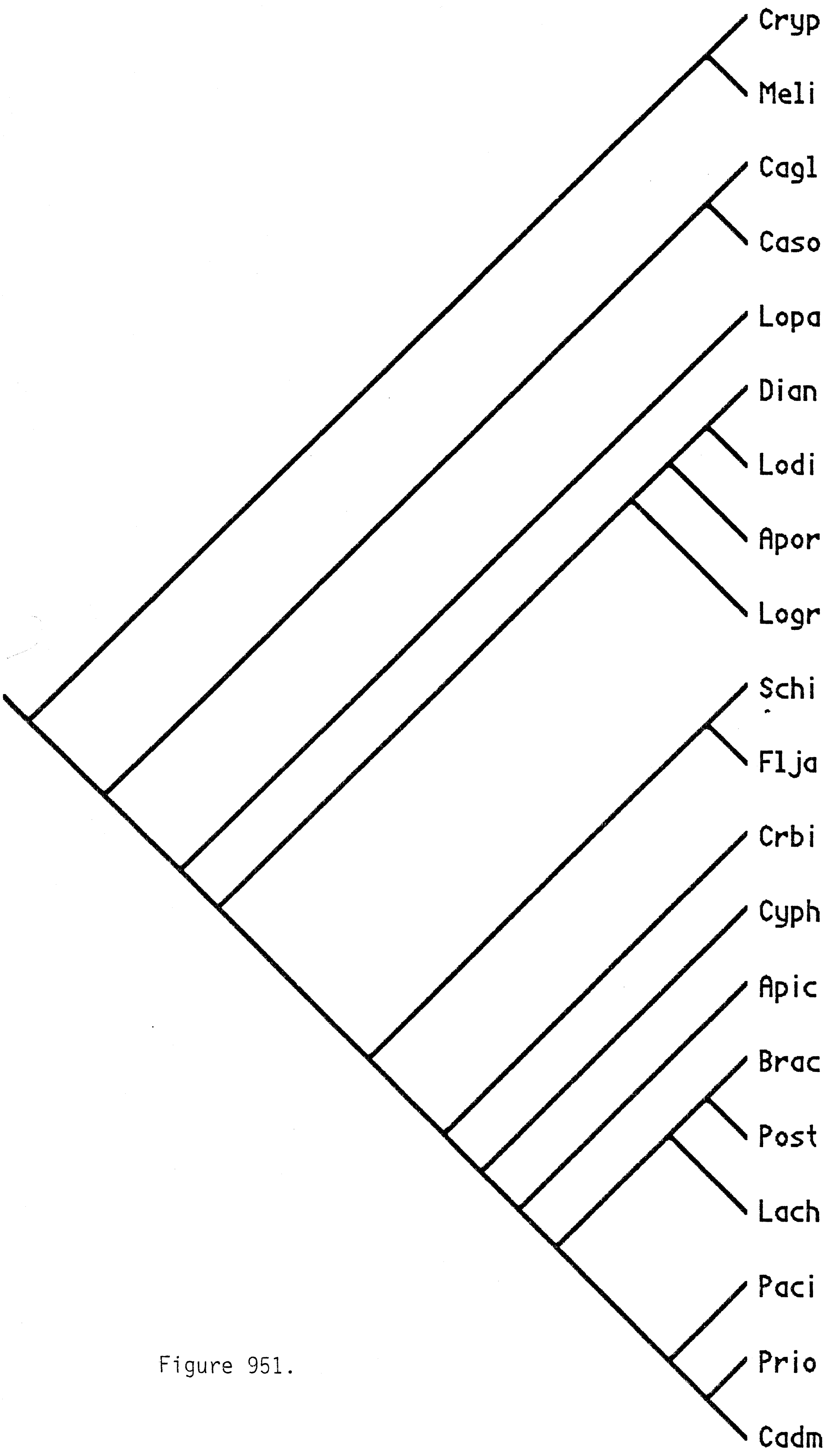

Cryp
Meli
Cagl
Caso
Lopa
Dian
Lodi
Apor
Logr
Schi
Flja
Crbi
Cyph
Apic
Brac
Post
Lach
Paci
Prio
Cadm

Figure 951.

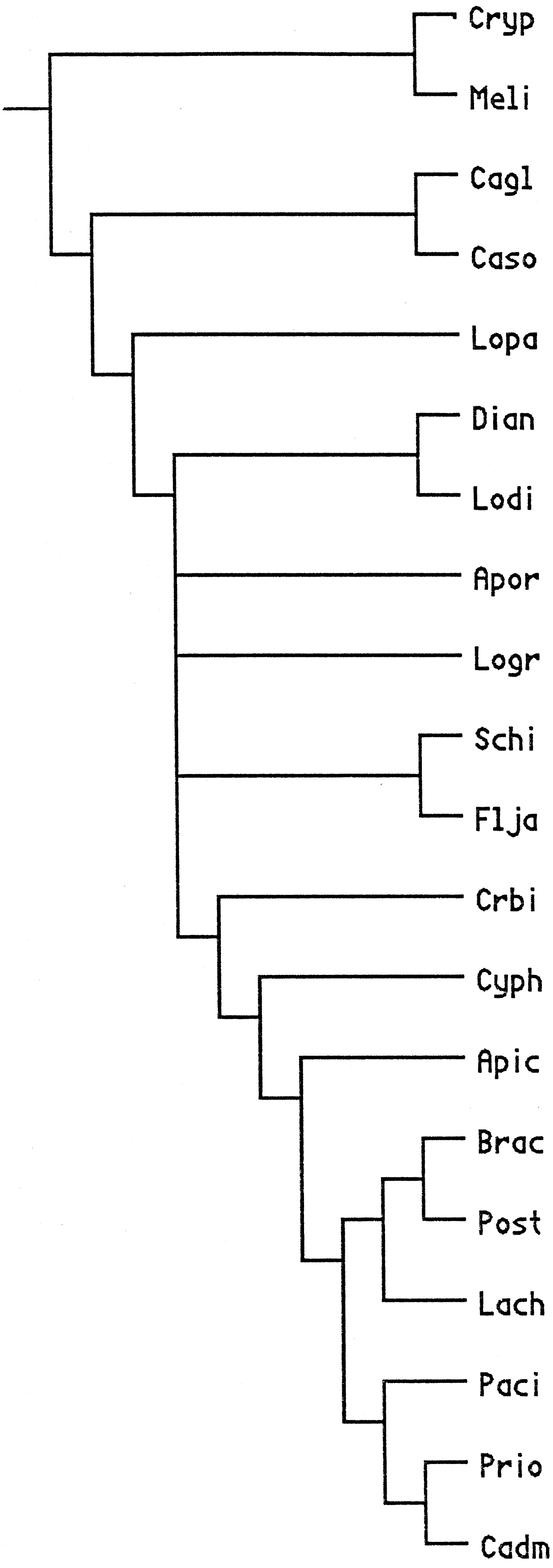

Cryp
Meli
Cagl
Caso
Lopa
Dian
Lodi
Apor
Logr
Schi
Flja
Crbi
Cyph
Apic
Brac
Post
Lach
Paci
Prio
Cadm

Figure 952.

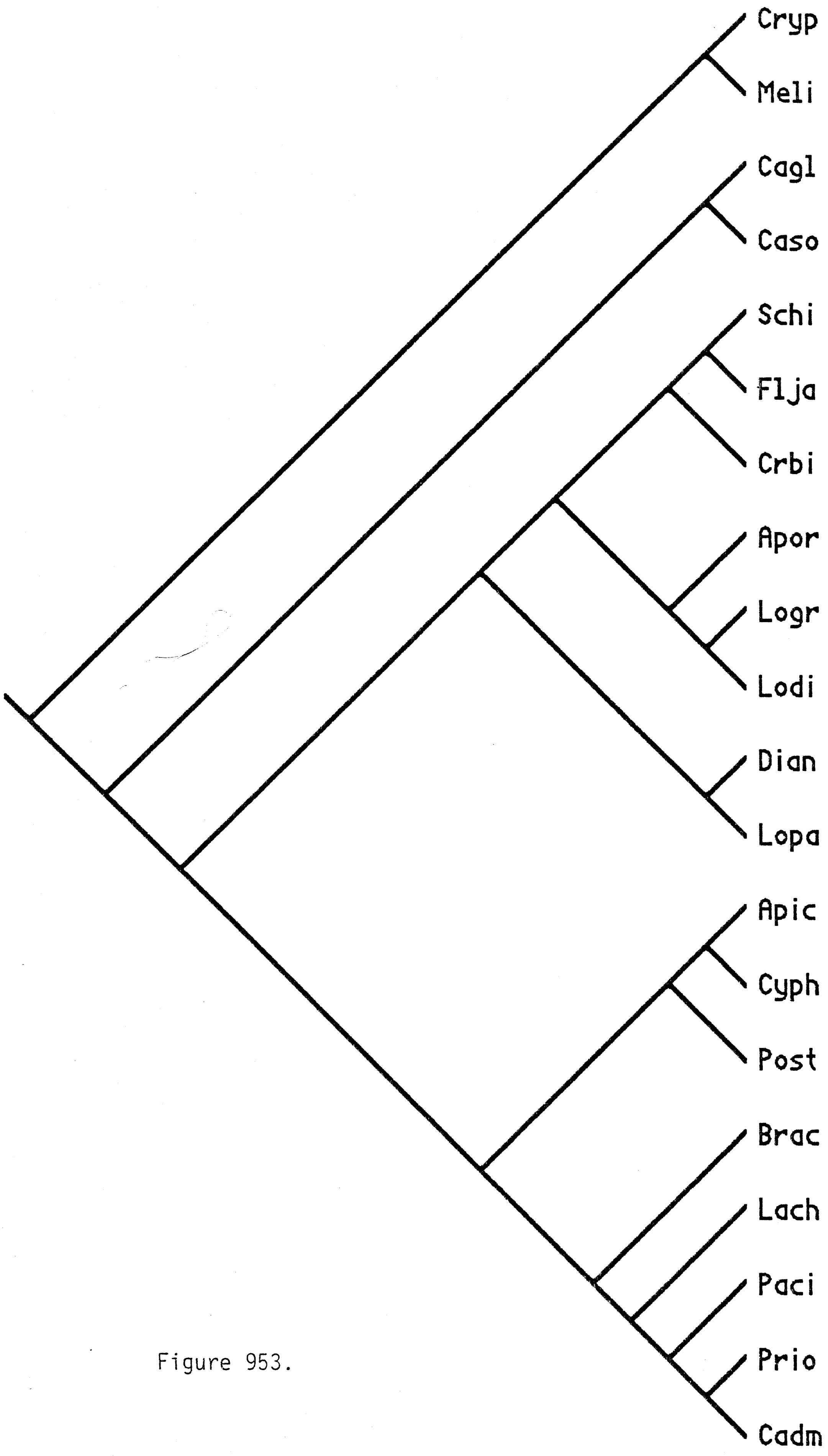

Cryp
Meli
Cagl
Caso
Schi
Flja
Crbi
Apor
Logr
Lodi
Dian
Lopa
Apic
Cyph
Post
Brac
Lach
Paci
Prio
Cadm

Figure 953.

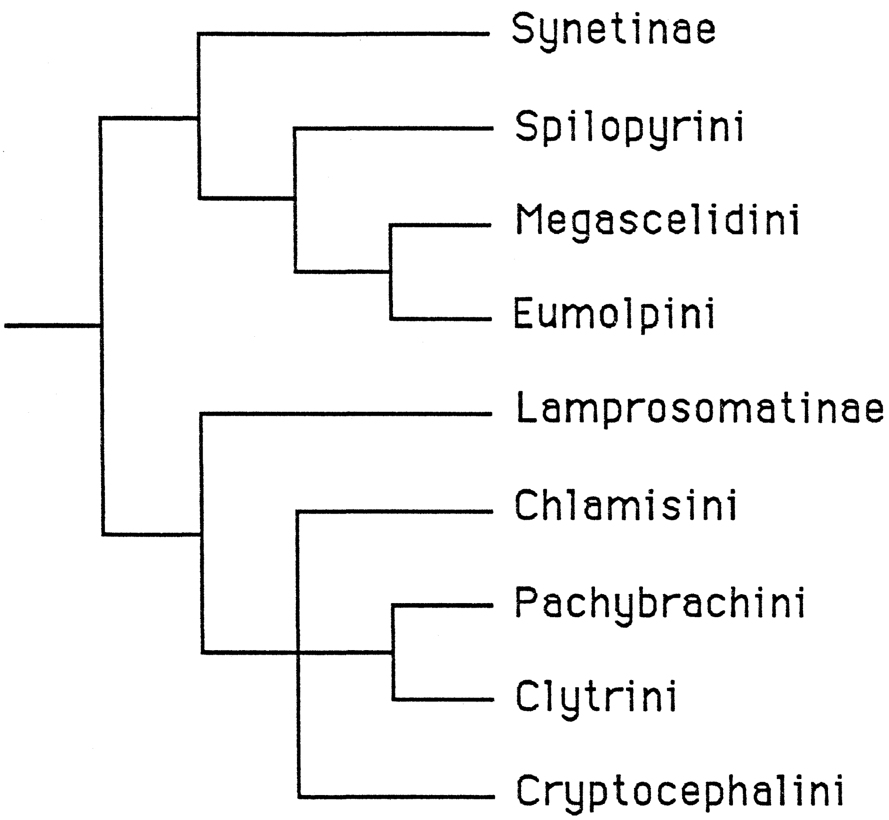


Figure 954.

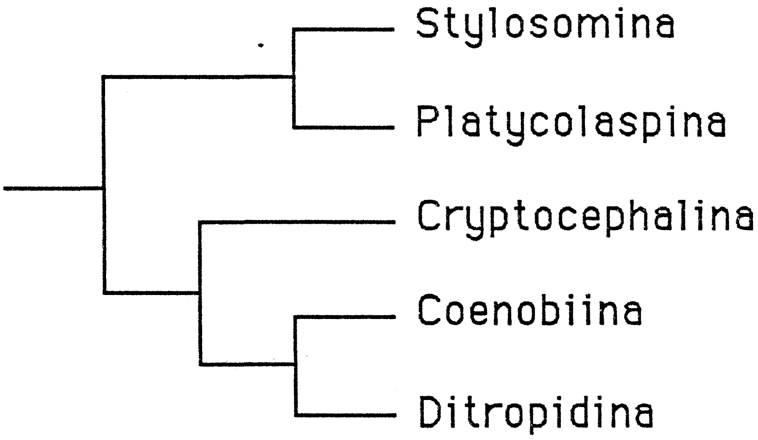


Figure 955.

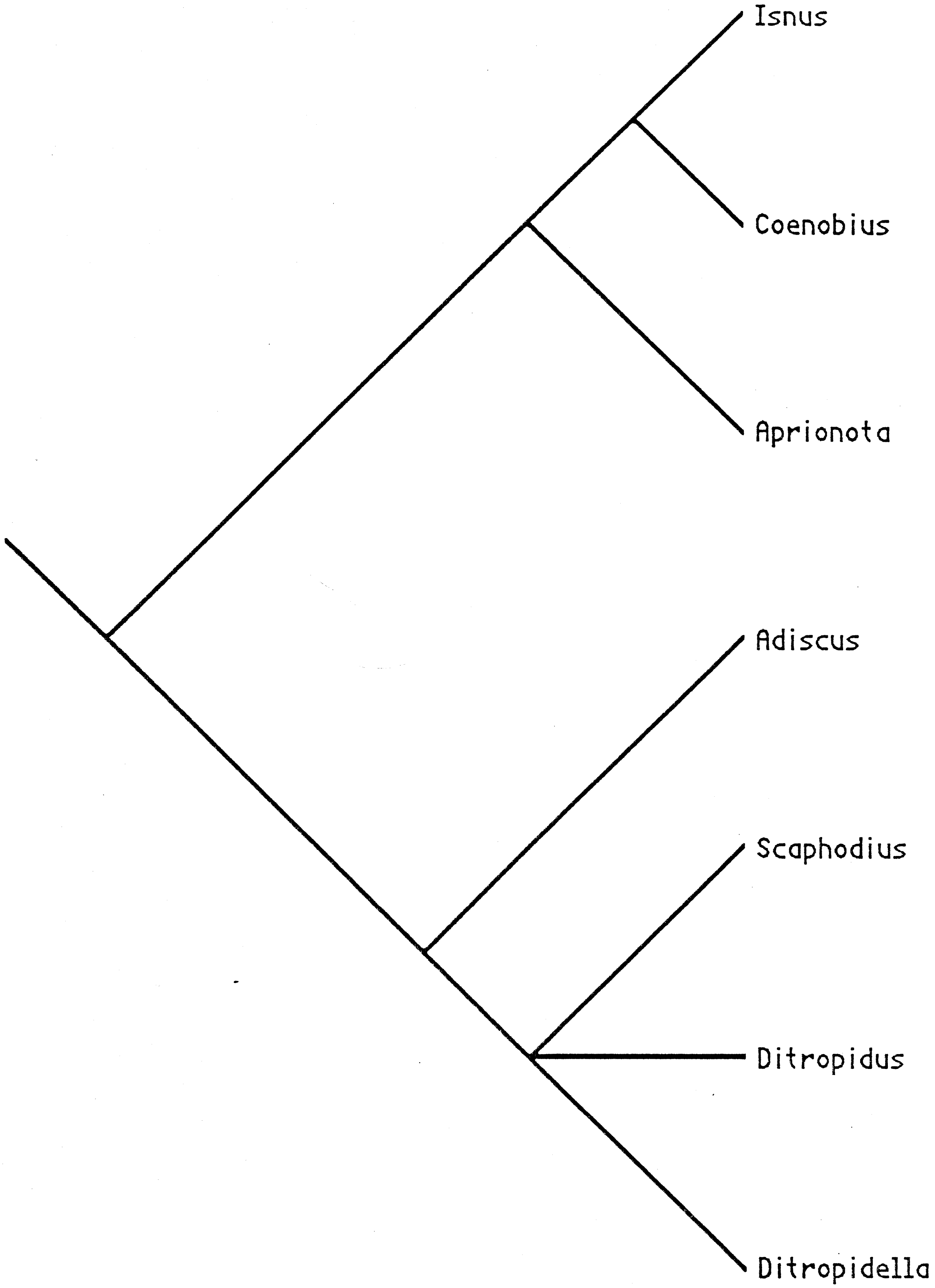

Isnus
Coenobius
Aprionota
Adiscus
Scaphodius
Ditropidus
Ditropidella

Figure 956.

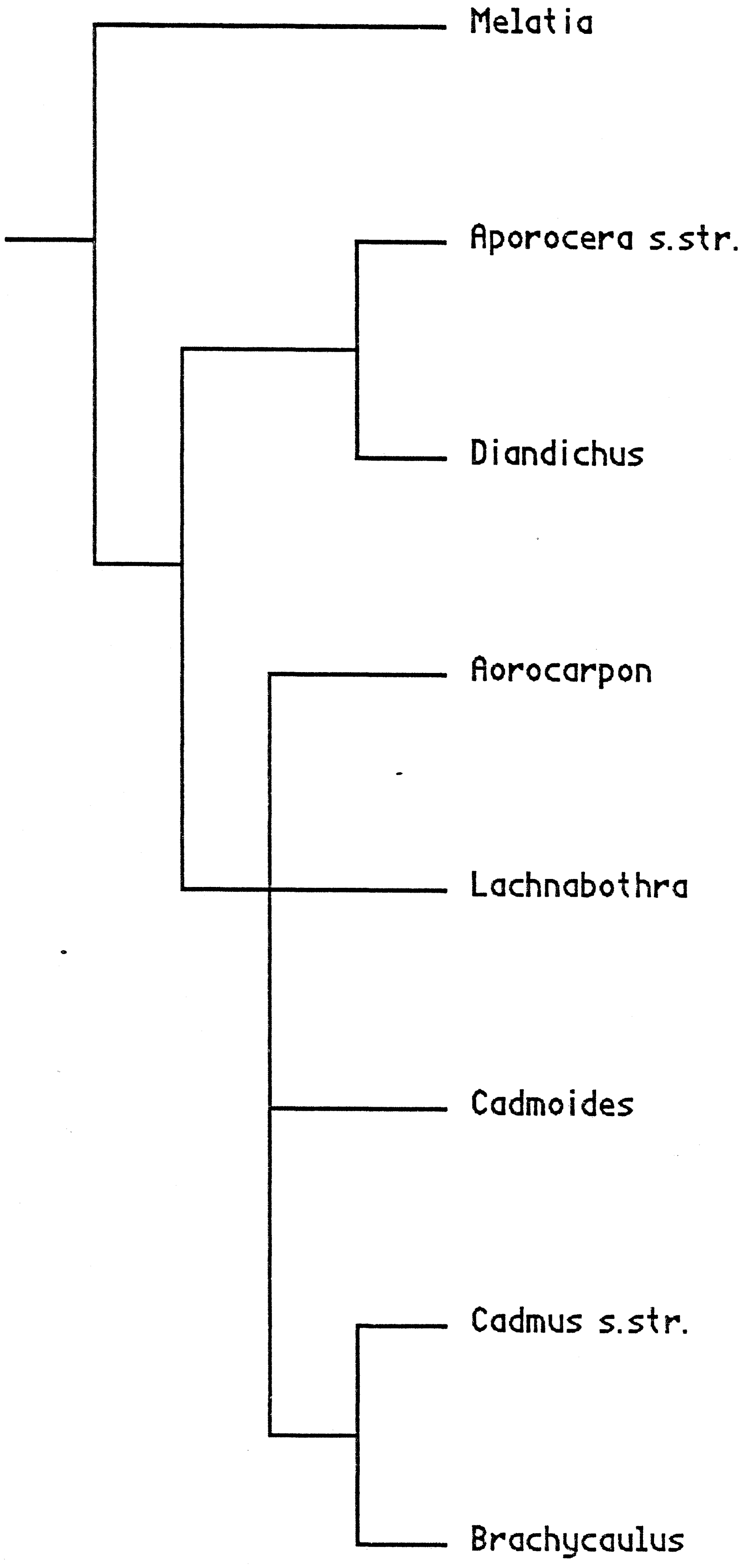

Melatia
Aporocera s.str.
Diandichus
Aorocarpon
Lachnabothra
Cadmoides
Cadmus s.str.
Brachycaulus

Figure 957.

Appendix A : List of material used for morphological analyses of scatoshell, larval, pupal and adult characters

Data for the specimens used in the scatoshell, larval, pupal and adult analyses are provided. The original name of each taxon is given in [], if different, together with the abbreviation used on the cladograms (Figs 927-954). The body lengths of adults are given. The larvae are all *ex* adults (with the parent data provided) unless otherwise noted. Abbreviations for depositories are given on pp. 17-18.

Eumolpinae

Spilopyrini

Macrolema sp. (= MACR); ♂=8.5mm, ♀ = 10mm.
♂, ♀ : Mount Fisher, Milla Milla 10.x.1979 N. Qld A. & M. Walford-Huggins [ANIC].

Spilopyra sumptuosa Baly (= SPIL); ♂= 10mm, ♀ = 11mm.
♂: Glen Aplin S. Q. 1948 A. Gemmell [ANIC].
♀ : St. Bernard, Mount Tamborine [ANIC].

Eumolpini

Pachnephorus sp. (= EUKI); ♂= 3mm, ♀ = 3.5mm.
♂, ♀ : Kinchega NP, NSW on *Epialtes cunninghamii* 25.ix.1985 C. Reid [ANIC].

Chrysochus auratus (F.) (= CHRY); ♂= 8mm, ♀ = 9mm.
♂,♀ : Dunnville, Ontario, Canada vi.1952 Plath [ANIC].

Edusella nr. *lineata* Blackburn (= EDUS); ♂= 4mm; ♀ = 4.5mm.
♂, ♀ , larvae : Black Mt. ACT 15.xi.1987 C. Reid & D. McCorquodale [ANIC].

Megascelini

Megascelis sp. (= MEGA); ♂= 3.5mm, ♀ = 4mm.
♂, ♀ : Ecuador Guayas Prov. Guayaquil 50m 18.ii.1981 H. F. Howden [ANIC].

Synetinae

Syneta adamsi Baly (= SYNE); ♂ = 5.5mm, ♀ = 7mm.
♂, ♀ : Japan C. Lewis 1910-320 Nicholson [BMNH].

Lamprosomatinae

Lamprosomatini

Lamprosoma elegans Jacoby (= LAMP); ♀ = 3.5mm.
2♀♀ : Mexico, Morelos, Cuernaraca vi.1934 5000' H. E. Hinton BM 1959-100 BM exch. 1984 [ANIC].

Lychnophaes purpureus Lacordaire (= LYCH); ♂ = 4mm, ♀ = 4.5mm.
♂, ♀ : Fry, Rio Janeiro Fry Coll 1905-100 BM exch 1984 [ANIC].

Oomorphus concolor Curtis (= OOMO); ♀ = 2.7mm.
many ♀ : Budleigh Salterton, S. Devon G. C. C. [BMNH]
larvae = Colynton [BMNH]

Cryptocephalinae

Chlamisini

Chlamisus mimosae Karren (= CHMI); ♂ = 2.5mm, ♀ = 3.5mm.
♂, ♀, larvae : Long Pocket Laboratory culture, Brisbane (ex. Brazil) [ANIC].

Chlamisus [*Brachycaulus*] *aterrimus* (Lea) (= CHAT); ♂ = 2.5mm, ♀ = 3mm.
♂: 15.16°S 144.59°E 14k NW Hope Vale Mission QLD 8-10 Oct. 1980 T. Weir [ANIC].
♀ : Kuranda xii.1949 J. G. Brooks bequest. Compared with holotypes of *C. australis* and *C. aterrimus*, C. Reid [ANIC].

Clytrini

Babiina

Babia quadriguttata Olivier (= BABI); ♀ = 5mm.
♀ : det. A. R. Moldenke '69 & cited in monograph [ANIC].

Clytrina

Aetheomorpha cryptocephaloides (Lacordaire) (= AETH); ♂ = 2.5mm, ♀ = 3.5mm.
♂, ♀ : Mutchilba N. Q. Dec. 1933 A. D. Selby F. E. Wilson coll. [MVM]

Clytra laeviuscula Ratzebourg (= CLYT); ♂ = 9.5mm, ♀ = 11mm.
♂, ♀ : Bogen, Danau [ANIC].

Labidostomis propinqua Faldeman (= LABI); ♂ = 10mm, ♀ = 11mm.
♂, ♀ : Persia, 1908 Asterabad 4-6. coll. O. Leonhard [ANIC].

Labidostomis sp. (= LABI)
larvae : nr Ghazrin Iran M. L. Cox [BMNH].

Smaragdina affine (Illiger) (= SMAR); ♂= 3.5mm, ♀ = 4mm.
larvae = Wychwood Pk, R. W. Lloyd [BMNH].

Smaragdina cyanea (F.) (= SMAR); ♂= 5mm, ♀ = 6mm.
♂, ♀ : Bogen, Danau v.1963 C. G. C. Gooding coll., donated ANIC 1979 [ANIC].

Ischiopachina
Ischiopachys bicolor (Olivier) (= ISCH); ♀ = 9mm.
♀ : Cayenne [ANIC].

Megalostomina
Megalostomis pyropyga Lacordaire (= MEGO); ♂= 8mm, ♀ = 9mm.
♂, ♀ : Rio Balsas Gro. Mex. Wickham [ANIC].

Pachybrachini
Unplaced larva (= CryA)
(1, not associated with adults) : Canal Zone Barro Colorado Id rotten flowers of *Pseudobombax* 19.ii-9.iii.1975 [ANIC].

Acolastus tuberculatus Jacoby (= ACOL); ♂= 3mm, ♀ = 3.5mm.
♂, ♀ = 5954 Marshall coll., 1918-53 [BMNH].

Ambrotodes signatipennis Baly (= AMBR); ♂= 3.2mm, ♀ = 3.5mm.
♂= Bariloch Argentina Terr. Rio Negro F. & M. Edwards BM 1927-63 28.xi-1.xii.1926 [BMNH].
♀ = L. Nahuel Huapi Puerto Blest Argentina Terr. Rio Negro F. & M. Edwards BM 1927-63 2-3.iii.1926 [BMNH].

Griburius larvatus (Newman) (= GRIB); ♂= 5.5mm, ♀ = 6.5mm.
♀ : John George Gehring coll. Winter Park, Florida 30.iii.1929 [ANIC].

Metallactus sp. (= META); ♂= 4.8mm, ♀ = 6mm.
♂, ♀ = Argentina Salta ii.1944 Rosario del Frontiera El Herangle F. Monrós coll. 1959 [USNM].

Mylassa socia Stål (= MYLA); ♂= 3mm, ♀ = 3.3mm.
♂, ♀ : Reed, Fry coll. 1905.100 [BMNH].

Pachybrachis hieroglyphicus Laicharting (= PACH); ♂= 3.5mm, ♀ = 4mm.
♂, ♀ = Simbach Tun vi.1956 C. G. C. Gooding coll. [ANIC].

Stylosomina
Stylosomus tamaricis (L.) (= STYL); ♂= 1.5mm, ♀ = 2mm.
♂, ♀ = Aimargnes, E. Tisson coll. F. Knab [USNM].

Platycolaspina
Arnomus brouni Sharp (= ARNO); ♂= 2.7mm, ♀ = 3mm.
♂, ♀ : Coppermine Id, Chicken Is 28-31.x.1968 J. C. Watt, litter [DSIR]

Arnomus sp. (= ARNO)
larvae (not associated with adults) : Tookahune Mtn NZ coll. C. Lyal [ANIC].

Atenesus sp. nov. (= ATEN); ♂= 2.2mm, ♀ = 2.5mm.
♂, ♀ : 23.32S 133.38E Mt Solitaire 30k WNW Alice Springs NT 29.viii.1978 M. S. Upton [ANIC].

Atenesus sp. nov. (= ATEN); ♂= 1.7mm, ♀ = 2mm.
larvae : 3k W Cobar NSW on Cassia eremophila flws, mulga scrub 24.ix.1985 C. Reid, 444 [ANIC].

Leasia australis Jacoby (= LEAS); ♂ 1.5mm, ♀ = 1.5mm.
♂, ♀ = Augusta, WA (34.19S 115.10E) 14k WNW Foul Bay 13.xi.1969 E. B. Britton [ANIC].

Leasia [*Agetinella*] *minuta* Jacoby (= AGMI); ♂ 1.2mm, ♀ = 1.5mm.
♂, ♀ : Kings Park, Perth, WA, Acacia spp flowers 16-19.viii.1987 C. Reid, 1051 [ANIC].
larvae : Araluen Park, Perth, WA on Acacia flws 16-19.viii.1987 C. Reid 1054 [ANIC].

Leasia sp. 2 (= AGTW); ♂= 1.2mm, ♀ = 1.5mm.
♂, ♀ : 30k E Cobar NSW on Ac. hakeoides & A. doratoxylon flws 23.ix.1985, 450 [ANIC].

larvae : Ingalba NR 5k W Temora NSW on Ac. hakeoides flws 20.viii.1985 C. Reid, 393; 2k E Ardlethan NSW on Ac. doratoxylon & A. decora flws 30.ix.1985 C. Reid 437. [ANIC].

Platycolaspis australis Jacoby (= PLAT); ♂= 1.5mm, ♀ = 1.8mm.
♂, ♀, larvae = Bulls Head, Brindabella Range, ACT on Acacia dealbata flws 12.x.1985 C. Reid, 485 [ANIC].

Semelvillea acaciae sp. nov. (= SEAC); ♂= 5mm, ♀ = 6mm.
♂, ♀, larvae = Barrington Tops SF, NSW on Ac. barringtonensis & melanoxylon, Dilgry R. Loop, 31.53S 151.32E 1200m 25.xi.1985 C. Reid, 557 [ANIC].

Semelvillea nothofagi sp. nov. (= SENO); ♂= 2.5mm, ♀ = 3mm.
♂, ♀ = Cobark Park, Barrington Tops SF, NSW, on Nothofagus moorei 25.xi.1986 C. Reid, 911 [ANIC].
larvae : Barrington Tops SF, NSW on Nothofagus moorei, Dilgry R. Loop, 31.53S 151.32E 1200m 26.xi.1985 C. Reid, 556; ditto but 25.xi.1986, 910 [ANIC].

Semelvillea waraganj sp. nov. (= SEGC); ♂= 3.2mm, ♀ = 4mm.
larvae : Piccadilly Circus ACT on E. pauciflora powerline clearing 10.xii.1984 C. Reid, 3 [ANIC].

Coenobiina
Aprionota [*Coenobius*] *inconstans* Lea (= APIN); ♂= 1.3mm, ♀ = 1.8mm.
♂, ♀ = 10 k S Black Springs NSW Acacia 3.xii.1984 C. Reid, 53 [ANIC].
larvae : Crummelin Reserve Pearl Beach NSW on Ac. linifolia flws 17.ii.1986 C. Reid 881; Kioloa SF 6k SW Kioloa NSW on Acacia flws 22.ii.1986 C. Reid 836 [ANIC].

Aprionota [*Loxopleurus*] *ruficollis* Bryant (= LORU); ♂= 1.7mm, ♀ = 2mm.
♂, ♀ : Fiji Viti Levu I. Lami 0-200m xii.1978 (♂), ii.1981 (♀) N. H. L. Krauss coll. [BBMH]

Aprionota [*Pycnophthalma*] *tutuilana* Maulik (= PYCN); ♂= 1.5mm, ♀ = 1.8mm.
♂, ♀ : Fagatogo Tutuilana Samoa 8.25.40 900f beating shrubbery ECZimmerman coll. [BPBM].

Aprionota sp. Tonga (= APTO); ♂= 1.5mm, ♀ = 2mm.
♂, ♀ : Tomga Eua I. Ohonua 2.1956 N. L. H. Krauss [BPBM].

Coenobius triangulum Suffrian (= COEN); ♂= 1.5mm, ♀ = 2mm.
♂, ♀ = Malvern, Natal xii.01 Jacoby coll. 1909-289 [BMNH].

Isnus discoidalis Jacoby (= ISNU); ♀ = 1.5mm.
2♀♀ = N. W. Rhodesia Kashitu N. of Broken Hill vi.1915 H. C. Dollman tree flowers [BMNH].

Ditropidina

Adiscus grandis (Baly) (= DIOR); ♂= 4mm, ♀ = 4.5mm.
♂= Quop W. Sarawak G. E. Bryant 30.iii.1914 Pres. by Imp. Bur. Ent. Brit. Mus. 1923-65. [BMNH].
♀ = Puak Sarawak 1.v.1914 G. E. Bryant. G. Bryant coll. 1919-147. [BMNH].

Ditropidella nr *jacobyi* Baly (= DISE); ♂= 1.5mm, ♀ = 1.8mm.
♂= Stirling Ra. NP (Bluff Knoll Rd) WA on Jarrah 31.xii.1985 C. Reid, 729 [ANIC].
♀ = North Walpole Rd 6k N Walpole WA on Jarrah 2.i.1986, 738 [ANIC].
larvae : Porongurup NP (SE corner) WA on Jarrah 29.xii.1985 C. Reid, 724 [ANIC].

Ditropidella nr *jacobyi* Baly (= DIFI); ♂= 1.8mm, ♀ = 2.2mm.
♂, ♀, larvae = Piccadilly Circus ACT on E. pauciflora powerline clearing 10.xii.1984 C. Reid, 5 [ANIC].

Ditropidus [*Elaphodes*] *aeneolus* Chapuis (= ELAE); ♂= 2mm, ♀ = 2.5mm.
♂, ♀ : Tallarook VIC on Ac. mearnsii 26.vi.1985 P. G. Kelly [ANIC].
larvae : CSIRO Black Mtn Canberra ACT on Ac terminalis 28.vii.1985 C. Reid 398 [ANIC].

Ditropidus [*Elaphodes*] nr *aeneolus* (= ELON); ♂= 2.2mm, ♀ = 2.8mm.
larvae : 35k W Balranald NSW (Sturt H'way) on Ac. pendula 15.v.1986 C. Reid 862 [ANIC].

Ditropidus antennarius Chapuis (= DITA); ♂= 2.5mm, ♀ = 3mm.
larvae : Sawpit Ck 7K W Gundaroo NSW on E. macrorhyncha 7.ii.1985 C. Reid, 215 [ANIC].

Ditropidus nr *antennarius* Chapuis (= DITA); ♂ = 2.5mm, ♀ = 3mm.
♂, ♀ : 11.09S 132.09E Black Point Coburg Peninsula NT 30.i.1977 E. D. Edwards [ANIC].

Ditropidus [*Elaphodes*] *cervinus* Suffrian (= ELCE); ♂ = 2mm, ♀ = 3.5mm.
♂, ♀ : P. G. Kelly coll. [ANIC].
larvae : Cook, Canberra, ACT on Ac dealbata 30.xii.1984 C. Reid, 246 [ANIC].

Ditropidus comans Chapuis (= DICS); ♂ = 1.8mm, ♀ = 2mm.
♂, ♀ : 35 k W Balranald NSW on Ac. pendula 15.v.1986 C. Reid, 872 [ANIC].

Ditropidus concolor Saunders (= DICO); ♂ = 3mm, ♀ = 3.5mm.
larvae : Sawpit Ck 7k W Gundaroo NSW on Ac. dealbata 30.xii.1984 C. Reid 105 [ANIC].

Ditropidus fugitivus Chapuis (= DITS); ♂ = 3.5mm, ♀ = 3.5mm.
larvae : 20k NE Cervantes WA on Acacia flws 20-23.viii.1987 C. Reid 1059 [ANIC].

Ditropidus [*Polyachus*] *geminus* Chapuis (= POGE); ♂ = 2.5mm, ♀ = 3mm.
♂, ♀ = Inglewood Vict. C. Oke [MVM]

Ditropidus [*Elaphodes*] *pilula* Chapuis (= ELPI); ♂ = 2.5mm, ♀ = 3.5mm.
♂, ♀ : Black mtn ACT on Eucalyptus 6.iii.1985 C. Reid, 261 [ANIC].
larvae : Congo, Moruya NSW at light trap 17.iii.1985 C. Reid 277 [ANIC].

Ditropidus [*Tappesia*] *saundersi* Baly (= TASA); ♀ = 3mm.
♀ : NSWales [ANIC].
♀ : Birchip V. viii.1903 [MVM]

Ditropidus [*Prasonotus*] *submetallicus* Suffrian (= PRSU); ♂ = 4.7mm, ♀ = 5mm.
♂ : Stirling Ra. NP, WA Bluff Knoll Rd (280m) at base of Xanthorhoea leaves 31.xii.1985 C. Reid, 765 [ANIC].
♀, larvae : Porongurup NP (SE corner), WA at base of Xanthorhoea leaves 29.xii.1985 C. Reid & P. J. Gullan, 767 [ANIC].

Ditropidus [*Bucharis*] *suffriani* Baly (= BUSU); ♀ = 3.3mm.
♀ : New Guinea, Baly coll. [BMNH].

Ditropidus [*Euditropidus*] *variabilis* Lea (= EUVA); ♂= 3mm, ♀ = 4mm.
♂, ♀ : Tweed R. 14.iii.1901 WWF [ANIC].

Ditropidus sp. WA (= DIWA); ♂= 1.3mm, ♀ = 1.5mm.
♂, ♀ : Serpentine Falls WA 32.22S 116.00E 17.xi.1969 by beating E. B. Britten [ANIC].

Ditropidus sp. 469 (= DIFO); ♂= 2mm, ♀ = 2.3mm.
♂, ♀, larvae : Kinchega NP, NSW SE shore Lake Menindee on Ac. bivenosa flowers 27.ix.1985 C. Reid, 469 [ANIC].

Ditropidus sp. 522 (= PLEO); ♂= 2.8mm, ♀ = 3mm.
Larvae : Bywong Hill 5k NE Sutton NSW on Eucalyptus 3.xi.1985 C. Reid 522 [ANIC].

Ditropidus sp. 865 (= NRPO); ♂= 2mm, ♀ = 3mm.
♂, ♀, larvae = 35k W Balranald NSW (Sturt H'way) on Ac. pendula 15.v.1986 C. Reid & P. J. Gullan, 865 [ANIC].

Scaphodius striatocollis Montrouzier (= SCST); ♂= 2mm, ♀ = 2.5mm.
♂= New Caledonia Noumea : Anse Vata 30m 8.viii.1979 G. A. Samuelson coll. Bishop Mus. Acc. no. 1979-380 Rubiaceae. [BPBM].
♀ = New Caledonia Anse Vata 23.x.1958 C. R. Joyce coll. [BPBM].

Cryptocephalina

Aporocera [*Schizosternus*] *albogularis* Chapuis (= SCAL); ♂= 3.2mm, ♀ = 3.8mm.
♂= Bundaberg Q nr Bin Bin Rg.15-20.xii.1974 H. Frauca [ANIC].
♀ = 25.35S 151.57E 5.5k SSW of Mt Biggenden Qld 11.x.1984 I. Naumann, J. Cardale at light [ANIC].
larvae : 5k SW Tamborine Qld on bloodwood 22.xi.1986 C. Reid, 912 [ANIC].

Aporocera [*Idiocephala*] *albolinea* Saunders (= IDAL); ♂= 3.5mm, ♀ = 4.5mm.
larvae : Piccadilly Circus ACT on E. pauciflora powerline clearing 16.xii.1984 C. Reid 20 [ANIC].

Aporocera apicalis Saunders (= APAN); ♂= 4mm, ♀ = 5.5mm.
♂: Bundaberg Qld (nr Bin Bin Rg.) 15-20.xii.1974 H. Frauca [ANIC].
♀ : Bluff Rg. Biggenden Q 17.xii.1984 H. Frauca [ANIC].

Aporocera [*Loxopleurus*] *atra* Saunders (= LOAT); ♂= 3mm, ♀ = 4.5mm.
larvae : Piccadilly Circus ACT on Euc pauciflora powerline clearing 10.xii.1984 C. Reid, 6 [ANIC].

Aporocera [*Cadmus*] *aurantiaca* Chapuis (= CAAU); ♂= 6mm, ♀ = 7mm.
♂, ♀ : Black Mtn ACT at light x.1987 C. Reid, 1181 [ANIC].
larvae : 20k SE Braidwood NSW wet sclerophyll (200m), on Eucalyptus 31.x.1985 C. Reid, 497 [ANIC].

Aporocera [*Ochrosopsis*] *australis* Saunders (= OCAU); ♂= 5.8mm, ♀ = 6mm.
♂: Echuca VIC 27.11.78 P. G. Kelly [ANIC].
♀ : Armidale NSW 19.11.80 P. G. Kelly [ANIC].

Aporocera [*Cryptocephalus*] *bihamata* Chapuis (= CRBI); ♂= 5mm, ♀ = 7mm.
♀ : St. Lucia Brisbane SE Qld ix.1983 R. de Keyser [ANIC].
larvae : 18k SW Braidwood NSW on E. viminalis 30.i.1986 C. Reid 797 [ANIC].

Aporocera [*Cryptocephalus*] *bynoei* Saunders (= CRBY); ♂= 4.5mm, ♀ = 5.5mm.
larvae : Stirling Ra. NP WA (Bluff Knoll Rd) on Jarrah 31.xii.1985 C. Reid 728 [ANIC].

Aporocera [*Cryptocephalus*] *casta* Suffrian (= CRCA); ♂= 3mm, ♀ = 4mm.
larvae : Stirling Ra. NP WA (S. R. Caravan Park) on E. wandoo 30.xii.1985 C. Reid 726 [ANIC].

Aporocera [*Cyphodera*] *chlamydiformis* Baly (= CYCH); ♂= 5mm, ♀ = 6mm.
♂, ♀, larvae : Honeysuckle Ck T. S. ACT old quarry 1100m on E. rubida 2.iii.1986 C. Reid, 826 [ANIC].

Aporocera [*Idiocephala*] *consors* Boisduval (= IDCO); ♂= 3mm, ♀ = 4.5mm.
♂: Mt Barrow Rd 890m Tas 15-17.ii.1980 A. Newton & M/ Thayer beating Acacia dealbata [ANIC].
♀ : Mt Franklin ACT on Ac dealbata 23.i.1985 C. Reid 146 [ANIC].
larvae : Kioloa NSW on Ac mearnsii roadside 7.i.1985 C. Reid 126 [ANIC].

Aporocera [*Euphyma*] *flaviventris* Saunders (= EUFL); ♂= 3mm, ♀ = 3.5mm.
♂: Bendigo Vict. YM2968 19.i.1984 P. G. Kelly [ANIC].
♀ : Deakin ACT by sweeping grass 16.i.1974 E. B. Britton [ANIC].

larvae : Bruce Canberra ACT on Eucalyptus 6.ii.1985 C. Reid 208 [ANIC].

Aporocera [*Loxopleurus*] *gravata* Chapuis (= LOGR); ♂ = 3mm, ♀ = 4mm.
♂, ♀ : Watalga Ra. via Rosedale Q 17.iv.1975 H. Frauca [ANIC].
larvae : Copeland Tops 15k W Gloucester NSW on Ac. irrorata 600m 26.xi.1985 C. Reid 546 [ANIC].

Aporocera [*Dicenopsis*] *haematodes* Boisduval (= CRHA); ♂ = 5.5mm, ♀ = 7mm.
♂, ♀ : Piccadilly Circus ACT on E. pauciflora powerline clearing 16.xii.1984 C. Reid 16 [ANIC].
larvae : Guthega Power Sta. Kosciusko NP NSW on E. viminalis 24.iii.1985 C. Reid 282 [ANIC].

Aporocera [*Loxopleurus*] nr *inconstans* Lea (= LOIN); ♂ = 2.2mm, ♀ = 2.8mm.
larvae : Warrumbungle Mtn Motel 10k W Coonabarabran NSW Eucalyptus 24.xi.1985 C. Reid, 643 [ANIC].

Aporocera [*Cryptocephalus*] *iridipennis* Chapuis (= CRIR); ♂ = 4.5mm, ♀ = 5.5mm.
larvae : 5k SW Tambo rine Qld on bloodwood 22.xi.1986 C. Reid 919 [ANIC].

Aporocera [*Cryptocephalus*] *jacksoni* Boisduval (= CRJA); ♂ = 3.8mm, ♀ = 5mm.
♂, ♀ : Piccadilly Circus ACT on E. pauciflora powerline clearing 16.xii.1984 C. Reid 18 [ANIC].
larvae : Dicky Cooper Ck Kosciusko NP NSW on E. pauciflora & E. perriniana 29.i.1985 C. Reid [ANIC].174

Aporocera [*Rhombosternus*] *jocosa* Baly (= RHJO); ♂ = 3mm, ♀ = 4mm.
♂ : Coree Creek 18.xii.1938 W. K. Hughes [ANIC].
♀ : Barrington Tops SF NSW on Eucalyptus Dilgry R. Loop 1300m 26.xi.1985 C. Reid, 564 [ANIC].
larvae : Campbell Pk Mt Ainslie ACT on Eucalyptus 13.xi.1985 C. Reid, 532 [ANIC].

Aporocera [*Loxopleurus*] *libertina* Suffrian (= LOLI); ♂ = 2.8mm, ♀ = 3.5mm.
♂ : Bushworth SF Vic 29.xi.1975 G. G. Burns comp. with type of L. libertinus C. Reid [ANIC].
♀ : Dunolly Vic 12.xi.1970 G. G. Burns comp. with type of L. libertinus C. Reid [ANIC].
larvae : 4k SE Mt Barker popln. SA on Ac. pycnantha 15.xii.1985 C. Reid 693 [ANIC].

Aporocera [*Ochrosopsis*] *melanocephala* Saunders (= OCME) ♂ = 3.5mm, ♀ = 4mm.
larvae : 18k SW Braidwood NSW in cop on E. viminalis 30.i.1986 C. Reid 796 [ANIC].

Aporocera [*Loxopleurus*] *paupercula* Germar (= LOPA); ♂ = 1.3mm, ♀ = 2mm.
♂, ♀ : Winburndale NR 12m E Bathurst NSW 6.xii.1974 J. Cardale [ANIC].

Aporocera [*Idiocephala*] *pulchella* Saunders (= IDPU); ♂ = 4mm, ♀ = 5.5mm.
larvae : 5k SW Tambo rine Qld on bloodwood 22.xi.1986 C. Reid 920 [ANIC].

Aporocera [*Chariderma*] *pulchella* Baly (= CHPU); ♂ = 9mm, ♀ = 10.5mm.
♂ : Herberton 30.xi.1947 3782 B. J. Selman det. [DPIB]
♀ : Herberton BM exch.[ANIC].

Aporocera [*Cryptocephalus*] *scabrosa* Olivier (= CRSC); ♂ = 4mm, ♀ = 5.5mm.
larvae : New Chums Rd Brindabella Ra. ACT on Ac. dealbata powerline clearing 20.i.1985 C. Reid 143 [ANIC].

Aporocera [*Cryptocephalus*] *speciosa* Guerin-Meneville (= CRSP); ♂ = 4mm, ♀ = 5mm.
larvae : Pierce's Ck Forest Sett. Cotter ACT on Helichrysum semipapposum 10.iii.1985 K. Pullen, P. Gullan, C. Reid 263 [ANIC].

Aporocera [*Cadmus*] *stictica* Suffrian (= OCAU); ♂ = 5mm, ♀ = 6.5mm.
larvae : Sawpit Ck 16k W Jindabyne Kosciusko NP NSW on E. dalrympleana powerline clearing 24.iii.1985 C. Reid 285 [ANIC].

Aporocera [*Ochrosopsis*] *subfasciata* Saunders (= OCSU); ♂ = 3.5mm, ♀ = 4mm.
larvae : Dicky Cooper Ck Kosciusko NP NSW on E. pauciflora fire regrowth 29.i.1985 C. Reid 176 [ANIC].

Aporocera [*Mitocera*] *viridipennis* Saunders (= MIVI); ♂ = 6mm, ♀ = 7.5mm.
♂, ♀ : Maggs Mtn Hut Tas eucalypt 6.ii.1980 R. H. Green [QVML]
larvae : Sawpit Ck 16k W Jindabyne Kosciusco NP NSW on E. dalrympleana & E. stellulata powerline clearing 24.iii.1985 C. Reid 284 [ANIC].

Aporocera [*Chloroplisma*] *viridis* Saunders (= CHVI); ♂ = 3mm, ♀ = 4mm.
♂, ♀, larvae : Black Springs NSW on E. pauciflora 3.xii.1984 C. Reid 34 [ANIC].

Aporocera sp. 1049 (= LODI); ♂= 2.7mm, ♀ = 3mm.
♂: Lancelin WA 23.ix.1974 K. & E. Carnaby [ANIC].
♀: Quilergup WA 33.46S 115.39E 4.x.1981 I. D. Naumann & J. C. Cardale [ANIC].
larvae : 30k S Eneabba WA on Hibbertia flws 20-23.viii.1987 C. Reid, 1049 [ANIC].

Aporocera (*Diandichus*) *analis* Chapuis (= DIAN); ♂= 2.5mm, ♀ = 3mm.
♂, ♀: Coast Rge Qld nr Biggenden 19.viii.1976 H. Frauca [ANIC].
larvae : 2k E Ardlethan NSW on Ac. doratoxylon & A. decora flws 30.ix.1985 C. Reid, 436 [ANIC].

Aporocera (*Diandichus*) sp. 435 (= DIAF); ♂= 2.5mm, ♀ = 3.2mm.
larvae : 2k E Ardlethan NSW on Ac. doratoxylon flws 30.ix.1985 C. Reid, 435 [ANIC].

Cadmus (*Aorocarpon*) [*Ochrosopsis*] *apicalis* Saunders (= OCAP) ♂= 3.5mm, ♀ = 5mm.
larvae : 17k SE Braidwood NSW on E. pauciflora 31.x.1985 C. Reid 507 [ANIC].

Cadmus (*Aoropcarpon*) sp. 289 (=NRLA); ♂= 3mm, ♀ = 4mm.
larvae : Sawpit Ck 16k W of Jindabyne Kosc. NP, NSW on E. dalrympleana 24.3.1985 C.Reid 289 [ANIC].

Cadmus (*Aorocarpon*) [*Loxopleurus*]*pauxillus* Chapuis (= CAPE); ♂= 3.5mm, ♀ = 5mm.
larvae : Congo nr Moruya NSW at light trap, feed on eucalypt 17.iii.1985 C. Reid 317 [ANIC].

Cadmus (*Aorocarpon*) [*Brachycaulus*] *posticalis* Lea (= BRPO); ♂= 2.7mm, ♀ = 3.5mm.
♂: Cabbage Tree Ck, c 20k NW Batemans Bay NSW on Ac. trachyphloeia 3.ii.1986 C. Reid, 806 [ANIC].
♀, larvae : Mongarlowe R. c 20k SE Braidwood NSW on Ac. irrorata by river 16.iii.1985, 320 [ANIC].

Cadmus (*Brachycaulus*) *ferrugineus* Fairmaire (= BRFE); ♂= 4.5mm, ♀ 6.5mm.
♂: Eltham Vic J. E. Dixon [ANIC].
♀: 3k NW Mt. Schofield, Lake George Ra. NSW on E. mannifera 21.ii.1985 C. Reid, 236 [ANIC].
larvae : Cook, Canberra, ACT on Eucalyptus 11.iii.1985 C. Reid 270 [ANIC].

Cadmus (*Brachycaulus*) *mammillatus* Lea (= BRMA); ♂= 2.5mm, ♀ = 3.8mm.
♂, ♀ : Rushworth Vict 19.i.1975 P. G. Kelly [ANIC].

Cadmus australis (Boisduval) (= CAAS); ♂= 6mm, ♀ = 8mm.
♂, ♀ : Maggs Mtn Hut Tas. Eucalypt foliage 13.1.1976 R. H. Green [QVML]

Cadmus [*Prionopleura*] nr *bifasciatus* Saunders (= CABI); ♂= 6.5mm, ♀ = 9mm.
larvae : Billy Billy Rocks, Tidbinbilla ACT on Eucalyptus 25.xi.1984 C. Reid 33 [ANIC].

Cadmus [*Prionopleura*] *crucicollis* Boisduval (= CACR); ♂ = 6mm, ♀ = 7.5mm.
larvae : Summit Mt Gingera ACT on E. pauciflora 23.i.1985 C. Reid, 154 [ANIC].

Cadmus litigiosus Boheman (= CALI); ♂= 6mm, ♀ = 8mm.
larvae : Summit Mt Gingera ACT on E. pauciflora 23.i.1985 C. Reid, 151 [ANIC].

Cadmus [*Paracadmus*] *luctuosus* Chapuis (= PALU); ♂= 5mm, ♀ = 6mm.
♂, ♀ : Honeysuckle Ck T. S. ACT old quarry 1100m on E. stellulata (♂) & rubida (♀) 2.iii.1986 C. Reid, 824 [ANIC].
larvae : Pilliga Scrub 30k E Baradine NSW on E. trachyphloeia 25.xi.1985 C. Reid 552 [ANIC].

Cadmus [*Prionopleura*] nr *luteus* Chapuis (= CALU); ♂= 7mm, ♀ = 9mm.
larvae : 17k SE Braidwood NSW on E. pauciflora 31.x.1985 C. Reid 508 [ANIC].

Cadmus [*Prionopleura*] *rugicollis* Gray (= PRRU); ♂= 6mm, ♀ = 8.5mm.
♂, ♀ : Coonabarabran NSW 24.viii.1972 P. G. Kelly [ANIC].
larvae : 11k E Coonabarabran NSW E. mannifera heathy swamp 27.viii.1986 C. Reid 908 [ANIC].

Cadmus (*Cadmoides*) *pacificus* Suffrian (= CAPA); ♂= 4.5mm, ♀ = 6mm.
♂, ♀, larvae : Honeysuckle Ck T. S. ACT old quarry 1100m on E. rubida 2.iii.1986 C. Reid, 829 [ANIC]

Cadmus (*Cadmoides*) *strigillatus* Chapuis (= CAST); ♂= 5mm, ♀ = 6.5mm.
larvae : Barrington Tops SF NSW Dilgry R. Loop on Eucalyptus 1400m 26.xi.1985 C. Reid, 538 [ANIC].

Cadmus (*Lachnabothra*) *braccatus* Klug (= LAHO); ♂= 5mm, ♀ = 5.5mm.
♂, ♀, larvae : Kioloa NSW on low vegetation 7-8.1.1985 C.Reid [ANIC].

Cryptocephalus [*Bassareus*] *brunnipes* Olivier (= BASS); ♂= 5mm, ♀ = 5.5mm.
♂, ♀ : Georgia [MACL].

Cryptocephalus coryli L. (= CRCO); ♂= 6mm, ♀ = 7mm.
♂, ♀, larvae : Box Hill R. W. Lloyd [BMNH].

Cryptocephalus incertus Olivier (= CRIN); ♀ = 3.8mm.
♀ : Georgia [MACL].

Cryptocephalus moraei L. (= CRMO); ♂= 3.5mm, ♀ = 4.5mm.
♂, ♀, larvae : 5k N Amalfi, Campania Italy on grass, Castanea wood 28.vi.1986 P. J. Gullan, 882 [ANIC].

Cryptocephalus parvulus Müller (= CRPA); ♂= 3.2mm, ♀ = 3.8mm.
larvae : New Forest M. L. Cox [BMNH].

Cryptocephalus sericeus L. (= CRSE); ♂= 4.5mm, ♀ = 6mm.
♂, ♀ : Waidischiat, Karawanken Austria vii.1965 C. G. L. Gooding donation 1979 [ANIC].

Diachus auratus (F.) (=DIAC); ♀ 1.5mm.
♀ : New Hebrides, Erromango Id, Navolou 13.iii.1978 N.L.H. Krauss coll. [BPBM].

Lexiphanes coenobita Suffrian (= LEXI); ♂= 3mm, ♀ = 3.3mm.
♂, ♀ : Rio San Javier Santa Fe Argentina G. E. Bryant G. Bryant coll. 1919-147. [BMNH].

Melatia [*Cadmus*]*glochidionis* Gressitt (= CAGL); ♂= 1.7mm, ♀ = 2.5mm.
♂, ♀ : Cairns [SAM].

Melatia [*Cadmus*]*solomonensis* Bryant (= CASO); ♂= 3mm, ♀ = 4mm.
♂, ♀ = Solomon Islands Bougainville Island Konga Village (Buin) 6.ii-21.iii.1961 W. W. Brandt [ANIC].

Melixanthus intermedius Baly (= MELI); ♂= 3mm, ♀ = 3.5mm.
♂, ♀ : Singapore C. J. Saunders BM 1933-227 [BMNH].

Stegnocephala hebetata Suffrian (= STEG); ♂= 3.2mm, ♀ = 3.8mm.
♂, ♀ = Para Baly coll. [BMNH].

Appendix B.

I am afraid Australian workers must make up their minds to the fact that if they are to postpone describing the insects of their country until they have ascertained them to be new by comparison with types (in the case of genera or species that have been insufficiently described in Europe) they will have to leave the work to be done almost entirely outside Australia. For my own part, I am convinced that the best course to adopt is to regard all descriptions that are insufficient for recognition as non-existent (unless one can get at the types through one's own friends), and although unquestionably the result will often prove to be that one's nomenclature will have to be subsequently corrected, I regard the author of the original insufficient description as the person on whom must be laid the responsibility for any confusion that may occur.

Thomas Blackburn (1894 : 145)

Appendix B : Catalogue of Australasian Camptosomata.

This catalogue includes every name used in Australian Camptosomata, up to and including the present work. Furthermore all names from the south-west Pacific are listed, including New Caledonia, New Guinea, New Hebrides, New Zealand, Palau, Samoa, Solomon Islands and Truk. The New Guinea Cryptocephalina fauna is included, but the Ditropidina are almost all listed as *incertae sedis* because the original descriptions are insufficient for correct subtribal diagnosis, which will require examination of the type material. I have also included taxa from south-east Asia and the Malay Archipelago which belong to the genera *Aporocera* and *Melatia*. This includes *Melinobius longipes* Jacoby, described from Burma. Revisions of the status of species names are generally based on the study of type material (as indicated) but in some cases have relied on a collection (in the Australian National Insect Collection, Canberra) of 35mm colour slides of types in the British Museum or on original literature.

Genera and species are arranged alphabetically.

For each genus entry the following information is given : original author, date and page number(s) of description or citation, together with higher taxon placement if different; all Australasian context citations; all other citations for endemic Australasian genera, but only major works for non-endemic genera; aspect of citation, if part of specialised study, for example "wing venation". Synonymy is given chronologically.

For each species entry the following information is given : name in agreement with gender of present genus; original author, date and page number(s) of description, together with higher taxon placement if different, original spelling if different and type locality(ies); all other citations including aspect if part of specialised study. Synonymy and all combinations are given chronologically.

Symbols : * = non-Australian taxon; † = syntype or holotype seen. *Nomina nuda* are included alphabetically, but placed in []. These brackets are also used to isolate text discussing nomenclatural problems or classificatory problems.

INFORMAL GROUP **Camptosomata**

1. SUBFAMILY **Lamprosomatinae.** Lacordaire 1848 : 559; Monrós 1960b : 3.
1.1 TRIBE **Lamprosomatini.** Lacordaire 1848 : 559.

Type genus : *Lamprosoma* Kirby 1818 : 445.

1.1.1 Genus ****Oomorphus*** Curtis 1831 : 347; Clavareau 1913 : 224 (jun. syn. of *Lamprosoma*); Monrós 1956a : 45-46 (valid genus); Monrós 1960 : 5 (full bibliography).

Type species : *Byrrhus concolor* Sturm, by original designation (Curtis 1831 : 347).

****caledonicus*** Monrós 1958 : 32, fig. 3 (New Caledonia); Monrós 1960b : 7.
****microbius*** Monrós 1958 : 32, fig. 4 (New Caledonia); Monrós 1960b : 7.

2. SUBFAMILY **Cryptocephalinae.** Gyllenhal 1813 : 582; Watt 1975 : 33.
2.1 TRIBE **Chlamisini.** Gressitt 1946 : 84; Karren 1972 : 896. [**Art. 39**]

Type genus : *Chlamisus* Rafinesque, 1815 : 116.

2.1.1 Genus ***Chlamisus*** Rafinesque 1815 : 116; Gressitt 1965 : 445; Karren 1972 : 908 [full synonymy and reference list given]; Seeno and Wilcox 1982 : 43.

Type species : *Chlamys foveolata* Knoch, by subsequent designation (Navajas 1946; Karren 1972); nec *Clytra gibbosa* F. (Gressitt and Kimoto 1961), which was not included in original description.

= ***Exema*** Lacordaire1848 : 844, *nec sensu* Karren 1966; Gressitt 1961 (jun. syn. of *Chlamisus*); Karren 1966 : 651-653 (valid); Seeno and Wilcox 1982 : 43 (valid)

Type species : *Chlamys intricata* Kollar 1824, by subsequent designation (Jacoby 1908; Karren 1966 : 651)

†***aterrimus*** Lea 1904 : 447-448 (*Cadmus*; Cleveland Bay); Clavareau 1913 : 208; **comb. nov.**
= †*australis* Bryant 1943 : 219 (Koah); **syn. nov.**
mimosae Karren 1989 : 255 (Brazil) [introduced]
****rhododendri*** Gressitt 1965 : 447-448 (New Guinea)
****rotundatus*** Gressitt 1965 : 448-449 (New Guinea)
****wisselensis*** Gressitt 1965 : 446-447 (New Guinea)

2.2 TRIBE **Clytrini**. Lacordaire 1848 : 9.

2.2.1 SUBTRIBE **Clytrina**. Lacordaire 1848 : 9.

Type genus : *Clytra* Lacharting 1781.

2.2.1.1 Genus ***Aetheomorpha*** Lacordaire 1848 : 311; Jacoby 1908 : 123; Clavareau 1913 : 45 (sg. of *Diapromorpha*); Gressitt and Kimoto 1961 : 86 (valid genus); Gressitt 1965 : 385; Seeno and Wilcox 1982 : 32.

Type species : *Aetheomorpha nematoides* Lacordaire (Jacoby 1908; Gressitt and Kimoto 1961)

cryptocephaloides Lacordaire 1848 : 315 (Australia); Clavareau 1913 : 45.
**papuana* Gressitt 1965 : 389-390 (New Guinea).

2.3 TRIBE **Pachybrachini**. Chapuis 1874 : 163.

Type genus : *Pachybrachis* Chevrolat 1837.

2.3.1 Genus ***Metallactus*** Suffrian 1866 : 248-9; Chapuis 1874 : 167; Clavareau 1913 : 92; Seeno and Wilcox 1982 : 37.

Type species : not known, apparently not designated.

nigrofasciatus Suffrian 1866 : 363 (Brazil); Fiebrig 1910 : 248, plate 8, figs 19-21 (biology); Clavareau 1913 : 93; Julien 1987 : 6 (biological control agent). [failed introduction]
patagonicus Suffrian 1866 : 353 (Patagonia); Clavareau 1913 : 93; MacFadyen 1987 : 329-331 (biology, biological control agent). [failed introduction]

[TRIBE **Achenopini**. Chapuis 1874. There are no Australasian members of this tribe]

2.4 TRIBE **Cryptocephalini.** Gyllenhal 1813 : 582.

Type genus : *Cryptocephalus* Geoffroy in Müller 1764.

[SUBTRIBE **Stylosomini.** The supposed Australian and New Zealand genera are placed in Platycolaspina; there are therefore no Australasian members of this subtribe]

2.4.1 SUBTRIBE **Platycolaspina** this work, **subtribe nov.**

Type genus : *Platycolaspis* Jacoby 1908.

2.4.1.1 Genus ***Leasia*** Jacoby 1907 : 148 (in Clytrini); Clavareau 1913 : 77; Tillyard 1926 : 235; Monrós 1951 : 451-6 (Cucujoidea, morphology, phylogeny); Jolivet 1957 : 84-5 (wing venation, phylogeny); Crowson 1967 : 152 (Clytrini, phylogeny); Seeno and Wilcox 1982 : 184 (Cucujoidea).

Type species : *Leasia australis* Jacoby by monotypy

= ***Agetinella*** Jacoby 1908 : 26-27 (in Eumolpini); Clavareau 1914 : 177; Seeno and Wilcox 1982 : 65. **syn. nov.**

Type species : *Agetinella minuta* Jacoby, by monotypy

†***australis*** Jacoby 1907 : 148 (Karridale, North Australia [sic]); Clavareau 1913 : 77; Monrós 1951 : 451-6 (morphology); Jolivet 1957 : 84-5 (wing venation)
†***minuta*** Jacoby 1908 : 27 (*Agetinella*; Swan River); Clavareau 1914 : 177; **comb. nov.**

2.4.1.2 Genus ***Platycolaspis*** Jacoby 1908 : 27 (in Eumolpini); Clavareau 1914 : 34; Seeno and Wilcox 1982 : 58.

Type species : *Platycolaspis australis* Jacoby, by monotypy

†***australis*** Jacoby 1908 : 28 (Hobart); Clavareau 1914 : 177; Lea 1915 : 102, 110;

2.4.1.3 Genus *Atenesus* Weise 1923 : 4-5; Seeno and Wilcox 1982 : 37 (Stylosomini).

Type species : *Atenesus mjoebergi* Weise, designation this work

†*fuscitarsis* Weise 1923 : 5, note 1 (Champion Bay)
†*mjoebergi* Weise 1923 : 5 (Malanda)

2.4.1.4 Genus **Arnomus* Sharp 1876 : 99; Broun 1880 : 619; Clavareau 1913 : 87; Tillyard 1926 : 235; Jolivet 1957 : 89 (wing venation); Kasap and Crowson 1976 : 104 (larva); Seeno and Wilcox 1982 : 37 (Stylosomini)

Type species : *Arnomus brouni* Sharp, by monotypy

*†***brouni*** Sharp 1876 : 99-100; Broun 1880 : 619; Clavareau 1913 : 87; Hudson 1934 : 104; Jolivet 1957 : 89 (wing venation)
*†***curtipes*** Broun 1893 : 1390; Clavareau 1913 : 87
  = †*impressus* Broun 1913 **syn. nov.**
  = †*viridicollis* Broun 1909 : 286-7 **syn. nov.**
†***marginalis*** Broun 1893 : 1390-1; Clavareau 1913 : 87
†***signatus*** Broun 1909 : 287-8; Clavareau 1913 : 87; Hudson 1934 : 104 (host)
  = †*fulvus* Broun 1915 : 342 **syn. nov.**
  = †*vicinus* Broun 1915 : 342-3 **syn. nov.**

2.4.1.5 Genus ***Semelvillea*** Reid, this work, **gen. nov.**

Type species : *Semelvillea acaciae* Reid, by original designation

†***acaciae*** Reid, this work, **sp. nov.**
†***bunyae*** Reid, this work, **sp. nov.**
†***eungellae*** Reid, this work, **sp. nov.**
†***hirsuta*** Reid, this work, **sp. nov.**
†***nothofagi*** Reid, this work, **sp. nov.**
†***parva*** Reid, this work, **sp. nov.**
†***punctata*** Reid, this work, **sp. nov.**
†***waraganji*** Reid, this work, **sp. nov.**

2.4.2 SUBTRIBE **Coenobiina** this work, **subtribe nov.**

Type genus : *Coenobius* Suffrian 1857.

[Genus *__Coenobius__* Suffrian 1857 : 61-4; Suffrian 1859 : 5, 9; Chapuis 1874 : 177; Chapuis 1875 : 81; Weise 1903 : 32-3; Jacoby 1908 : 182-3; Clavareau 1913 : 122; Lea 1920 : 252; Gressitt 1955; Jolivet 1957 : 93 (wing venation); Bryant and Gressitt 1957 : 9; Gressitt and Kimoto 1961; Kimoto and Gressitt 1981 : 326; Gressitt 1982 : 719; Seeno and Wilcox 1982 : 38.

Type species : *Coenobius triangulum* Suffrian, by subsequent designation (Jacoby 1908 : 182; Gressitt and Kimoto 1961)

All Australian species formerly referred to this genus have been placed elsewhere, in *Aprionota* Maulik and *Ditropidus* Erichson.]

2.4.2.1 Genus ***Aprionota*** Maulik 1929 : 178; Gressitt 1957 : 246 (subgen. of *Ditropidus*); Seeno and Wilcox 1982 : 38; **stat. rev.**

Type species : *Aprionota lucida* Maulik (Samoa) by original designation and monotypy

= ***Pycnophthalma*** Maulik 1929 : 180; Bryant and Gressitt 1957 : 13; Seeno and Wilcox 1982 : 38; **syn. nov.**

Type species : *Pycnophthalma tutuilana* Maulik (Samoa) by original designation and monotypy

= *__Cephalocryptus__* Gressitt 1955 : 6-8 (subgenus of *Coenobius*); Seeno and Wilcox 1982 : 38; **syn. nov.**

Type species : *Coenobius* (*Cephalocryptus*) *macarangae* Gressitt, by original designation

__aenea__ Bryant 1936 : 242-243 (*Pycnophthalma*, New Hebrides); **comb. nov.**
†__apicale__ Bryant in Bryant and Gressitt 1957 : 14-15 (*Pycnophthalma*, Fiji); **comb. nov.**
__aureopilosa__ Bryant 1925 : 591 (*Coenobius*, Fiji); Bryant and Gressitt 1957 : 14 (*Pycnophthalma*); **comb. nov.**

brandti* Gressitt 1965 : 401-402 (*Coenobius*, New Guinea); **comb. nov.

collaris* Gressitt 1965 : 400-401 (*Coenobius*, New Guinea); **comb. nov.

**corrugata* Gressitt 1957 : 247 (Samoa)

costipennis* Bryant 1945 : 421 (*Loxopleurus*, Fiji); Bryant and Gressitt 1957 : 16; **comb. nov.

constricticollis* Jacoby 1896 : 383-4 (*Bucharis*, Sumatra); **comb. nov.

cuprea* Bryant 1942 : 508 (*Pycnophthalma*, Fiji); Bryant and Gressitt 1957 ; 14; **comb. nov.

*†*genistomae* Gressitt in Bryant and Gressitt 1957 : 10 (*Coenobius*, Fiji); **comb. nov.**

*†*glochidionis* Gressitt 1955 : 7-8 (*Coenobius*, Palau); **comb. nov.**

†*inconstans* Lea 1920 : 253-4 (*Coenobius*; Mount Tambourine, Armidale, Forest Reefs, Jenolan, Leura, Sydney); Lea 1920 : 401; **comb. nov.**

†*insulicola* Lea 1920 : 402-3 (*Coenobius*; Pelsart Island); Britton and Stanbury 1980 : 265; **comb. nov.**

kamoensis* Gressitt 1965 : 405-406 (*Coenobius*, New Guinea): **comb. nov.

kleinhoviae* Gressitt 1965 : 403-404 (*Coenobius*, New Guinea); **comb. nov.

laratana* Gressitt 1965 : 404-405 (*Coenobius*, New Guinea); **comb. nov.

[*lauensis* Gressitt, subspecies of *marginipennis* Bryant (*q.v.*)]

leveri* Bryant 1942 : 509 (*Pycnophthalma*, Fiji); Bryant and Gressitt 1957 : 15; **comb. nov.

leveri* Bryant 1943 : 567 (*Loxopleurus*, Fiji); Bryant and Gressitt 1957 : 16; **comb. nov.

†*longicornis* Lea 1920 : 401-2 (*Coenobius*; Cairns); **comb. nov.**

*†*lucida* Maulik 1929 ; 179, fig. 1 (Samoa); Gressitt 1957 : 246;

*†*lucida subpallida* Gressitt 1957 : 246-247 (Samoa)

*†*macarangae* Gressitt 1955 : 8-10, fig. 1b (*Coenobius* sg. *Cephalocryptus*, Palau and Truk); **comb. nov.**

*†*marginipennis* Bryant 1938 : 249 (*Coenobius*, Fiji); Bryant and Gressitt 1957 : 10; **comb. nov.**

marginipennis lauensis* Gressitt in Bryant and Gressitt 1957 : 10-11 (*Coenobius*, Fiji); **comb. nov.

oculatus* Jacoby 1896 : 382-3 (*Bucharis*, Sumatra); **comb. nov.

pallidipes* Gressitt 1965 : 402-403 (*Coenobius*, New Guinea); **comb. nov.

†*parvoniger* Lea 1920 : 254 (*Coenobius*; Cairns); Lea 1920 : 401; **comb. nov.**

pipturus* Gressitt 1965 : 406-407 (*Coenobius*, New Guinea); **comb. nov.

*†*producticollis* Gressitt in Bryant and Gressitt 1957 : 11-12 (*Coenobius*, Fiji); **comb. nov.**

****rotumanus*** Gressitt in Bryant and Gressitt 1957 : 17-18 (*Loxopleurus*, Fiji); **comb. nov.**

*†***ruficollis*** Bryant in Bryant and Gressitt 1957 : 16-17 (*Loxopleurus*, Fiji); **comb. nov.**

†***spissus*** Lea 1920 : 402 (*Coenobius*; Sydney); Lea 1926 : 286; Britton and Stanbury 1980 : 286; **comb. nov.**

****subaeneus*** Gressitt 1955 : 10-11 (*Coenobius* sg. *Cephalocryptus*, Truk); **comb. nov.**

[*subpallidus* Gressitt, subspecies of *lucidus* Maulik (*q.v.*)]

*†***tutuilana*** Maulik 1929 : 181, fig. 2 (*Pycnophthalma*, Samoa); Gressitt 1957 : 247-248; **comb. nov.**

****tutuilana upoluana*** Gressitt 1957 : 248 (*Pycnophthalma*, Samoa); **comb. nov.**

[*upoluana* Gressitt, subspecies of *tutuilana* Maulik (*q.v.*)]

****vitiensis*** Bryant 1943 : 566 (*Loxopleurus*, Fiji); Bryant and Gressitt 1957 : 17; **comb. nov.**

*†***zimmermani*** Gressitt in Bryant and Gressitt 1957 : 12-13 (*Coenobius*, Fiji); **comb. nov.**

2.4.3 SUBTRIBE **Ditropidina** this work, **subtribe nov.**

Type genus : *Ditropidus* Erichson 1842.

2.4.3.1 Genus *Ditropidella*, this work. **gen. nov.**

Type species : *Coenobius binotatus* Lea 1920, this designation.

†***binotata*** Lea 1920 : 254-5 (*Coenobius*; Sydney, Galston, Tamworth, Birchip); Goudie 1927 : 303; Gressitt 1955 : 9; Britton and Stanbury 1980 : 249 **comb. nov.**

†***carinata*** Lea 1920 : 241 (*Ditropidus*, Dividing Range); Lea 1920 : 222; **comb. nov.**

†***jacobyi*** Baly 1877 : 380 (Gawler Town); Masters 1887 : 575; Clavareau 1913 : 118; Lea 1920 : 384, 399, 400; Lea 1920 : 220, 240, 241; Lea 1926 : 286; **comb. nov.**

†***sculptipennis*** Lea 1920 : 399 (*Ditropidus*, Geraldton); Lea 1920 : 222; **comb. nov.**

2.4.3.2 Genus ***Ditropidus*** Erichson 1842 : 120; Chevrolat 1837 : 449 (*nom. nud.*); Fogg 1859 : 333-4 (trans. of Erichson); Suffrian 1859 : 5, 9, 23-5 (sen. syn. of

Pleomorpha Saunders); Suffrian 1866 : 2; Baly 1865 : 61; Chapuis 1874 : 155-6, 159 and 181-2; Lea 1902 : 429; Lea 1904 : 330; Froggatt 1907 : 201; Fauvel 1907 : 152; Clavareau 1913 : 116 (sen. syn. of *Pleomorpha* Saunders); Lea 1920 : 218-220; Tillyard 1926 : 235; Goudie 1927 : 303; Maulik 1929 : 178; Bryant and Gressitt 1957 : 13; Jolivet 1957 : 92 (wing venation); Gressitt 1982 : 719; Van den Berg 1982 : 52-3 (hosts); Seeno and Wilcox 1982 : 38 (sen. syn. of *Pleomorphus* Saunders and *Aprionota* Maulik); Hawkeswood 1988 : 99 (host).

Type species : *Cryptocephalus* (subgenus *Ditropidus*) *ochropus* Erichson, by subsequent revisor (Gressitt 1965)

= ***Pleomorpha*** Saunders 1847 : 472; Saunders 1847 : 268; Suffrian 1859 : 5, 25 (jun. syn. of *Ditropidus*); Clavareau 1913 : 116 (jun. syn. of *Ditropidus*); Seeno and Wilcox 1982 : 38 (jun. syn. of *Ditropidus*)

Type species : *Pleomorpha ruficollis* Saunders, this work

= ***Elaphodes*** Suffrian 1859 :16-8; Suffrian 1859 : 9; Suffrian 1866 : 2; Chapuis 1874 : 155, 159, 180-2; Baly 1877 : 378; Lea 1904 : 330; Clavareau 1913 : 115; Jolivet 1957 : 92 (wing venation); Gressitt 1965 : 390; Seeno and Wilcox 1982 : 38; **syn. nov.**

Type species : *Elaphodes cervinus* Suffrian, by subsequent revisor (Gressitt 1965)

= ***Prasonotus*** Suffrian 1859 : 10-12; Suffrian 1859 : 9; Suffrian 1866 : 2; Baly 1865 : 61; Chapuis 1874 : 159 (*Prosonotus* [sic]), 177-8, 181, 183; Lea 1904 : 331; Clavareau 1913 : 121; Jolivet 1957 : 93 (wing venation); Seeno and Wilcox 1982 : 38;

Type species : *Prasonotus submetallicus* Suffrian, this work.

= ***Bucharis*** Baly 1865 : 61-2; Chapuis 1874 : 159 and 178-9; Weise 1903 : 33; Clavareau 1913 : 122; Weise 1916 : 6; Weise 1923 : 6-7; Jolivet 1957 : 93 (wing venation); Gressitt 1965 : 399; Kimoto and Gressitt 1981 : 326; Seeno and Wilcox 1982 : 38; **syn. nov.**

Type species : *Bucharis suffriani* Baly, by subsequent revisor (Gressitt 1965)

= ***Pleomorphus*** Chapuis 1874 : 182-3; Suffrian 1866 : 2 (*nom. nud.*); Chapuis 1874 : 159; Clavareau 1913 : 121; Lea 1920 : 221 (jun. syn. of *Ditropidus* by inclusion of type species); Jolivet 1957 : 92 (wing venation); Seeno and Wilcox 1982 : 38; **syn. nov.**

Type species : *Ditropidus histerinus* [sic] Suffrian, by original designation [two names were proposed for inclusion but *P. putridus* had not been described and was therefore a *nomen nudum.* There is no evidence that "*histerinus* Suffrian" was anything other than a *lapsus* for *Ditropidus histeroides* Suffrian].

= ***Polyachus*** Chapuis 1875 : 81; Clavareau 1913 : 113; Jolivet 1957 : 91 (wing venation); Seeno and Wilcox 1982 : 38; **syn. nov.**

Type species : *Polyachus geminus* Chapuis 1875, by monotypy

= ***Tappesia*** Baly 1877 : 378-9; Clavareau 1913 : 202 (in Cryptocephalini); Jolivet 1957 : 96; Seeno and Wilcox 1982 : 39 (in Cryptocephalini); **syn. nov.**

Type species : *Tappesia saundersi* Baly, by monotypy

= ***Euditropidus*** Lea 1920 : 243; Seeno and Wilcox 1982 : 38; **syn. nov.**

Type species : *Euditropidus variabilis* Lea 1920, by original designation

†***abdominalis*** Chapuis 1875 : 79 (Clarence River); Masters 1887 : 571; Lea 1902 : 430; Clavareau 1913 : 116; Lea 1920 : 221, 223, 231; Lea 1920 : 396;
†***aciculatus*** Chapuis 1875 : 78 (Australia); Chapuis 1879 : 77; Masters 1887 : 572; Clavareau 1913 : 116; Lea 1920 : 220; Lea 1920 : 388
aeneipennis Boisduval 1835 : 588 (*Cryptocephalus*; New Holland); Saunders 1847 : 473 (*Pleomorpha*; ? identity); Saunders 1847 : 269; Suffrian 1859 : 152 (*Ditropidus*, ? identity); Chapuis 1879 : 76; Masters 1887 : 572; Clavareau 1913 : 116; Lea 1920 : 221;
[*aeneipennis* Dejean, in Chevrolat 1837 : 449 is a nomen nudum]
†***aeneolus*** Chapuis 1875 : 82 (*Elaphodes*, Sydney); Masters 1887 : 570; Clavareau 1913 : 115; Lea 1920 : 247; **comb. nov.**
†***albertisi*** Chapuis 1876 : 337-8 (Somerset, Cape York); Masters 1887 : 572; Clavareau 1913 : 116; Lea 1920 : 220; Lea 1921 : 383
†***albiceps*** Lea 1920 : 233-4 (Oodnadatta); Lea 1920 : 221

albohirsutus Baly 1871 : 383 (*Elaphodes*); Masters 1887 : 570 (*albohirtus* [sic]); Clavareau 1913 : 115 (*Elaphodes*); Lea 1921 : 260 (*Ditropidus*)

amabilis Baly 1877 : 383 (Cape York); Baly 1877: 384; Masters 1887 : 572; Clavareau 1913 : 116; Lea 1920 : 220; Lea 1920 : 382

†***amentatus*** Lea 1920 : 255 (*Polyachus*; Australia, South Australia); **comb. nov.**

†***amictus*** Chapuis 1875 : 82-3 (*Elaphodes*, Brisbane); Chapuis 1879 : 75; Masters 1887 : 570; Lea 1902 : 419; Clavareau 1913 : 115; Weise 1916 : 4; Lea 1920 : 248 (? = *epilachnoides* Chapuis); **comb. nov.**

†***angustifrons*** Chapuis 1875 : 80; Masters 1887 : 572; Lea 1902 : 428; Clavareau 1913 : 116; Lea 1920 : 221;

antennarius Baly 1877 : 382 (Moreton Bay); Masters 1887 : 572; Lea 1902 : 424, 430; Clavareau 1913 : 116; Lea 1920 : 383-4 (sen. syn. of *antennarius* Chapuis and *baccaeformis* Chapuis); Lea 1920 : 218, 220;

= *antennarius* Chapuis 1879 : 76 (Gayndah), nec Baly 1877; Masters 1887 : 572; Clavareau 1913 : 116 (= *chapuisi* nom. nov.); Lea 1920 : 383-4 (jun. syn. of *antennarius* Baly); Lea 1920 : 220

= *baccaeformis* Chapuis 1879 : 76 (Gayndah); Masters 1887 : 572; Clavareau 1913 : 116; Lea 1920 : 383 (jun. syn. of *antennarius* Baly); Lea 1920 : 220;

= *chapuisi* Clavareau 1913 : 116 nec Baly 1876 (nom. nov. for *antennarius* Chapuis)

†***anthracinus*** Erichson 1842 : 234 note (New Holland); Suffrian 1859 : 2, 34-5; Masters 1887 : 572; Clavareau 1913 : 116; Lea 1920 : 221

= †*punctivarius* Lea 1921 : 408-9 (Hobart, Launceston); Lea 1920 : 222; Britton and Stanbury 1980 : 281; **syn. nov.** [types are identical]

†***apiciflavus*** Chapuis 1875 : 77 (New Holland); Masters 1887 : 572; Lea 1902 : 421, 430; Clavareau 1913 : 116; Lea 1920 : 394; Lea 1920 : 220; Lea 1921 : 392;

†***apicipennis*** Lea 1921 : 391-2 (Sea Lake, Murray River, Moonta); Lea 1920 : 220; Goudie 1927 : 303

†***armatus*** Lea 1921 : 398-9 (north-west Australia, King George Sound); Lea 1920 : 396: Lea 1920 : 221: Britton and Stanbury 1980 : 247

[*ater* Boisduval; Lea 1920 : 221 (nom. nud.)]

†***aurichalceus*** Suffrian 1859 : 32-4 (Melbourne); Suffrian 1859 : 31; Masters 1887 : 572; Clavareau 1913 : 116; Lea 1920 : 382; Lea 1920 : 221, 234; Lea 1921 : 403, 407;

= †*oblongipennis* Lea 1920 : 232-3 (Tasmania, Frankford, Launceston, Hobart, Victorian Alps, Forest Reefs); Lea 1920 : 221; Lea 1921 : 409; Britton and Stanbury 1980 : 273; **syn. nov.** [types are identical]

†***basiceps*** Lea 1921 : 390-1 (Oodnadatta, Quorn); Lea 1920 : 220;

†***basiventris*** Lea 1921 : 398 (Long Reach); Lea 1920 : 220;

bicolor Chapuis 1879 : 76 (Peak Downs); Masters 1887 : 572; Clavareau 1913 : 116; Lea 1920 : 221;

bicolor Baly 1877 : 386 (*Polyachus*; Gawler Town); Masters 1887 : 578; Clavareau 1913 : 113; **comb. nov.**

bimaculatus Lea 1920 : 392-3 (Dalby); Lea 1920 : 220

biplagiatus Baly 1871 : 389-390 (Moreton Bay, north-west Australia); Masters 1887 : 572; Clavareau 1913 : 116; Lea 1920 : 220

†***boops*** Suffrian 1859 : 43-5 (Australia); Masters 1887 : 572; Clavareau 1913 : 116; Lea 1920 : 221

†***brachysomus*** Lea 1902 : 428 (Geraldton); Clavareau 1913 : 116; Lea 1920 : 221, 234; Lea 1921 : 405

†***brevicollis*** Lea 1921 : 226-7; Lea 1920 : 399; Lea 1920 : 222, 236; Britton and Stanbury 1980 : 250

†***brevis*** Lea 1921 : 405-6 (Darwin); Lea 1920 : 221

†***brunneipennis*** Lea 1920 : 399-400 (Swan River and Karridale); Lea 1920 : 222, 241;

†***caeruleipennis*** Lea 1920 : 231-2 (north-west Australia); Lea 1920 : 221; Britton and Stanbury 1980 : 251

†***caeruleus*** Lea 1920 : 397 (Rottnest Island, Vasse River, Sydney); Lea 1920 : 221, 235

†***carbonarius*** Baly 1871 : 384 (Western Australia); Masters 1887 : 572; Lea 1902 : 431; Clavareau 1913 : 116; Lea 1920 : 221; Lea 1921 : 399, 410;

= †*subsimilis* Lea 1902 : 422 (Geraldton); Clavareau 1913 : 120; Lea 1920 : 389; Lea 1920 : 221, 231, 245; **syn. nov.** [*subsimilis*, with red pronotum, is the ♀ of the entirely dark ♂ *carbonarius*]

†***carinaticeps*** Lea 1920 : 395-6 (Forest Reefs); Lea 1920 : 221

†***cavifrons*** Chapuis 1875 : 81 (Australia); Chapuis 1876 : 338; Masters 1887 : 572; Clavareau 1913 : 116; Lea 1920 : 221

†***cervinus*** Suffrian 1859 : 18-20 (*Elaphodes*, Port Philip); Masters 1887 : 571; Clavareau 1913 : 115; Lea 1920 : 246-7 (sen. syn. of tigrinus Chapuis); Lea 1920 : 249; **comb. nov.**

= †*tigrinus* Chapuis 1875 : 83 (*Elaphodes*, Sydney, Victoria); Masters 1887 : 571; Lea 1902 : 419; Froggatt 1907 : 201 (host); Clavareau 1913 : 115; Lea 1920 : 246, 252 (jun. syn. of *cervinus* Suffrian 1859); Van den Berg 1982 : 52 (host)

chapuisi Baly 1876 : 462 (*Bucharis*, Gawler Town); Masters 1887 : 570; Clavareau 1913 : 122; Lea 1921 : 260 (*chapuisii* [sic], = *Ditropidus*);

†***clypealis*** Lea 1921 : 397-8 (Port Lincoln, Sydney); Lea 1920 : 221

clypeatus Weise 1916 : 7-8 (Bucharis; Fremantle, Geraldton); Weise 1923 : 7 (*Ditropidus*)

†***coccinelloides*** Lea 1920 : 251-2 (*Elaphodes*, Brisbane, Hunter River); Britton and Stanbury 1980 : 252; **comb. nov.**

†***coelestis*** Lea 1902 : 425 (Geraldton); Clavareau 1913 : 116; Lea 1920 : 396: Lea 1920 : 221, 223, 237; Lea 1920 : 399;

†***coerulescens*** Chapuis 1875 : 78 (Pine Mountain); Masters 1887 : 573; Clavareau 1913 : 116 ; Lea 1920 : 221; Lea 1921 : 223

†***cognatus*** Lea 1921 : 404 (Peterborough, Murray River); Lea 1920 : 396; Lea 1920 : 221

†***comans*** Chapuis 1875 : 75 (Port Lincoln); Masters 1887 : 573; Clavareau 1913 : 116; Lea 1920 : 387; Lea 1920 : 220; Lea 1921 : 382

*†***compactus*** Sharp 1881 : 50-1 (*Scaphodius*; New Zealand); Clavareau 1913 : 115; **comb. nov.**

†***comptus*** Chapuis 1875 : 75 (Australia); Masters 1887 : 573; Clavareau 1913 : 116; Lea 1920 : 220;

concolor Saunders 1847 : 61 (*Pleomorpha*; Australia); Saunders 1847 : 269-270; Suffrian 1859 : 165-6 (*Ditropidus*); Masters 1887 : 573 (sen. syn. of *ater* Saunders and *cistellus* Germar); Lea 1902 : 425, 430; Clavareau 1913 : 117 (sen. syn. of *ater* Saunders and *cistellus* Germar); Lea 1920 : 396-7; Lea 1920 : 221-3, 226 (sen. syn. of *ater*, *cistellus* and *maxillosus* Suffrian); Lea 1921 : 393, 399, 408; Goudie 1927 : 303; Jolivet 1957 : 92 (wing venation)

= *ater* Saunders 1847 : 61 (*Pleomorpha*; Western Australia) nec Boisduval 1835; Saunders 1847 : 270; Suffrian 1859 : 166 (*Ditropidus*); Masters 1887 : 573 (jun. syn. of *concolor* Saunders); Clavareau 1913 : 117 (jun. syn. of *concolor* Saunders); Lea 1920 : 221-2 (jun. syn. of *concolor* Saunders)

= *cistellus* Germar 1848 : 242-3 (Adelaide); Suffrian 1859 : 25-7, 28, 29 (? jun. syn. of *Pleomorpha concolor* Saunders and *P. atra* Saunders); Chapuis 1876 : 337; Masters 1887 : 573 (jun. syn. of *concolor* Saunders); Clavareau 1913 : 117 (jun. syn. of *concolor* Saunders); Lea 1915 : 801 note; Lea1920 : 221-2 (jun. syn. of *cconcolor* Saunders)

= *maxillosus* Suffrian 1859 : 27-8 (Port Philip); Masters 1887 : 575; Clavareau 1913 : 118; Lea 1920 : 220-1 (jun. syn. of *concolor* Saunders); Jolivet 1978 : 176 (host); Hawkeswood 1988 : 98 ("nr" *maxillosa*; host).

†***congenitus*** Lea 1921 : 407-8 (Adelaide, Murray Bridge); Lea 1920 : 396; Lea 1920 : 221; Lea 1921 : 402, 404,

****constricticollis*** Jacoby 1896 : 383-4 (*Bucharis*; Pangherang-Pisang); **comb. nov.**

†***convexiusculus*** Chapuis 1879 : 76 (*Elaphodes*, Peak Downs); Masters 1887 : 571; Clavareau 1913 : 115; Lea 1920 : 387 (*Ditropidus*); Lea 1920 : 220

†***coriaceus*** Lea 1920 : 397-8 (Geraldton, Swan River, Dirk Hartog Island); Lea 1920 : 222; Britton and Stanbury 1980 : 253

cornutus Baly 1877 : 384-5 (Australia); Masters 1887 : 573; Clavareau 1913 : 117; lea 1920 : 385, 389; Lea 1920 : 220; Lea 1921 : 386

†***corrugatus*** Lea 1902 : 423 (Swan River); Clavareau 1913 : 117; Lea 1920 : 220

†***costatus*** Chapuis 1875 : 77 (Australia); Masters 1887 : 573; Clavareau 1913 : 117; Lea 1920 : 388, 397; Lea 221, 233-4; Lea 1921 : 222

costipennis Baly 1876 : 465 (Champion Bay); Masters 1887 : 573 (*costatipennis* [sic]); Clavareau 1913 : 117; Lea 1920 : 221

†***crassipes*** Lea 1920 : 225-6 (north-west Australia, Derby); Lea 1920 : 220; Lea 1921 : 383;

†***cribriceps*** Lea 1921 : 396 (Bluff); Lea 1921 : 402; Lea 1920 : 221

†***cribricollis*** Lea 1921 : 385-6 (Australia); Lea 1920 : 220

†***cribripennis*** Lea 1920 : 226-7 (Geraldton, Perth, Swan River, Rottnest Island); Lea 1920 : 220; Lea 1921 : 383; Britton and Stanbury 1980 : 254

†***cuneatus*** Chapuis 1875 : 76 (Clarence River); Masters 1887 : 573; Lea 1902 : 430; Clavareau 1913 : 117; Lea 1917 : 626; Lea 1920 : 220; Goudie 1927 : 303

†***cupreus*** Chapuis 1875 : 78 (Brisbane); Chapuis 1879 : 77; Masters 1887 : 573; Lea 1902 : 427-8; Weise 1908 : 3; Clavareau 1913 : 117; Lea 1920 : 221

†***cupricollis*** Lea 1921 : 382-3 (Morgan); Lea 1920 : 220; Lea 1921 ; 260

davisii Saunders 1847 : 472 (*Pleomorpha*; near Adelaide); Saunders 1847 : 268-9, plate 15, fig. 4; Suffrian 1859 : 25, 165-6 (*Ditropidus*); Suffrian 1866 : 2; Chapuis 1874 : 182; Masters 1887 : 573 (*dawisi* [sic]); Clavareau 1913 : 117; Lea 1917 : 626; Lea 1920 : 220-1; Lea 1921 : 221-2; Lea 1921 : 391-2; Goudie 1927 : 303

dimidiatus Baly 1871 : 389 (north Australia, ?Brisbane); Masters 1887 : 573; Lea 1902 : 431; Clavareau 1913 ; 117; Lea 1920 : 220; Lea 1920 : 382-3

discicollis Lea 1921 : 382 (Mount Lofty); Lea 1920 : 220

†***distinguendus*** Chapuis 1875 : 79 (Swan River); Masters 1887 : 574; Weise 1908 : 2; Clavareau 1913 : 117; Lea 1920 : 389; Lea 1920 : 221;

†***dohrni*** Chapuis 1879 : 76 (*Elaphodes*, Gayndah, Sydney); Masters 1887 : 571; Lea 1902 : 419; Clavareau 1913 : 115; **comb. nov.**

†***doriae*** Chapuis 1876 : 336-7 (Somerset, Cape York); Masters 1887 : 574; Clavareau 1913 : 117; Lea 1920 : 386; Lea 1920 : 221; Lea 1921 : 223; Lea 1921 : 401; Gressitt 1965 : 396, 399;

[*dubius* Lea, var. of *vagans* Lea (*q.v.*)]

duboulai Baly 1871 : 385 (Champion Bay); Masters 1887 : 574 (*duboulayi* [sic]); Clavareau 1913 : 117 (*duboulayi* [sic]); Lea 1920 : 221, 235;

†*elutus* Lea 1902 : 421 (Forest Reefs); Clavareau 1913 : 117; Lea 1920 : 220; Weise 1923 ; 8

†***epilachnoides*** Chapuis 1875 : 82 (*Elaphodes*, Sydney); Chapuis 1876 : plate 115, fig. 5; Masters 1887 : 571; Lea 1902 : 419; Clavareau 1913 : 115; Lea 1920 : 248, 250; Gressitt 1965 : 391; **comb. nov.**

†***epistomalis*** Weise 1908 : 2-3 (Dirk Hartog); Clavareau 1913 : 117

evelynensis Weise 1923 : 12 (Evelyne)

†***facialis*** Baly 1876 : 466 (Gawler Town); Masters 1887 : 574; Clavareau 1913 : 117; Lea 1920 : 221; Lea 1920 : 398

†***fasciatus*** Baly 1871 : 390-1 (Champion Bay); Masters 1887 : 574; Clavareau 1913 : 117; Lea 1920 : 386, 391-2; Lea 1920 : 220;

= *canescens* Chapuis 1875 : 75 (Adelaide, Brisbane, Pine Mountain); Masters 1887 : 573; Lea 1902 : 431; Clavareau 1913 : 116; Lea 1917 : 626; Lea 1920 : 386 (jun. syn. of *fasciatus* Baly); Lea 1920 : 220

fasciatus var ***pictipes*** Lea 1920 : 386 (Cue)

ferrugineus Weise 1923 : 15-6 (*Elaphodes*, Cedar Creek); **comb. nov.**

†***festivus*** Suffrian 1859 : 14-16 (*Prasonotus*, Port Philip); Suffrian 1859 : 12; Masters 1887 : 570; Clavareau 1913 : 121; **comb. nov.**

= †*suffriani* Chapuis 1875 : 78 (*Ditropidus*; Sydney); Chapuis 1876 ??: plate 115, fig. 6; Masters 1887 : 578; Lea 1902 : 430; Clavareau 1913 : 120; Lea 1920 : 220; **syn. nov.**

†***flavipennis*** Lea 1921 : 384-5 (Oodnadatta); Lea 1920 : 220, 229;

†***flavipes*** Lea 1920 : 224-5 (Leigh Creek, Oodnadatta, Morgan); Lea 1920 : 220; Lea 1921 : 260; Britton and Stanbury 1980 : 259

†***flavoapicalis*** Lea 1920 : 241-2 (Warren River); Lea 1920 : 222

†***flavolateralis*** Lea 1920 : 238-9 (Huon River, Devonport, Burnie, Port Lincoln, Kangaroo Island, Mount Gambier); Lea 1920 : 239; Lea 1920 : 222;

†***foveiventris*** Lea 1921 : 399-400 (Port Lincoln); Lea 1920 : 221

[*frater* Lea, in Goudie 1927 : 303 [*nomen nudum*; Lea appears to have forgotten to describe this species]]

†***frontalis*** Chapuis 1875 : 80 (Australia); Masters 1887 : 574; Lea 1902 : 397; Clavareau 1913 : 117; Lea 1920 : 397; Lea 1920 : 221; Lea 1921 : 397, 410; Gressitt 1965 : 395

†***fugitivus*** Chapuis 1875 : 77 (Swan River); Masters 1887 : 574; Lea 1902 : 422,430; Clavareau 1913 : 117; Lea 1920 : 221, 245; Weise 1923 : 7

fulgidus Suffrian 1859 : 28-9 (Australia); Masters 1887 : 574; Clavareau 1913 : 117; Lea 1920 : 221

****fulvicollis*** Bryant 1949 : 929 (New Guinea); Bryant 1949 : 922; Gressitt 1965 :

fulvicornis Weise 1923 ; 11-12 (Glen Lamington)

****fulvipes*** Baly 1865 : 63 (*Bucharis*; Morty Island); Clavareau 1913 : 122; Weise 1923 : 6; **comb. nov.**

fulvus Baly 1871 : 388-9 (Western Australia); Masters 1887 : 574; Weise 1908 : 2; Clavareau 1913 : 117; Lea 1920 : 220; Lea 1921 : 387

†***gagates*** Lea 1921 : 409-410 (Blue Mountains, Jenolan, Mount Victoria, Dividing Range); Lea 1920 : 221; Britton and Stanbury 1980 : 261

†***gagatinus*** Erichson 1842 : 234 note (New Holland); Suffrian 1859 : 2, 35-6, 37, 38; Masters 1887 : 574; Lea 1902 : 426; Clavareau 1913 ; 118; Lea 1920 : 221

†***geminatus*** Chapuis 1875 : 79 (Parao River); Masters 1887 : 574; Clavareau 1913 : 118; Lea 1920 : 221

†***geminus*** Chapuis 1875 : 81 (*Polyachus*; Pine Mountain, Sydney, Adelaide); Masters 1887 : 579; Clavareau 1913 : 113; Lea 1920 : 245; Jolivet 1957 : 91 (wing venation) **comb. nov.**

†***geniculatus*** Lea 1920 : 391-2 (Geraldton); Lea 1920 : 220

†***gibbicollis*** Lea 1921 : 381-2 (Mount Lofty); Lea 1920 : 220; Lea 1921 : 382

†***gibbulus*** Suffrian 1859 : 41-3 (Australia); Masters 1887 : 574; Clavareau 1913 : 118; Lea 1920 : 221; Weise 1923 ; 10

†***glaber*** Lea 1921 : 406 (Sydney); Lea 1920 : 221;

†***globulus*** Lea 1921 : 383-4 (Australia); Lea 1920 : 220

globus Boisduval 1835 : 589 (*Cryptocephalus*; New Holland); Suffrian 1859 : 152 (*Ditropidus*, ? identity); Masters 1887 : 574 (sen. syn. of *saprinodes* Suffr.); Clavareau 1913 : 118 (sen. syn. of *saprinodes* Suffrian); Lea 1920 : 221 (? sen. syn. of *saprinodes* Suffrian and *seminulum* Germar)

[*globus* Dejean, in Chevrolat 1837 : 449, is a *nomen nudum*]

†***glossatus*** Lea 1921 : 393-4 (Port Lincoln, Mount Lofty, Ardrossan, Lucindale, Coromby, Diamond Creek, Georgetown); Lea 1920 : 221; Lea 1921 : 403; Britton and Stanbury 1980 : 261

†***godeffroyi*** Chapuis 1879 : 77 (Peak Downs); Masters 1887 : 575; Clavareau 1913 ; 118; Lea 1920 : 220

granulosus Baly 1876 : 462-3 (*Bucharis*; Champion Bay); Masters 1887 : 570; Clavareau 1913 : 122; **comb. nov.**

†***gymnopterus*** Lea 1917 : 625-6 (Parachilna); Lea 1920 : 391; Lea 1920 : 220, 225, ;226; Lea 1921 : 383

†***haemorrhoidalis*** Lea 1920 : 400-1 (*Elaphodes*, Hobart); **comb. nov.**

†***halticoides*** Lea 1920 : 401 (*Elaphodes*, Bridgetown); **comb. nov.**

hirticollis Baly 1871 : 384-5 (Western Australia); Masters 1887 : 575; Clavareau 1913 : 118; Lea 1917 : 626; Lea 1920 : 220; Lea 1921 : 260

histeroides Suffrian 1859 : 31-2 (Australia); Chapuis 1874 : 183 (*histerinus* [sic], = *Pleomorphus*); Chapuis 1876 : plate 116, fig.1 (*histerinus* [sic]); Masters 1887 : 578; Clavareau 1913 : 121 (= *Pleomorphus histerinus*, Chapuis); Lea 1920 : 221 (*Ditropidus*); Jolivet 1957 : 92 (wing venation);

†***holoporphyrus*** Lea 1902 : 420 (Sydney); Clavareau 1913 : 118; Lea 1920 : 220

†***ignitus*** Lea 1921 : 222-3 (Cairns, Bowen); Lea 1920 : 220

†***imitator*** Lea 1920 : 229 (Australia); Lea 1920 : 220

†***imperialis*** Chapuis 1876 : 335-6 (Somerset, Cape York); Masters 1887 : 575; Clavareau 1913 : 118; Lea 1920 : 389; Lea 1920 : 221; Lea 1921 : 399

†***impuncticollis*** Lea 1920 : 393-4 (Karridale); Lea 1920 : 220

†***inconspicuus*** Lea 1921 : 263 (Sydney); Lea 1926 : 286

†***indistinctus*** Lea 1921 : 401 (Leigh Creek); Lea 1920 : 396; Lea 1920 : 221; Lea 1921 : 404; Britton and Stanbury 1980;

†***insignis*** Lea 1920 : 394-5 (Mullewa); Lea 1920 : 221

†***insularis*** Lea 1902 : 424-5 (Rottnest Island); Clavareau 1913 : 118; Lea 1920 : 389; Lea 1920 : 221; Lea 1921 : 400;

= *chalceus* Lea 1902 : 426, 427; Clavareau 1913 : 116; Lea 1920 : 389 (jun. syn. of *insularis* Lea); Lea 1920 :221

= *lateralis* Lea 1902 : 428; Clavareau 1913 : 118; Lea 1920 : 428 (jun. syn. of *insularis* Lea); Lea 1920 : 221

†***intonsus*** Lea 1902 : 419-420 (Whitton); Clavareau 1913 : 118; Lea 1920 : 220, 225; Lea 1920 : 391; Lea 1921 : 382, 384

jansoni Baly 1876 : 466 (Rockhampton); Masters 1887 : 575; Clavareau 1913 : 118; Lea 1920 : 221; Weise 1923 : 7;

†***labiatus*** Chapuis 1875 : 80 (Melbourne, Brisbane); Chapuis 1876 : 337; Masters 1887 : 575; Clavareau 1913 : 118; Lea 1920 : 222; Lea 1920 : 400; Lea 1921 : 410

†***lacordairei*** Chapuis 1875 : 75-6 (Australia); Chapuis 1879 : 77; Masters 1887 : 575; Clavareau 1913 : 118; Lea 1920 : 220

laetus Baly 1876 : 464-5 (South Australia); Masters 1887 : 575; Clavareau 1913 : 118; Lea 1920 : 221; Lea 1921 : 407

†***laevicollis*** Lea 1902 : 424 (Pinjarrah, Swan River, Darling Ranges, Vasse); Clavareau 1913 : 118; Lea 1920 : 382, 390; Lea 1920 : 220

laevigatus Baly 1877 : 380-1 (*Ditropidus*; North Australia); Masters 1887 : 575; Lea 1902 : 421; Clavareau 1913 : 118; Lea 1920 : 221; Weise 1923 : 14 (*Polyachus*);

laeviusculus Weise 1923 : 11 (Tambourine)

†***laminatus*** Chapuis 1875 : 79-80 (Sydney, Port Denison, Rockhampton, Cape York); Chapuis 1879 : 76; Masters 1887 : 575; Blackburn 1888 : 1472; Clavareau 1913

: 118; Lea 1920 : 222; Lea 1920 : 388; Lea 1921 : 399; Hawkeswood 1988 : 98 (host)

†***larinus*** Lea 1902 : 418 (*Elaphodes*, Behn River, north-west Australia); Clavareau 1913 : 115; **comb. nov.**

†***latericollis*** Lea 1920 : 228-9 (Brisbane); Lea 1920 : 220, 229

lateritius Chapuis 1879 : 76 (Gayndah); Masters 1887 : 575; Clavareau 1913 : 118; Lea 1920 : 220

†***lateroapicalis*** Lea 1920 : 237-8 (Forest Reefs, Armidale, West Tamar, Launceston, Huon River, Frankford, King Island, Lucindale, Mount Lofty, Kangaroo Island); Lea 1920 : 222, 239, 240; Britton and Stanbury 1980 : 267

[*latibasis* Lea 1921 : 385 (*Prasonotus*, nom. nud.)]

†***laticollis*** Lea 1920 : 393 (Brisbane); Lea 1920 : 220

†***latifrons*** Lea 1920 : 390-1 (Condobolin); Lea 1920 : 220

latifrons Weise 1923 : 8-9 (Yarrabah), nec Lea 1920

†***lentulus*** Chapuis 1875 : 81 (Tasmania, Brisbane, Parao River); Chapuis 1876 : 338; Masters 1887 : 575; Lea 1902 : 431, 454; Clavareau 1913 : 118; Lea 1917 : 626; Lea : 388; Lea 1920 : 221, 233; Lea 1921 : 397, 410; Lea 1926 : 286

lepidus Weise 1923 : 7-8 (Lamington Plateau)

lineolatus Weise 1923 : 14-5 (*Elaphodes*, Cedar Creek); **comb. nov.**

†***lobicollis*** Lea 1920 : 396-7 (Brisbane); Lea 1920 : 221; Lea 1921 : 224

†***longipes*** Lea 1921 : 390 (Leigh Creek); Lea 1920 : 220

†***longus*** Lea 1921 : 388-9 (Cue); Lea 1920 : 220

lucidulus Chapuis 1876 : 340-1 (*Coenobius*; Somerset, Cape York); Masters 1887 : 578; Lea 1902 : 425; Clavareau 1913 : 123; Lea1920 : 252-3; Weise 1923 : 14 (= *Polyachus*) **comb. nov.**

†***macrocephalus*** Lea 1920 : 242-3 (Australia, Geraldton, Swan River, Bridgetown, Mount Lofty, Port Lincoln); Lea 1920 : 222; Britton and Stanbury 1980 : 269

†***macrops*** Lea 1921 : 394-5 (Australia, Port Lincoln); Lea 1920 : 221; Lea 1921 : 396-7;

†***maculicollis*** Chapuis 1875 : 76-7 (Sydney); Masters 1887 : 575; Lea 1902 : 430; Clavareau 1913 : 118; Lea 1920 : 387-8; Lea 1920 : 221; Weise 1923 : 11

= †*erythroderes* Lea 1920 : 244-5 (*Euditropidus*; Mount Tambourine); **syn. nov.**

= †*niger* Lea 1920 : 244 (*Euditropidus*; Dorrigo); **syn. nov.**

= †*maculicollis* Weise 1923 : 13-4 (*Polyachus*; Glen Lamington); **syn. nov.** [*maculicollis* includes colour varieties with completely dark dorsum (*niger*) or completely red pronotum (*erythroderes*)]

†***maculifrons*** Chapuis 1875 : 78 (King George Sound); Masters 1887 : 575; Clavareau 1913 : 118; Lea 1920 : 221

†***majorinus*** Lea 1921 : 393 (Mount Lofty); Lea 1920 : 221; Lea 1921 : 394

†***mandibularis*** Lea 1902 : 422 (Swan River); Clavareau 1913 : 118; Lea 1920 : 221; Lea 1920 : 392

marginicollis Baly 1876 : 463-4 (Polyachus; Swan River); Masters 1887 : 579; Clavareau 1913 : 113 **comb. nov.**

martius Baly 1876 : 463 (*Bucharis*; Moreton Bay); Baly 1877 : 386; Masters 1887 : 570; Clavareau 1913 : 122; Weise 1923 : 6; Jolivet 1957 : 93 (wing venation); **comb. nov.**

†***melasomus*** Lea 1902 : 426 (Forest Reefs); Clavareau 1913 : 119; Lea 1920 : 222; Lea 1920 : 397; Lea 1921 : 397, 403, 410

†***metallicus*** Lea 1920 : 394 (Sheffield); Lea 1920 : 220; Britton and Stanbury 1980 : 272

†***micans*** Lea 1902 : 427-8 (Geraldton); Clavareau 1913 : 119; Lea 1920 : 221;

†***michaelseni*** Weise 1908 : 3 (Dirk Hartog, Brown Station); Clavareau 1913 : 119

†***minutus*** Lea 1920 : 239-240 (Dividing Range, Gisborne, Launceston, Turner's Marsh, Hobart, Mount Wellington, Huon River, Swansea, Frankford, Wilmot, Burnie); Lea 1920 : 222; Lea 1926 : 286; Britton and Stanbury 1980 : 273

†***mirus*** Lea 1920 : 392 (Moree); Lea 1920 : 220

mjoebergi Weise 1916 : 3-4, plate 1, fig. 2 (*Elaphodes*, Kimberley district); **comb. nov.**

modestus Weise 1923 : 10-11 (Cedar Creek)

†***modicus*** Lea 1921 : 383 (Bowen); Lea 1920 : 220

murinus Chapuis 1879 : 75 (*Elaphodes*, Rockhampton); Masters 1887 : 571; Lea 1902 : 419; Clavareau 1913 : 115; Lea 1920 : 247; **comb. nov.**

nanus Weise 1923 : 9-10 (Glen Lamington)

†***nigribasis*** Lea 1921 : 387-8 (Australia, Swan River); Lea 1920 : 220, 256;

†***nigricollis*** Lea 1902 : 422-3 (Loftus); Clavareau 1913 : 119; Lea 1920 : 220; Lea 1920 : 389; Lea 1921 : 387

†***nigripennis*** Lea 1902 : 421 (Galston, Tamworth); Clavareau 1913 : 119; Lea 1920 : 221; Lea 1920 : 389-390

†***nigriventris*** Lea 1921 : 388 (Leigh Creek); Lea 1920 : 220

†***nigrovarius*** Lea 1920 : 250 (*Elaphodes*, South Australia, Port Lincoln, Murray Bridge); **comb. nov.**

†***nitiduloides*** Chapuis 1879 : 76 (Sydney); Masters 1887 : 576; Lea 1902 : 426, 430; Clavareau 1913 : 119; Lea 1920 : 222; Lea 1921 : 409, 410

†***nobilis*** Chapuis 1875 : 81 (Swan River, Queensland, Cape York); Masters 1887 : 576; Clavareau 1913 : 119; Lea 1920 : 222

notatus Weise 1923 : 7 (nom. nov. for *fasciatus* Weise nec Baly)

= *fasciatus* Weise 1916 : 6, plate 1, fig. 4 (*Bucharis*, Kimberley District); Weise 1923 : 7 (*Ditropidus notatus* Weise)

†***oblongus*** Lea 1902 : 419 (*Elaphodes*, Thursday Island); Clavareau 1913 : 115; Lea 1920 : 249; Britton and Stanbury 1980 : 276; **comb. nov.**

†***obscuripennis*** Lea 1921 : 403-4 (Leigh Creek, Parachilna); Lea 1920 : 222

†***obsidianus*** Chapuis 1879 : 76 (Gayndah, Peak Downs); Masters 1887 : 576; Clavareau 1913 : 119; Lea 1920 : 222;

†***obtusus*** Chapuis 1875 : 76 (Adelaide, Pine Mountain); Masters 1887 : 576; Clavareau 1913 : 119; Lea 1920 : 220; Lea 1921 : 391

†***ochropus*** Erichson 1842 : 233-4 (Tasmania); Suffrian 1859 : 2, 40-1; Masters 1887 : 576; Lea 1902 : 427, 454; Clavareau 1913 : 119; Lea 1920 : 382; Lea 1920 : 221, 232; Lea 1921 : 394, 396-7, 409

odewahnii Baly 1871 : 387 (South Australia); Masters 1887 : 576 (*odewahni* [sic]); Lea 1902 : 431; Clavareau 1913 : 119; Lea 1920 : 383; Lea 1920 : 220, 234; Lea 1921 : 397, 407

†***opaciceps*** Lea 1921 : 227 (Sydney, Galston, Como, Mount Tambourine, Dalby, Bribie Island); Lea 1920 : 222; Britton and Stanbury 1980 : 277

ophthalmicus Suffrian 1859 : 45-7 (Australia); Masters 1887 : 576; Clavareau 1913 : 119; Lea 1920 : 222

†***opulentus*** Chapuis 1875 : 77 (Australia); Masters 1887 : 576; Clavareau 1913 : 119; Lea 1920 : 221;

†***ornatus*** Baly 1876 : 467-8 (Western Australia); Masters 1887 : 576; Lea 1902 : 431; Clavareau 1913 : 119; Lea 1920 : 385; Lea 1920 : 220, 227

= †*alphabeticus* Lea 1920 : 227-8 (South Australia, Port Lincoln); Lea 1920 : 220; Britton and Stanbury 1980 : 245; **syn. nov.** [this is a minor colour variant of *ornatus*]

†***ovatulus*** Chapuis 1875 : 80 (Sydney); Masters 1887 : 576; Clavareau 1913 : 119; Lea 1920 : 221

pallens Chapuis 1879 : 77 (*Pleomorphus*; Peak Downs); Masters 1887 : 578; **comb. nov.**

†***pallidipennis*** Chapuis 1875 : 76 (Pine Mountain); Masters 1887 : 576; Lea 1902 : 424; Weise 1908 : 2; Clavareau 1913 : 119; Lea 1920 : 220

= †*dolichognathus* Lea 1920 : 255-6 (*Polyachus*; Australia, South Australia); Britton and Stanbury 1980 : 256; **syn. nov.**

†***pallidus*** Lea 1920 : 245 (*Euditropidus*; Leigh Creek); **comb. nov.**

†***pallipes*** Lea 1920 : 240-1 (Dividing Range); Lea 1920 : 222

†***palmerstoni*** Blackburn 1888 : 1472 (Northern Territory); Clavareau 1913 : 119; Lea 1920 : 222; Lea 1921 : 401, 406

parviceps Weise 1923 : 7 (nom. nov. for *angustifrons* Weise)
= *angustifrons* Weise 1916 : 8-9 (*Bucharis*, Kimberley District), nec Chapuis 1875; Weise 1923 : 7 (= *parviceps* Weise)

pascoei Baly 1877 : 381 (Melbourne); Masters 1887 : 576; Lea 1902 : 421, 431; Clavareau 1913 : 119; Lea 1920 : 221

†*pastus* Chapuis 1875 : 77 (Sydney); Chapuis 1879 : 77; Masters 1887 : 576; Clavareau 1913 : 119; Lea 1920 : 220, 232

phalacroides Baly 1876 : 464 (Gawler Town); Masters 1887 : 576; Clavareau 1913 : 119; Lea 1920 : 222; Hawkeswood 1983 : 156-8 (host)

pictus Baly 1877 : 382 (Western Australia); Masters 1887 : 576; Lea 1902 : 423, 431; Clavareau 1913 : 119; Lea 1920 : 220

†*pilula* Chapuis 1875 : 83 (*Elaphodes*, Melbourne, Port Denison); Chapuis 1879 : 76; Masters 1887 : 571; Lea 1902 : 419; Clavareau 1913 : 115; Weise 1916 : 3; Lea 1920 : 246, 250; **comb. nov.**

politus Weise 1923 : 6 (*Bucharis*; Glen Lamington); **comb. nov.**

†*puberulus* Chapuis 1875 : 75 (Swan River); Masters 1887 : 577; Clavareau 1913 : 119; Lea 1920 : 387; Lea 1920 : 220, 225

†*pubescens* Lea 1920 : 223-4 (Leigh Creek); Lea 1920 : 220; Lea 1920 : 391; Britton and Stanbury 1980 : 280

†*pubicollis* Chapuis 1875 : 75 (Australia); Chapuis 1879 : 76; Masters 1887 : 577; Lea 1902 : 430; Clavareau 1913 : 119; Lea 1915 : 801; Lea 1917 : 626; Lea 1920 : 220, 223; Lea 1920 : 387, 391; Lea 1921 : 383; Lea 1921 : 260

pulchellus Baly 1876 : 468 (Adelaide); Masters 1887 : 577; Clavareau 1913 : 119; Lea 1920 : 385; Lea 1920 : 220

**pulcher* Gressitt 1965 : 399, Fig. 4b (New Guinea);

†*pulicosus* Lea 1902 : 424 (Bridgetown); Weise 1908 : 2; Clavareau 1913 : 119; Lea 1920 : 220, 255

†*punctatostriatus* Lea 1921 : 262 (Baudin Point)

†*puncticollis* Lea 1921 : 405 (Blue Mountains, Sydney); Lea 1920 : 397; Lea 1920 : 222

†*punctipennis* Lea 1921 : 395-6 (Western Australia, Mullewa); Lea 1920 : 221; Lea 1921 : 396-7;

†*punctulum* Chapuis 1875 : 80 (Sydney, Adelaide, Fiji); Masters 1887 : 577; Lea 1902 : 430; Clavareau 1913 : 120; Lea 1920 : 387, 398; Lea 1920 : 222, 235; Lea 1921 : 226; Bryant and Gressitt 1957 : 13 (? identity)

pusillus Weise 1923 : 9 (Tambourine); Weise 1923 : 11

†***putridus*** Chapuis 1879 : 77 (*Pleomorphus*; Peak Downs, Rockhampton); Chapuis 1874 : 183 (*nom. nud.*); Masters 1887 : 578; Clavareau 1913 : 121 (*putridus* Suffrian [sic]); **comb. nov.**

†***pygidialis*** Lea 1920 : 395 (Sydney); Lea 1920 : 222; Lea 1921 : 225; Lea 1921 : 402, 405

†***pyriformis*** Suffrian 1859 : 29-31 (Sydney); Masters 1887 : 577; Clavareau 1913 : 120; Lea 1920 : 222

†***quadratipennis*** Lea 1921 : 402-3 (Leigh Creek, Port Lincoln, Adelaide); Lea 1920 : 396; Lea 1920 : 222; Lea 1921 : 224-5; Lea 1921 : 402, 404-5

†***rhizobioides*** Lea 1920 : 400 (*Elaphodes*, Dalmorton); **comb. nov.**

†***rivularis*** Lea 1920 : 235-6 (Capel River, Vasse River, Swan River); Lea 1920 : 222; Britton and Stanbury 1980 : 282

†***rotundatus*** Lea 1920 : 234 (Geraldton); Lea 1920 : 222

†***rotundiformis*** Lea 1920 : 235 (Cairns District); Lea 1920 : 222; Lea 1920 : 398; Lea 1921

†***rufescens*** Chapuis 1875 : 76 (Port Denison, Cape York); Masters 1887 : 577; Lea 1902 : 424; Clavareau 1913 : 120; Lea 1920 : 220

ruficaudis Baly 1877 : 35 (*Prasonotus*, New South Wales); Masters 1887 : 570; Lea 1902 : 419; Lea 1904 : 352, 422; Clavareau 1913 : 121; **comb. nov.**

†***ruficollis*** Saunders 1847 : 472-3 (*Pleomorpha*; Van Diemen's Land); Saunders 1847 : 269; Suffrian 1859 : 165-6 (*Ditropidus*); Masters 1887 : 577; Lea 1902 : 454; Clavareau 1913 : 120; Lea 1920 : 385; Lea 1920 : 221, 231;

= †*elegantulus* Baly 1877 : 381-2 (Australia); Masters 1887 : 574; Lea 1902 : 431; Clavareau 1913 : 117; Lea 1920 : 383-5; Lea 1920 : 221, 230, 231, 233, 245; **syn. nov.**

= †*rufipes* Saunders 1847 : 473 (*Pleomorpha*; Van Diemen's Land); Saunders 1847 : 269; Suffrian 1859 : 165-6 (*Ditropidus*); Chapuis 1879 : 76; Masters 1887 : 577; Lea 1902 : 431, 454; Clavareau 1913 : 120; Lea 1920 : 221; **syn. nov.**

[in *ruficollis* the ♂ has a red pronotum (*elegantulus*) and the ♀ is entirely metallic green (*rufipes*)]

†***rufimanus*** Lea 1920 : 398-9 (Mount Lofty); Lea 1920 : 222

rufocupreus Baly 1871 : 386-7 (Western Australia, Champion Bay); Masters 1887 : 577; Clavareau 1913 : 120; Lea 1920 : 220

rufovarius Chapuis 1875 ; 82 (*Elaphodes*, Carpentaria); Masters 1887 : 571; Lea 1902 : 419; Clavareau 1913 : 115; Weise 1916 : 5; Lea 1920 : 248; **comb. nov.**

†***rutilus*** Chapuis 1875 : 82 (*Elaphodes*, Port Denison); Masters 1887 : 571; Lea 1902 : 419; Clavareau 1913 : 115; Lea 1920 : 246, 250; **comb. nov.**

sanguinolentus Chapuis 1879 : 75 (*Elaphodes*, Gayndah); Masters 1887 : 571; Clavareau 1913 : 115; **comb. nov.**

saprinoides Suffrian 1859 : 47-8 (Australia); Clavareau 1913 : 120 (jun. syn. of *globus* Boisduval); Lea 1920 : 221-2 (*saprinodes* [sic],? = *globus* Boisduval)

†***saundersi*** Baly 1877 : 379 (Gawler Town); Masters 1887 : 570; Clavareau 1913 : 202; **comb. nov.**

= †*multimaculatus* Lea 1920 : 250-1 (*Elaphodes*; Australia, New South Wales, Cobar); **syn. nov.**

schmelzi Chapuis 1879 : 77 (Peak Downs); Masters 1887 : 577; Clavareau 1913 : 120; Lea 1920 : 220

†***scitulus*** Lea 1902 : 427 (Swan River, Geraldton); Lea 1902 : 427; Weise 1908 : 3; Clavareau 1913 : 120; lea 1920 : 390; Lea 1920 : 221

†***sculpturatus*** Lea 1921 : 261-2 (Baudin Island, Baudin Point)

†***scutellaris*** Lea 1921 : 406-7 (Australia, Murray Bridge, Kangaroo Island); Lea 1920 : 222

†***scutellaris*** Chapuis 1875 : 83 (*Elaphodes*, Sydney); Masters 1887 : 571; Clavareau 1913 : 115; Lea 1920 : 247-8; **comb. nov.**

†***semicircularis*** Baly 1876 : 466-7 (Australia); Masters 1887 : 577; Clavareau 1913 : 120; Lea 1920 : 220

†***semicrudus*** Lea 1920 : 230-1 (Victorian Alps, Hobart, Mount Wellington, Huon River, Sheffield, Kangaroo Island); Lea 1920 : 221, 245; Britton and Stanbury 1980 : 284

†***seminulum*** Germar 1848 : 242 (syn. of *globus* Boisduval ?, Adelaide); Suffrian 1859 : 38-40 (not syn. with *globus* Boisduval); Chapuis 1879 : 76; Masters 1887 : 577; Clavareau 1913 : 120; Lea 1920 : 397; Lea 1920 : 221 (? syn. of *globus* Boisduval); Weise 1923 : 11

septempunctatus Weise 1916 : 4-5 (*Elaphodes*, Kimberley District);

serenus Baly 1876 : 468-9 (South Australia); Masters 1887 : 577; Clavareau 1913 : 120; Lea 1920 : 385; Lea 1920 : 220; Lea 1921 : 391

†***signifer*** Chapuis 1875 : 83 (*Elaphodes*, Adelaide); Masters 1887 : 571; Clavareau 1913 : 115; Lea 1920 : 248-250, 252; **comb. nov.**

†***similis*** Lea 1920 : 237 (Mount Lofty, Port Lincoln, Adelaide, Kangaroo Island, Lucindale); Lea 1920 : 222

†***simplex*** Lea 1920 : 249-250 (*Elaphodes*, Cairns District, Peel Island); Lea 1920 : 252; **comb. nov.**

†***sobrinus*** Lea 1902 : 426 (Swan River); Clavareau 1913 : 120; Lea 1920 : 390, 397; Lea 1920 : 221; Lea 1921 : 397, 402, 410;

†***solitus*** Lea 1921 : 223-4 (Mount Lofty, Mecklenburg, Adelaide, Moonta, Kilkerran, Parachilna, Quorn, Dividing Range, Sydney, Forest Reefs); Lea 1920 : 222; Lea 1921 : 224; Lea 1921 : 406; Britton and Stanbury 1980 : 286

†***splendidus*** Chapuis 1875 : 78 (Adelaide); Masters 1887 : 577; Clavareau 1913 : 120; Lea 1920 : 221; Goudie 1927 : 303

†***straminipennis*** Weise 1908 : 1-2 (Denham); Clavareau 1913 : 120 (sen. syn. of var. *obscurifrons* Weise 1908)

= *straminipennis* var. *obscurifrons* Weise 1908 : 2; Clavareau 1913 : 120 (jun. syn. of *straminipennis* Weise 1908)

†***striatipennis*** Lea 1921 : 400 (Good Island, Thursday Island); Lea 1920 : 222; Lea 1921 : 223

†***striatopunctatus*** Lea 1902 : 426 (Darling Range); Clavareau 1913 : 120; Lea 1920 : 390; Lea 1920 : 222; Lea 1921 : 224; Lea 1921 : 397; Lea 1926 : 286

†***striatus*** Lea 1921 : 385 (Boulder); Lea 1920 : 220

†***strigiceps*** Lea 1902 : 427 (Galston, Sydney, Glen Innes); Clavareau 1913 : 120; Lea 1920 : 221; Gressitt 1965 : 394

†***strigicollis*** Lea 1920 : 234 (Port Lincoln); Lea 1920 : 222; Lea 1921 : 402

strigosus Baly 1871 : 385-6 (Champion Bay); Masters 1887 : 577; Clavareau 1913 : 120; Lea 1920 : 120

†***subaeneus*** Chapuis 1875 : 79 (Tasmania); Masters 1887 : 578; Lea 1902 : 430, 454; Clavareau 1913 : 120; Lea 1920 : 388; Lea 1920 : 221-2; Lea 1921 : 409-410

†***subarmatus*** Lea 1920 : 396 (Swan River); Lea 1920 : 397; Lea 1920 : 222

subcylindricus Baly 1877 : 385 (Western Australia); Masters 1887 : 578; Clavareau 1913 : 120; Lea 1920 : 220

submetallescens Baly 1877 : 383-4 (Gawler Town); Masters 1887 : 578; Clavareau 1913 : 120; Lea 1920 : 390; Lea 1920 : 220

†***submetallicus*** Suffrian 1859 : 12-14 (*Prasonotus*; Western Australia); Baly 1877 : 36 (*submetallescens* [sic]; Masters 1887 : 570; Lea 1904 : 351-2 (sen. syn. of *morbillosus* Baly, *morbillosus* Chapuis, *chapuisi* Blackburn), 422; Clavareau 1913 : 121; Jolivet 1957 : 93 (wing venation); **comb. nov.**

= *chapuisi* Blackburn 1891 : 139 (*Prasonotus*, nom. nov. for *morbillosus* Chapuis nec Baly [sic]): Lea 1904 : 351-2 (jun. syn. of *submetallicus* Suffrian); Clavareau 1913 : 121

= †*morbillosus* Chapuis 1876 : plate 115, fig. 4 (*Prasonotus*, Swan River); 1879 : 75; Blackburn 1891 : 139 (= *chapuisi* Blackburn, nom. nov.); Lea 1904 : 333, 351 (jun. syn. of *submetallicus* Suffrian); Clavareau 1913 : 121

= †*morbillosus* Baly 1877 : 35-6 (*Prasonotus*, New South Wales, Western Australia), nec Chapuis 1876; Masters 1887 : 570; Lea 1904 : 333, 351-2 (jun. syn. of *submetallicus* Suffrian); Clavareau 1913 : 121;

†***subsuturalis*** Lea 1920 : 399 (Tweed River); Lea 1920 : 222

****suffriani*** Baly 1865 : 62-3, plate 3, fig. 8 (*Bucharis*, Dory, Mysol) [nec *Ditropidus suffriani* Chapuis]; Chapuis 1874 : 178; Clavareau 1913 : 122; Gressitt 1965 : 399; **comb. nov.**

tarsalis Lea 1902 : 423-4 (Armidale); Clavareau 1913 : 120; Lea 1920 : 220. [nb. unique type specimen is missing]

tarsatus Baly 1871 : 387-8 (Western Australia, Champion Bay); Masters 1887 : 578; Clavareau 1913 : 121; Lea 1920 : 220; Lea 1921 : 389; Lea 1921 : 261

†***tenuifrons*** Lea 1920 : 236-7 (North Queensland, Cairns District); Lea 1920 : 222

tessellatus Weise 1916 : 5 (Kimberley District); **comb. nov.**

†***tibialis*** Chapuis 1875 : 79 (Sydney, Clarence River, Brisbane, Fiji); Masters 1887 : 578; Lea 1902 : 430; Clavareau 1913 : 121; Lea 1920 : 386-7; Lea 1920 : 221; Lea 1921 : 406; Bryant and Gressitt 1957 : 13; Gressitt 1965 : 393, 397, 399;

trabeatus Chapuis 1879 : 76 (Peak Downs); Masters 1887 : 578; Lea 1902 : 428; Clavareau 1913 : 121; Lea 1920 : 222; Lea 1921 : 396

†***tranquillus*** Lea 1920 : 398 (Sydney, Como); Lea 1920 : 222, 237; Lea 1921 : 226-7; Britton and Stanbury 1980 : 289

triangulifer Lea 1921 : 408 (Charters Towers); Lea 1920 : 222

tricolor Weise 1923 : 16 (*Elaphodes*, Tambourine); **comb. nov.**

†***tropicus*** Lea 1921 : 224-5 (North-west Australia, Roebuck Bay, Thursday Island, Cairns, Bowen); Lea 1920 : 397; Lea 1920 : 22; Lea 1921 : 407; Britton and Stanbury 1980 ; 290

†***vagans*** Lea 1921 : 225-6 (Darwin, Cairns, Charters Towers, Brisbane, Blue Mountains, Wentworth Falls, Sydney, Galston, Como, Windsor, Port Lincoln, Murray Bridge, Quorn); Lea 1920 : 398; Lea 1920 : 222, 237; Britton and Stanbury 1980 : 291

vagans var. ***dubius*** Lea 1921 : 226

†***variabilis*** Lea 1920 : 243-4 (*Euditropidus*; Tweed River); **comb. nov.**

†***variiceps*** Lea 1920 : 229-230 (Mount Lofty, Port Lincoln); Lea 1920 : 220; Britton and Stanbury 1980 : 291

= †*marginipennis* Lea 1921 : 392 (Mount Lofty); Lea 1920 : 220; **syn. nov.** [in *variiceps* the pronotum is red in the ♂, metallic in the ♀ (*marginipennis*)]

†***variicollis*** Lea 1921 : 386-7 (Port Lincoln, Mount Lofty); Lea 1920 : 220

†**ventralis** Lea 1921 : 400-1 (Darwin); Lea 1920 : 222

†***venustus*** Lea 1902 : 428 (Brisbane); Clavareau 1913 : 121; Lea 1920 : 388, 390; Lea 1920 : 222, 235; Lea 1921 : 407

verticalis Weise 1923 : 7 (nom. nov. for *ruficollis* Weise nec Saunders)

= *ruficollis* Weise 1916 : 7 (*Bucharis*; Fremantle, Perth), nec Saunders 1844; Weise 1923 : 7 (*Ditropidus*, = *verticalis* Weise, nom. nov.)

†***vicarius*** Lea 1921 : 225 (North Queensland, Cairns, National Park, Ourimbah, Sydney); Lea 1920 : 222; Lea 1920 : 399; Lea 1921 : 226; Britton and Stanbury 1980 : 292

†***vigilans*** Lea 1902 : 425 (Tweed River); Clavareau 1913 : 121; Lea 1920 : 222-3, 231; Lea 1920 : 396; Weise 1923 : 7

†***viridiaeneus*** Lea 1902 : 420 (Bunbury); Clavareau 1913 : 121; Lea 1920 : 394; Lea 1920 : 220

†***viridimicans*** Lea 1921 : 410 (Blue Mountains, Jenolan, Illawarra, Sydney, Dividing Range); Lea 1920 : 222

†***viriditinctus*** Lea 1921 : 396-7 (Mount Lofty); Lea 1920 : 221; Lea 1921 : 408

vittiger Chapuis 1879 : 75 (*Elaphodes*, Rockhampton); Masters 1887 : 571; Clavareau 1913 : 116; Lea 1920 : 249; **comb. nov.**

vulpinus Suffrian 1859 : 20-2 (*Elaphodes*, Australia); Masters 1887 : 571; Clavareau 1913 : 116; Lea 1920 : 392; Lea 1920 : 245-6 (sen. syn. of *illotus* Lea); Goudie 1927 : 303; Jolivet 1957 : 92 (wing venation); **comb. nov.**

= *illotus* Lea 1902 : 418-9 (Inverell); Clavareau 1913 : 115; Lea 1920 : 245 (jun. syn. of *vulpinus* Suffrian 1859)

****wallacei*** Baly 1877 : 379-380 (Mysol); Clavareau 1913 : 121; Bryant 1949 : 929

†***whitei*** Lea 1915 : 800-1 (Flat Rock Hole); Lea 1917 : 626; Lea 1920 : 391; Lea 1920 : 220, 223, 226

†***xanthostomus*** Suffrian 1859 : 36-8 (Australia); Masters 1887 : 578; Clavareau 1913 : 121; Lea 1920 : 221

†***xanthurus*** Lea 1902 : 420-1 (Karridale, Bunbury, Swan River); Clavareau 1913 : 121; Lea 1920 : 220; Lea 1921 : 392

†***ziczac*** Lea 1920 : 249 (*Elaphodes*, Bundaberg, Rockhampton); Lea 1920 : 250; **comb. nov.**

incertae sedis, described in *Ditropidus* : some probably belong in *Aprionota.*

****aenescens*** Gressitt 1965 : 397-9 (*Ditropidus*, New Guinea);

****angularis*** Gressitt 1965 : 392-3 (*Ditropidus*, New Guinea);

****fulvicollis*** Bryant 1949 : 921 (*Ditropidus*, New Guinea); Gressitt 1965 : 393;

****minutus*** Jacoby 1896 : 381-2 (*Bucharis*; Sumatra); Clavareau 1913 : 122; Weise 1923 : 15 (*Polyachus*);

***montanus** Bryant 1949 : 928-9 (*Ditropidus*, New Guinea); Bryant 1949 : 922;
***posticalis** Gressitt 1965 : 393-4 (*Ditropidus*, New Guinea);
***punctulatus** Gressitt 1965 : 396-7 (*Ditropidus*, New Guinea)
***subiridescens** Gressitt 1965 : 390-1 (*Elaphodes*, New Guinea);
***varicolor** Gressitt 1965 : 395-6 (*Ditropidus*, New Guinea);
***viridis** Gressitt 1965 : 394-5 (*Ditropidus*, New Guinea);

2.4.3.3 Genus ***Scaphodius** Chapuis 1874 : 179-180; Chapuis 1874 : 159; Fauvel 1907 : 150; Clavareau 1913 : 114; Jolivet 1957 : 92 (wing venation); Seeno and Wilcox 1982 : 38;

Type species : *Scaphodius comptus* Chapuis, by monotypy

= ***Nyetra** Baly 1877 : 33; Jolivet 1957 : 92 (wing venation); Seeno and Wilcox 1982 : 38; **syn. nov.**

Type species : *Nyetra forcipata* Baly, by monotypy

***aeneus** Fauvel 1907 : 152 (*Ditropidus*, New Caledonia); **comb. nov.**
***†bifasciatus** Fauvel 1907 : 151 (New Caledonia); Clavareau 1913 : 114;
***†forcipata** Baly 1877 : 33 (New Caledonia); Jolivet 1957 : 92 (wing venation); **comb. nov.**
***nitidus** Fauvel 1907 : 152 (*Ditropidus*, New Caledonia); **comb. nov.**
***†opacicollis** Fauvel 1907 : 152 (*Ditropidus*, New Caledonia); **comb. nov.**
***†pictipennis** Fauvel 1907 : 151-2 (New Caledonia); Clavareau 1913 : 115;
***striaticollis** Montrouzier 1861 : 397 (*Cryptocephalus* or *Monachus*, New Caledonia); Fauvel 1907 : 150-1 (sen. syn. of *Scaphodius comptus* Chapuis); Clavareau 1913 : 115; Jolivet 1957 : 92 (wing venation)
= **comptus* Chapuis 1874 : 180 (New Caledonia); Fauvel 1907 : 150-1 (jun. syn. of *striaticollis* Montrouzier); Clavareau 1913 : 115 (valid sp.);
***striolatus** Fauvel 1907 : 152 (*Ditropidus*, New Caledonia); **comb. nov.**
***sulcatus** Fauvel 1907 : 152 (*Ditropidus*, New Caledonia); **comb. nov.**

incertae sedis, described in *Monachus*, probably *Scaphodius*
***oxythorax** Montrouzier 1861 : 303 (*Cryptocephalus* or *Monachus*, New Caledonia);
***pallens** Montrouzier 1861 : 303 (*Cryptocephalus* or *Monachus*, New Caledonia);

2.4.4 SUBTRIBE **Cryptocephalina** Gyllenhal 1813 : 582.

Type genus : *Cryptocephalus* Geoffroy in Müller 1764.

2.4.4.1 ***Aporocera*** Saunders 1842 : 68-9 (subg. of *Cryptocephalus*); Saunders 1845 : 149; Chapuis 1874 : 188-9; Baly 1877 : 28, 31; Lea 1904 : 331; Clavareau 1913 : 202, 204; Jolivet 1957 : 96 (wing venation); Seeno and Wilcox 1982 : 39; Ohmart, Stewart and Thomas 1983 : 403 (*Cryptocephalus*; host); Hawkeswood 1988 : 98 (*Cryptocephalus*; host).

2.4.4.4.1 Subgenus ***Aporocera*** s. str.

Type species : *Aporocera apicalis* Saunders, by subsequent designation (Baly 1877 : 28)

= ***Dicenopsis*** Saunders 1842 : 70 (subgenus of *Cryptocephalus*); Saunders 1845 : 142; Chapuis 1874 : 189 (jun. syn. of *Cryptocephalus* Geoffroy); Baly 1877 : 30 (jun. syn. of *Ochrosopsis* Saunders); Lea 1904 : 331 (*Cryptocephalus*); **syn. nov.**

Type species : *Cryptocephalus haematodes* Boisduval, by monotypy

= ***Mitocera*** Saunders 1842 : 70 (subg. of *Cryptocephalus* Geoffroy); Saunders 1845 : 151; Chapuis 1874 : 189 (jun. syn. of *Cryptocephalus* Geoffroy); Baly 1877 : 30 (jun. syn. of *Ochrosopsis* Saunders); Lea 1904 : 331 (valid); Clavareau 1913 : 203; Jolivet 1957 : 96 (wing venation); Gressitt 1965 : 407 (subg. of *Cryptocephalus* Geoffroy); Morrow 1977 : 102, 106 (hosts); Kimoto and Gressitt 1981 : 334; Seeno and Wilcox 1982 : 39; Ohmart, Stewart and Thomas 1983 : 403 (host); **syn. nov.**

Type species : *Mitocera viridipennis* Saunders, by monotypy.

= ***Ochrosopsis*** Saunders 1843 : 59 (subg. of *Cryptocephalus*); Saunders 1845 : 151-2; Chapuis 1874 : 189 (jun. syn. of *Cryptocephalus* Geoffroy); Baly 1877 : 379; Baly 1877 : 30 (sen. syn. of *Chloroplisma* Saunders, *Dicenopsis* Saunders, *Mitocera* Saunders); Baly 1877 : 224, 227; Lea 1904 : 331; Clavareau 1913 : 204; Jolivet 1957 : 96; Gressitt 1965 : 407 (jun. syn. of *Cryptocephalus* Geoffroy);

Kimoto and Gressitt 1981 : 334; Seeno and Wilcox 1982 : 39; Ohmart, Stewart and Thomas 1983 : 403; **syn. nov.**

Type species : *Ochrosopsis australis* Saunders, by subsequent designation (Saunders 1845 : 152)

= ***Idiocephala*** Saunders 1843 : 317 (subg. of *Cryptocephalus*, nom. nov. for *Anodonta* Saunders); Saunders 1845 : 142-3; Chapuis 1874 : 189 (jun. syn. of *Cryptocephalus* Geoffroy); Baly 1877 : 30 (jun. syn. of *Ochrosopsis* Saunders), 31 (jun. syn. of *Aporocera* Saunders [!]); Baly 1877 : 227; Lea 1904 : 331; Clavareau 1913 : 202; Weise 1923 : 22 (sen. syn. of *Anteriscus* Weise); Jolivet 1957 : 96; Gressitt 1965 : 407 (jun. syn. of *Cryptocephalus*); Kimoto and Gressitt 1981 : 334; Seeno and Wilcox 1982 : 39; Ohmart, Stewart and Thomas 1983 : 403 (host); **syn. nov.**

Type species : *Anodonta roei* Saunders, by subsequent designation (Saunders 1845 : 142); *Cryptocephalus speciosus* Guerin-Meneville [!] (Gressitt 1965; misreading of Baly 1877a : 31)

= ***Anodonta*** Saunders 1843 : 66-7, *nec* Lamarck 1799 : 87 (Mollusca); Saunders 1843 : 317 (= *Idiocephala*, nom. nov.)

= ***Chloroplisma*** Saunders 1847 : 293-4 (subgenus of *Cryptocephalus*); Chapuis 1874 : 189 (jun. syn. of *Cryptocephalus* Geoffroy); Baly 1877 : 30 (jun. syn. of *Ochrosopsis* Saunders); Lea 1904 : 331 (valid); Clavareau 1913 : 204; Jolivet 1957 : 96 (wing venation); **syn. nov.**

Type species : *Chloroplisma viridis* Saunders, by monotypy

= ***Loxopleurus*** Suffrian 1859 : 125-7; Chapuis 1874 : 159, 186-7; Chapuis 1876 : 44; Lea 1904 : 330-2; Clavareau 1913 : 124; Tillyard 1926 : 235; Bryant and Gressitt 1957 : 15-6; Jolivet 1957 : 93 (wing venation); Seeno and Wilcox 1982 : 38; **syn. nov.**

Type species : *Loxopleurus aereus* Suffrian, this work.

= ***Rhombosternus*** Suffrian 1859 : 141-3; Chapuis 1874 : 159, 187-9; Lea 1904 : 331; Clavareau 1913 : 126; Jolivet 1957 : 94 (wing venation); Seeno and Wilcox 1982 : 38; **syn. nov.**

Type species : *Rhombosternus sutor* Suffrian, this work.

= ***Schizosternus*** Chapuis 1876 : 44; Lea 1904 : 330-2 (sen. syn. of *Paracephala* Baly); Clavareau 1913 : 126 (sen. syn. of *Paracephala* Baly); Goudie 1927 : 304; Jolivet 1957 : 94 (wing venation); Seeno and Wilcox 1982 : 38 (sen. syn. of *Paracephala* Baly); **syn. nov.**

Type species : *Schizosternus albogularis* Chapuis, by monotypy

= ***Euphyma*** Baly 1877 : 224; Lea 1904 : 331; Seeno and Wilcox 1982 : 39 (jun. syn. of *Cryptocephalus*); **syn. nov.**

Type species : here designated *Idiocephala elegans* Saunders

= ***Chariderma*** Baly 1877 : 28-9; Lea 1904 : 331; Clavareau 1913 : 203; Jolivet 1957 : 96 (wing venation); Jolivet 1978 : 177 (host); Seeno and Wilcox 1982 : 39; **syn. nov.**

Type species : *Chariderma pulchella* Baly, by monotypy

= ***Paracephala*** Baly 1877 : 222-3, nec *Paracephala* Saunders 1868 : 63 (Buprestidae); Baly 1877 : 224; Lea 1904 : 331, 370 (jun. syn. of *Schizosternus* Chapuis); Clavareau 1913 : 126 (jun. syn. of *Schizosternus* Chapuis); Seeno and Wilcox 1982 : 38; **syn. nov.**

Type species : *Paracephala pectoralis* Baly, by original designation

= ***Cyphodera*** Baly 1877 : 25-6; Lea 1904 : 330, 331; Clavareau 1913 : 208 (subg. of *Cadmus*); Seeno and Wilcox 1982 : 40 (subg. of *Cadmus* Erichson); **syn. nov.**

Type species : *Cadmus chlamydiformis* Germar, by monotypy and original designation.

= ***Melinobius** Jacoby 1908 : 269; Clavareau 1913 : 202; **syn. nov.** [the description and illustrations are sufficient to indicate that this is a species of *Aporocera*]

Type species : *Melinobius longipes* Jacoby, by original designation and monotypy.

†***acenteta*** Lea 1904 : 434-5 (*Loxopleurus*; Huon River); Clavareau 1913 : 124; Britton and Stanbury 1980 : 244; **comb. nov.**

†***aciculata*** Chapuis 1875 : 92 (*Cryptocephalus*; Carpentaria); Masters 1887 : 582; Lea 1904 : 338, 370; Clavareau 1913 : 127; **comb. nov.**

†***aegra*** Chapuis 1875 : 96-7 (*Cryptocephalus*; Swan River); Masters 1887 : 583; Lea 1904 : 402; Clavareau 1913 : 128; Weise 1916 : 10 (*Schizosternus*); **comb. nov.**

†***aeneola*** Chapuis 1876 : 38 (*Loxopleurus*; Pine Mountain); Masters 1887 : 588; Lea 1904 : 434; Clavareau 1913 : 124; **comb. nov.**

†***albilinea*** Saunders 1843 : 67 (*Anodonta*, Van Diemen's Land); Saunders 1845 : 145 (*Idiocephala*); Suffrian 1859 : 104-7 (*Cryptocephalus*); Chapuis 1879 : 77; Masters 1887 : 583 (sen. syn. of *marginicollis* Saunders); Lea 1902 : 455; Lea 1904 : 377 (*Idiocephala*, sen. syn. of *marginicollis* Saunders); Clavareau 1913 : 202 (sen. syn. of *marginicollis* Saunders); **comb. nov.**

= *marginicollis* Saunders 1845 : 145 (New Holland); Masters 1887 : 583 (jun. syn. of *albilinea* Saunders); Lea 1904 : 377 (jun. syn. of *albilinea* Saunders); Clavareau 1913 : 202 (jun. syn. of *albilinea* Saunders);

†***albogularis*** Chapuis 1876 : 44-5 (type species of *Schizosternus*; New Holland); Masters 1887 : 588; Lea 1904 : 387 (sen. syn. of *Paracephala pectoralis* Baly); Clavareau 1913 : 126 (sen. syn. of *pectoralis* Baly); **comb. nov.**

= †*coccineus* Chapuis 1879 : 79 (*Schizosternus*; Gayndah); Masters 1887 : 588; Lea 1904 : 386-7, 427; Clavareau 1913 : 126; Jolivet 1957 : 94 (wing venation); **syn. nov.**

= †*delicatulus* Lea 1904 : 426-7 (*Schizosternus*; Gayndah, Rockhampton); Clavareau 1913 : 126; Britton and Stanbury 1980 : 256; **syn. nov.**

= †*filum* sensu Lea 1904 *nec* Chapuis 1875

= *pectoralis* Baly 1877 : 223-4 (type species of *Paracephala*; Cape York); Masters 1887 : 587; Lea 1904 : 370, 387 (jun. syn. of *Schizosternus albogularis* Chapuis); Clavareau 1913 : 126 (jun. syn. of *albogularis* Chapuis); [the dorsum of *albogularis* is variably coloured, including an entirely red form (*delicatulus*) and one with large yellow maculae (*coccineus*)]

†***albopictus*** Lea 1915 : 693 (*Cryptocephalus*; Portland); **comb. nov.**

†***antennalis*** Chapuis 1875 : 96 (*Cryptocephalus*, *attennalis* [sic], Wide Bay); Masters 1887 : 583 (*antennalis*); Lea 1904 : 367-8; Clavareau 1913 : 130; **comb. nov.**

antennata Baly 1876 : 460-1 (*Rhombosternus*; north-west Australia); Masters 1887 : 588; Lea 1904 : 381; Clavareau 1913 : 126; **comb. nov.**

†***apicalis*** Saunders 1842 : 69 (*Aporocera*; New South Wales); Saunders 1845 : 150, plate 9, fig. 4; Baly 1877 : 28 (type sp. of *Aporocera*); Masters 1887 : 587; Blackburn 1888 : 1474-5; Lea 1904 : 336, 382-3, 424; Clavareau 1913 : 204; Jolivet 1957 : 96 (wing venation)

= *bicolor* Saunders 1842 : 69 (New South Wales); Saunders 1845 : 149-150, plate 9, fig. 3; Baly 1877 : 28; Masters 1887 : 587; Lea 1904 : 336, 383, 424; Clavareau 1913 : 204; **syn. nov.** [this is a colour form of the variable species *apicalis*]

†***apicirufa*** Lea 1904 : 453 (*Cadmus*; South Australia); Clavareau 1913 : 205; Britton and Stanbury 1980 : 247; **comb. nov.**

†***appendiculata*** Lea 1904 : 393-4 (*Cryptocephalus*; Lane Cove, Clifton); Lea 1904 : 341; Clavareau 1913 : 130; Britton and Stanbury 1980 : 247; **comb. nov.**

†***argentata*** Chapuis 1875 : 92 (*Cryptocephalus*; Pine Mountain); Masters 1887 : 583; Lea 1904 : 370-1, 393 (sen. syn. of *Idicephala bella* Baly); Clavareau 1913 : 131 (sen. syn. of *bella* Baly); Hawkeswood 1985 : 164 (host); **comb. nov.**

= *bella* Baly 1877 : 225-6 (*Idiocephala*; Cape York); Masters 1887 : 583 (*Cryptocephalus*); Lea 1904 : 370-1 (jun. syn. of *Cryptocephalus argentatus* Chapuis); Clavareau 1913 : 131 (jun. syn. of *argentatus* Chapuis);

= †*fasciata* Weise 1923 : 21-2 (*Idiocephala*; Tambourine); **syn. nov.** [*argentatus* is widespread in north-eastern Australia and rather variable. There are several similar undescribed species. *Fasciata, bella* and *argentatus* are certainly synonymous.]

†***arrogans*** Chapuis 1875 : 99 (*Cadmus*; Adelaide, Sydney); Masters 1887 : 579; Clavareau 1913 : 205; **comb. nov.**

†***atra*** Saunders 1845 : 145-6 (*Idiocephala*, Van Diemen's Land); Masters 1887 : 583 (*Cryptocephalus*); Lea 1904 : 376 (sen. syn. of *Loxopleurus nigritus* Chapuis); Clavareau 1913 : 202 (sen. syn. of *nigritus* Chapuis); **comb. nov.**

= †*nigritus* Chapuis 1876 : 41 (*Loxopleurus*, Tasmania); Masters 1887 : 590; Lea 1904 : 376 (jun. syn. of *Idiocephala atra* Saunders); Clavareau 1913 : 202 (jun. syn. of *atra* Saunders);

†***atramentaria*** Chapuis 1876 : 41 (*Loxopleurus*; Sydney, Victoria); Masters 1887 : 589; Lea 1904 : 390, 437; Clavareau 1913 : 124; Goudie 1927 : 304; **comb. nov.**

†***attenuata*** Chapuis 1875 : 97 (*Cryptocephalus*; Australia); Masters 1887 : 583; Clavareau 1913 : 131; Weise 1916 : 10; **comb. nov.**

†***aurantiaca*** Chapuis 1875 : 98 (*Cadmus*; Sydney); Masters 1887 : 579; Lea 1904 : 358, 428; Clavareau 1913 : 205; **comb. nov.**

= †*monticola* Blackburn 1894 : 206 (*Rhombosternus*; Victorian Alps); Clavareau 1913 : 126; **syn. nov.**

auriculata Suffrian 1859 : 129-131 (*Loxopleurus*; Australia); Masters 1887 : 589; Lea 1904 : 388; Clavareau 1913 : 124; Goudie 1927 : 304; **comb. nov.**

aurifera Lea 1904 : 398 (*Cryptocephalus*; Sydney); Britton and Stanbury 1980 : 248; **comb. nov.**

†***australis*** Saunders 1843 : 59 (*Ochrosopsis*; Swan River); Saunders 1845 : 152, plate 9, fig. 6; Masters 1887 : 583 (*Cryptocephalus*); Lea 1904 : 348, 380; Clavareau 1913 : 204; **comb. nov.**

= †*erosa* Saunders 1843 : 59 (*Ochrosopsis*; Swan River); Saunders 1845 : 153; Masters 1887 : 584 (*Cryptocephalus*); Lea 1902 : 455; (*Cryptocephalus*); Lea 1904 : 380 (*Ochrosopsis*, *erosus* [sic] Saunders); Clavareau 1913 : 204; Goudie 1927 : 304 (*Cryptocephalus*); **syn. nov.** [this is the ♂ of *australis*]

= †*larinus* Lea 1904 : 404-5 (*Cryptocephalus*; Brisbane, Hunter River, Inverell, Armidale); Lea 1904 : 335, 407; Clavareau 1913 : 159; Britton and Stanbury 1980 : 267; **syn. nov.**

basizonis Lea 1904 : 414-5 (*Cryptocephalus*; Cairns); Clavareau 1913 : 132; Britton and Stanbury 1980 : 249; Weise 1923 : 20-1 (*Idiocephala*); **comb. nov.**

bellicosa Chapuis 1875 : 95 (*Cryptocephalus*; Melbourne); Chapuis 1879 : 77; Masters 1887 : 583; Clavareau 1913 : 133; Weise 1916 : 10; **comb. nov.**

****biformis*** Bryant 1949 : 926-8 (*Mitocera*; New Guinea); Bryant 1949 : 923; Gressitt 1965 : 417-9 (*Cryptocephalus*, subg. *Mitocera*); **comb. nov.**

†***bihamata*** Chapuis 1875 : 94 (*Cryptocephalus*; Pine Mountain, Brisbane); Chapuis 1879 : 77; Masters 1887 : 583; Lea 1904 : 411-2; Clavareau 1913 : 134; **comb. nov.**

†***blanda*** Lea 1904 : 395-6 (*Cryptocephalus*; Swan River, Pinjarrah, Darling Range); Clavareau 1913 : 136; **comb. nov.**

****brassi*** Gressitt 1965 : 417-8 (*Cryptocephalus*, subg. *Mitocera*; New Guinea); **comb. nov.**

bynoei Saunders 1845 : 146 (*Idiocephala*; New Holland); Masters 1887 : 583 (*Cryptocephalus*); Lea 1904 : 346 (*Cryptocephalus*), 373-4 (*Idiocephala*, host, sen. syn. of *Cryptocephalus convexicollis* Chapuis), 416; Clavareau 1913 : 202 (sen. syn. of *convexicollis* Chapuis); **comb. nov.**

= †*convexicollis* Chapuis 1875 : 91 (*Cryptocephalus*; Brisbane, Swan River, Rockhampton); Lea 1904 : 374 (jun. syn. of *Idiocephala bynoei* Saunders); Clavareau 1913 : 202 (jun. syn. of *bynoei* Saunders); [this synonymy is accepted here although the type of *bynoei* is missing and more than one species fits the description of it]

†***cariniventris*** Lea 1904 : 405 (*Cryptocephalus*; Brisbane); Lea 1904 : 335; Clavareau 1913 : 137; **comb. nov.**

†***carnifex*** Suffrian 1859 : 93-8 (*Cryptocephalus*; Australia); Masters 1887 : 583; Lea 1904 : 361 (jun. syn. of *haematodes* Boisduval); Clavareau 1913 : 153 (jun. syn. of *haematodes* Boisduval); Goudie 1927 : 303; **comb. nov. and stat. rev.** [the surface sculpture and aedeagi of *carnifex* Suffrian and *haematodes* Boisduval (sensu auctt.) are quite different].

†***casta*** Suffrian 1859 : 120-3 (*Cryptocephalus*; Western Australia); Masters 1887 : 583; Lea 1904 : 364; Clavareau 1913 : 138; Goudie 1927 : 303; **comb. nov.**

catoxantha Saunders 1845 : 150-1 (Port Essington); Baly 1877 : 28, 31 (Idiocephala), 31; Baly 1877 : 225; Masters 1887 : 588 (*Aporocera*); Blackburn 1888 : 1472-3 (*Idiocephala*); Lea 1904 : 338, 372; Clavareau 1913 : 202;

†***chalcea*** Chapuis 1876 : 40 (*Loxopleurus*; Australia); Masters 1887 : 589; Lea 1904 : 330, 391; Clavareau 1913 : 124; **comb. nov.**

chalybea Saunders 1843 : 59 (Port Essington); Saunders 1845 : 150; Baly 1877 : 28; Masters 1887 : 588; Lea 1904 : 424; Clavareau 1913 : 204

chlamydiformis Germar 1848 : 241 (*Cadmus*; Adelaide); Suffrian 1859 : 81-5; Baly 1877 : 26 (type-sp. of *Cyphodera*); Chapuis 1879 : 78 (*Cadmus*); Masters 1887 : 582 (*Cyphodera*); Lea 1904 : 386 (*Cyphodera*); Clavareau 1913 : 208 (*Cadmus*); Jolivet 1957 : 97 (wing venation); **comb. nov.**

chrysomelina Chapuis 1875 : 90 (*Cryptocephalus*; Port Denison); Baly 1877 : 31 (*Idiocephala*); Chapuis 1879 : 77 (*Cryptocephalus*); Masters 1887 : 584; Lea 1904 : 368-9; Clavareau 1913 : 138; Weise 1923 : 16 (*Idiocephala*); Hawkeswood 1988 : 96 (*Cryptocephalus*; host); **comb. nov.**

†***cicatricosa*** Chapuis 1875 : 102 (*Rhombosternus*; Adelaide); Masters 1887 : 588; Blackburn 1894 : 207; Lea 1904 : 450; Clavareau 1913 : 126; **comb. nov.**

= †*calomeloides* Lea 1904 : 450 (*Cadmus*; Victoria, South Australia, Gunning); Clavareau 1913 : 205; Britton and Stanbury 1980 : 251; **syn. nov.**

†***clara*** Lea 1904 : 399-400 (*Cryptocephalus*; north-west Australia); Lea 1904 : 341; Clavareau 1913 : 139; Britton and Stanbury 1980 : 252; **comb. nov.**

†***clavicornis*** Chapuis 1875 : 96 (*Cryptocephalus*; Sydney); Masters 1887 : 584; Lea 1904 : 365; Clavareau 1913 : 139; **comb. nov.**

†***coelestis*** Lea 1904 : 423-4 (*Cryptocephalus*; Gisborne); Clavareau 1913 : 139; Lea 1915 : 693; **comb. nov.**

†***collaris*** Chapuis 1876 : 39 (*Loxopleurus*; New Holland); Chapuis 1879 : 79; Masters 1887 : 589; Clavareau 1913 : 124; **comb. nov.**

composita Lea 1904 : 397 (*Cryptocephalus*; Gayndah); Clavareau 1913 : 140; Britton and Stanbury 1980 : 253; **comb. nov.**

†***compta*** Lea 1904 : 415-6 (*Cryptocephalus*; South Australia); Clavareau 1913 : 140; Goudie 1927 : 303; Britton and Stanbury 1980 : 253; **comb. nov.**

†***confinis*** Lea 1904 : 392 (*Cryptocephalus*; Jenolan); Lea 1904 : 340, 396; Clavareau 1913 : 140; **comb. nov.**

†***conjugata*** Chapuis 1875 : 96 (*Cryptocephalus*; Port Denison); Lea 1904 : 333, 340, 367-8, 403, 408; Clavareau 1913 : 140; Hawkeswood 1988 : 96 (host); **comb. nov.**

†***conjugata*** Chapuis 1876 : 39 (*Loxopleurus*; Sydney); Chapuis 1879 : 79; Masters 1887 : 589; Lea 1904 : 371, 391, 436; Clavareau 1913 : 124; **comb. nov.**

consors Boisduval 1835 : 588-9 (*Cryptocephalus*; Hobart); Suffrian 1859 : 101-3 (sen. syn. of *Idiocephala roei* Saunders); Masters 1887 : 584 (sen. syn. of *roei* Saunders); Blackburn 1891 : 139-140; Lea 1902 : 455; Lea 1904 : 343, 359-360, 363-4 (sen. syn. of *tricolor* Fabricius, *Idiocephala roei* Saunders, *I. atripennis* Saunders, *I. elegans* Saunders, *Loxopleurus plagicollis* Chapuis), 430; Clavareau 1913 : 140 (sen. syn. of *atripennis* Saunders, *elegans* Saunders, *plagicollis* Chapuis and *roei* Saunders); **comb. nov.**

= *elegans* Saunders 1845 : 143-4, plate 9 fig. 2 (*Idiocephala*; Hunter's River);] Suffrian 1859 : 103-4 (*Cryptocephalus*); Baly 1877 : 224 (*Euphyma*); Masters 1887 : 586 (sen. syn. of *axillaris* Stürm); Lea 1904 : 331 (*Cryptocephalus*, sen. syn. of *axillaris* Sturm), 363 (jun. syn. of *Cryptocephalus consors* Boisduval); Clavareau 1913 : 141 (jun. syn. of *consors*);

= †*roei* Saunders 1843 : 67 (*Anodonta*; Swan River); Saunders 1845 : 143 (*Idiocephala*); Masters 1887 : 584 (jun. syn. of *consors* Boisduval); Lea 1904 : 363 (jun. syn. of *Cryptocephalus consors* Boisduval); Clavareau 1913 : 141 (jun. syn. of *consors*);

= †*roei* var. *atripennis* Saunders 1843 : 67 (*Anodonta*; no locality); Saunders 1845 : 143 (*Idiocephala*); Lea 1904 : 333, 363 (jun. syn. of *Cryptocephalus consors* Boisduval); Clavareau 1913 : 141 (jun. syn. of *consors*);

= [*axillaris* Stürm; Suffrian 1859 : 104 (*nom. nud.*); Masters 1887 : 587 (*Euphyma*, jun. syn. of *elegans* Saunders); Lea 1904 : 331 (jun. syn. of *elegans* Saunders)

= †*plagicollis* Chapuis 1876 : 38 (*Loxopleurus*; Cape Shank); Masters 1887 : 590; Lea 1904 : 363 (jun. syn. of *Cryptocephalus consors* Boisduval); Clavareau 1913 : 141 (jun. syn. of *consors*);

= *tricolor* sensu Lea 1904, nec Fabricius 1801

†***conspicienda*** Lea 1904 : 413 (*Cryptocephalus*; New South Wales, Jindabyne, Sydney); Clavareau 1913 : 141; Britton and Stanbury 1980 : 253; **comb. nov.**

†***contigua*** Lea 1904 : 442-3 (*Loxopleurus*; Swan River, Darling Ranges); Lea 1904 : 343; Clavareau 1913 : 124; **comb. nov.**

†***convexicollis*** Lea 1904 : 421-2 (*Cryptocephalus*; Berrima, Bungendore, Queanbeyan); Masters 1887 : 584; Clavareau 1913 : 141; Britton and Stanbury 1980 : 253; **comb. nov.**

†***crassicornis*** Chapuis 1875 : 95-6 (*Cryptocephalus*; New Holland); Masters 1887 : 584; Lea 1904 : 331, 428-9 (*Schizosternus*); Clavareau 1913 : 126; Weise 1916 : 10-11; **comb. nov.**

cyanipennis Saunders 1843 : 67 (*Anodonta*; New Holland); Saunders 1845 : 144-5 (*Idiocephala*); Chapuis 1875 : 93 (*Cryptocephalus*); Chapuis 1879 : 77; Masters 1887 : 584; Lea 1904 : 342 (*Cryptocephalus*), 374-6 (*Idiocephala*, sen. syn. of *Cryptocephalus condensatus* Chapuis), 392, 395-6; Clavareau 1913 : 202 (sen. syn. of *I. condensata* Suffrian); Weise 1923 : 20; **comb. nov.**

= *condensatus* Suffrian 1859 : 118-120 (*Cryptocephalus*; Port Philip); Chapuis 1875 : 92; Baly 1877 : 31 (*Idiocephala*); Lea 1904 : 374-5 (jun. syn. of *cyanipennis* Saunders); Clavareau 1913 : 203 (jun. syn. of *cyanipennis* Saunders);

†***cyanophanus*** Chapuis 1879 : 78 (*Cryptocephalus*; Gayndah); Masters 1887 : 584; Clavareau 1913 : 144; **comb. nov.**

†***daemoniaca*** Suffrian 1859 : 133-5 (*Loxopleurus*; Australia); Chapuis 1879 : 79; Masters 1887 : 589; Clavareau 1913 : 124; **comb. nov.**

darwinii Saunders 1843 : 317 (*Idiocephala*; Sydney); Saunders 1845 : 148-9; Masters 1887 : 589 (*Loxopleurus*, sen. syn. of *subbrunneus* Saunders); Lea 1904 : 373; Clavareau 1913 : 126 (sen. syn. of *subbrunneus* Saunders); **comb. nov.**

†***dichroa*** Chapuis 1875 : 93 (*Cryptocephalus*; Port Denison, Sydney); Masters 1887 : 584; Lea 1904 : 371-2, 395; Clavareau 1913 : 145; Hawkeswood 1985 : 164; **comb. nov.**

†***difficilis*** Chapuis 1876 : 39-40 (*Loxopleurus*; Sydney); Masters 1887 : 589; Clavareau 1913 : 124; **comb. nov.**

discoidea Chapuis 1879 : 77-8 (*Cryptocephalus*; Peak Downs); Masters 1887 : 584; Clavareau 1913 : 146; **comb. nov.**

†***disconigra*** Lea 1904 : 445-6 (*Loxopleurus*; Sydney, South Australia); Clavareau 1913 : 124; **comb. nov.**

****discrepans*** Baly 1865 : 73-4 (*Cryptocephalus*; Morty Island); **comb. nov.**

†***distorta*** Lea 1904 : 410-1 (*Cryptocephalus*; Brisbane); Lea 1904 : 336, 345; Clavareau 1913 : 146; Britton and Stanbury 1980 : 256; **comb. nov.**

†***dolens*** Lea 1904 : 436-7 (*Loxopleurus*; Swan River); Clavareau 1913 : 124; **comb. nov.**

†***erudita*** Baly 1877 : 30 (*Cryptocephalus*; South Australia); Masters 1887 : 584; Lea 1904 : 380-1, 400 (*Cryptocephalus*); Clavareau 1913 : 204 (*Ochrosopsis*); Goudie 1927 : 304 (*Cryptocephalus*); **comb. nov.**

†***erythrotis*** Chapuis 1876 : 38-9 (*Loxopleurus*; Swan River); Masters 1887 : 589; Lea 1904 : 390-1; Clavareau 1913 : 125; **comb. nov.**

†***eumolpus*** Chapuis 1875 : 90-1 (*Cryptocephalus*; Port Denison); Chapuis 1876 : 345; Baly 1877 : 31 (*Idiocephala*); Masters 1887 : 585 (*Cryptocephalus*, *eumolphus* [sic]); Lea 1904 : 365 (*Cryptocephalus*); Clavareau 1913 : 148; Weise 1923 : 17 (*Idiocephala*); Hawkeswood 1988 : 96-7 (*Cryptocephalus*; host); **comb. nov.**

facialis Chapuis 1879 : 78 (*Cryptocephalus*; Gayndah); Masters 1887 : 585 (*fascialis* [sic]); Lea 1904 : 367; **comb. nov.**

†***fasciaticollis*** Lea 1904 : 452 (*Cadmus*; Mount Wellington); Clavareau 1913 : 206; Lea 1920 : 382; **comb. nov.**

†***filum*** Chapuis 1875 : 95 (*Cryptocephalus*; Adelaide); Baly 1877 : 223 (Paracephala); Masters 1887 : 587; Lea 1904 : 335, 370 (jun. syn. of *Schizosternus albogularis* Chapuis); Clavareau 1913 : 126; **comb. nov.**

†***flaviventris*** Saunders 1843 : 67 (*Anodonta*; New Holland); Saunders 1845 : 147 (*Idiocephala*, *flaventris* [sic]); Suffrian 1859 : 123-5 (*Cryptocephalus*); Baly 1877 : 31; Baly 1877 : 224 (*Euphyma*); Chapuis 1879 : 77 (*Cryptocephalus*); Masters 1887 : 586 (*Euphyma*); Lea 1904 : 336, 369, 377 (*Idiocephala*); Clavareau 1913 : 203; Weise 1923 : 21; **comb. nov.**

*†***fratercula*** Chapuis 1875 : 91 (*Cryptocephalus*; Fiji); Baly 1877 : 31 (*Idiocephala*, *fraternalis* [sic]); Bryant and Gressitt 1957 : 18 (*Cryptocephalus*); **comb. nov.**

****fulvofasciata*** Jacoby 1884 : 194-5 (*Cryptocephalus*; New Guinea); Gressitt 1965 : 417, fig. 13 (*Cryptocephalus*, subg. *Mitocera*); **comb. nov.**

†***fuscitarsis*** Lea 1904 : 441-2 (*Loxopleurus*; Western Australia, Swan River, Pinjarrah); Lea 1904 : 345; Clavareau 1913 : 125; **comb. nov.**

†***genialis*** Chapuis 1876 : 42 (*Loxopleurus*; Port Denison); Masters 1887 : 589; Lea 1904 : 330, 391; Clavareau 1913 : 125; **comb. nov.**

†***gibba*** Chapuis 1876 : 41 (*Loxopleurus*; Australia); Masters 1887 : 590; Lea 1904 : 432; Clavareau 1913 : 125; **comb. nov.**

= †*lugubris* Lea 1904 : 431-2 (*Loxopleurus*; Kiama, Sydney, Forest Reefs); Lea 1904 : 439; Clavareau 1913 : 125; Britton and Stanbury 1980 : 268; **syn. nov.**

†***gracilicornis*** Baly 1876 : 461-2 (*Rhombosternus*; Western Australia); Masters 1887 : 588; Clavareau 1913 : 126; **comb. nov.**

†***gracilior*** Chapuis 1875 : 91 (*Cryptocephalus*, Pine Mountain); Baly 1877 : 31 (*Idiocephala*, *gracilis* [sic]); Masters 1887 : 585 (*Cryptocephalus*); Lea 1904 : 368

(*Cryptocephalus*); Clavareau 1913 : 152; Weise 1923 : 17 (*Idiocephala*); Hawkeswood 1988 : 97 (*Cryptocephalus*; host); **comb. nov.**

†***gravata*** Chapuis 1876 : 41 (*Loxopleurus*, Brisbane); Chapuis 1879 : 79; Masters 1887 : 590; Lea 1904 : 349, 389; Clavareau 1913 : 125; Weise 1923 : 21 (*Idiocephala*); **comb. nov.**

haematodes Boisduval 1835 : 586-7 (*Cryptocephalus*; New Holland); Saunders 1842 : 70 (type species of *Dicenopsis*); Saunders 1845 : 142, plate 9, fig. 1; Suffrian 1859 : 93 (*Cryptocephalus*); Masters 1887 : 585; Lea 1902 : 455; Lea 1904 :361 (sen. syn. of *carnifex* Suffrian); Clavareau 1913 : 153 (sen. syn. of *carnifex* Suffrian); Goudie 1927 : 303; **comb. nov.**

hispida Chapuis 1879 : 77 (*Cryptocephalus*; Gayndah); Masters 1887 : 585; Clavareau 1913 : 154; **comb. nov.**

†***immatura*** Lea 1904 : 444-5 (*Loxopleurus*; Swan River, Pinjarrah); Clavareau 1913 : 125; **comb. nov.**

†***impressifrons*** Weise 1923 : 18-19 (*Idiocephala*, Atherton, Herberton, Cedar Creek); **comb. nov.**

†***inconstans*** Lea 1904 : 440-1 (*Loxopleurus*; South Australia); Clavareau 1913 : 125; **comb. nov.**

†***iridipennis*** Chapuis 1876 : 344-5 (*Cryptocephalus*; Sydney, Victoria); Masters 1887 : 585; Blackburn 1893 : 140 (*iridiventris* [sic], sen. syn. of *Idiocephala chapuisi* Baly); Lea 1904 : 369, 400; Clavareau 1913 : 157 (sen. syn. of *chapuisi* Baly); Brooks 1965 : 29 (host); Hawkeswood 1988 : 97-8 (host); **comb. nov.**

= *chapuisii* Baly 1877 : 224-5 (*Idiocephala*; Rockhampton); Masters 1887 : 584 (*Cryptocephalus*); Blackburn 1893 : 140 (*chapuisi* [sic], jun. syn. of *Cryptocephalus iridiventris* [sic] Chapuis); Lea 1904 : 369; Clavareau 1913 : 157 (*chapuisi* [sic], jun. syn. of *iridipennis* Chapuis);

= †*decens* Weise 1923 : 17-18 (*Idiocephala*; Tambourine, Colosseum); **syn. nov.** [the body in *iridipennis* varies from entirely metallic green to almost entirely reddish-yellow; this range encompasses *decens*]

jacksoni Guerin-Meneville, in Duperrey 1838 : 143-4 (*Cryptocephalus*; Port Jackson); Chapuis 1879 : 78; Masters 1887 : 585; Lea 1902 : 455; Lea 1904 : 337, 360, 365; Clavareau 1913 : 157; **comb. nov.**

jenolanensis Clavareau 1913 : 157 (nom. nov. pro *costipennis* Lea 1904, *nec* Duvivier 1891); **comb. nov.**

= †*costipennis* Lea 1904 : 424-5 (*Cryptocephalus*; Jenolan); Clavareau 1913 : 157 (preoc. by *costipennis* Duvivier 1891, = *jenolanensis* Clavareau);

jocosa Chapuis 1875 : 95 (*Cryptocephalus*; Victoria); Masters 1887 : 585; Lea 1904 :369 (sen. syn. of *Loxopleurus postremus* Chapuis, *Rhombosternus pretiosus*

Baly), 435; Clavareau 1913 : 158 (sen. syn. of *postremus* Chapuis and *pretiosus* Baly); **comb. nov.**

= †*postremus* Chapuis 1876 : 38 (*Loxopleurus*; Victoria); Masters 1887 : 590; Lea 1904 : 369 (jun. syn. of *Cryptocephalus jocosus* Chapuis); Clavareau 1913 : 157 (jun. syn. of *jocosus* Chapuis);

= †*pretiosus* Baly 1877 : 226-7 (*Rhombosternus*; Australia); Masters 1887 : 588; Lea 1904 : 369 (jun. syn. of *Cryptocephalus jocosus* Chapuis); Clavareau 1913 : 157 (jun. syn. of *jocosus* Chapuis);

****laeta*** Baly 1865 : 77-8 (*Loxopleurus*; Kai Island, Batchian); Jacoby 1884 : 195; Clavareau 1913 : 125; **comb. nov.**

†***laeviuscula*** Chapuis 1876 : 42 (*Loxopleurus*; Australia); Masters 1887 : 590; Lea 1904 : 391; Clavareau 1913 : 125; **comb. nov.**

lagopus Weise 1913 : 219 (*Cryptocephalus*, nom. nov. for *tricolor* Fabricius 1801 *nec* Rossi 1792); Clavareau 1913 : 159 (sen. syn. of *tricolor* F. *nec* Rossi); **comb. nov.**

= †*tricolor* Fabricius 1801 : 51 (*Cryptocephalus*; New Cambria), nec Rossi 1792; Masters 1887 : 587 (*Mitocera*); Lea 1904 : 343, 359-360, 363 (*Cryptocephalus*, sen. syn. of *consors* Boisduval), 430; Weise 1913 : 219 (preoc. name, replaced by *lagopus* Weise); Clavareau 1913 : 159 (jun. syn. of *lagopus* Weise) [the replacement name is valid according to ICZN Art 59b, although *tricolor* F. is no longer placed in *Cryptocephalus*]

†***lateriflava*** Lea 1904 : 430 (*Loxopleurus*; Swan River, Karridale); Clavareau 1913 : 125; **comb. nov.**

†***libertina*** Suffrian 1859 : 127-9 (*Loxopleurus*; Australia); Masters 1887 : 590; Clavareau 1913 : 125; Jolivet 1957 : 93 (wing venation); **comb. nov.**

= †*castor* Lea 1904 : 435 (*Loxopleurus*; South Australia, Swan River); Lea 1904 : 433, 436; Clavareau 1913 : 124; **syn. nov.**

†***lilliputana*** Lea 1904 : 409 (*Cryptocephalus*; Huon River); **comb. nov.**

****longipes*** Jacoby 1908 : 270 (*Melinobius*; Tenasserim); Clavareau 1913 : 202; **comb. nov.**

****maai*** Gressitt 1965 : 409-410 (*Cryptocephalus*, New Guinea); **comb. nov.**

†***marginipennis*** Lea 1904 : 438-9 (*Loxopleurus*; Mosmans Bay, Sydney); Clavareau 1913 : 125; **comb. nov.**

†***marmorata*** Lea 1904 : 427-8 (*Schizosternus*; South Australia); Clavareau 1913 : 126; Britton and Stanbury 1980 : 270; **comb. nov.**

†***mediocris*** Lea 1904 : 392-3 (*Cryptocephalus*; Endeavour River, Mackay); Clavareau 1913 : 164; Weise 1923 : 22 (*Idiocephala*); Britton and Stanbury 1980 : 271; **comb. nov.**

†***melanocephala*** Saunders 1843 : 59 (*Ochrosopsis*; New Holland); Saunders 1845 : 153; Suffrian 1859 : 107-9 (*Cryptocephalus*); Masters 1887 : 585; Lea 1902 : 455 (var. of *subfasciatus* Saunders); Lea 1904 : 378-9 (*Ochrosopsis*, *melanocephalus* [sic] Saunders, jun. [sic] syn. of *subfasciata* Saunders); Clavareau 1913 : 204 (sen. syn. of *subfasciatus* Saunders); **comb. nov.**

mercator Suffrian 1859 : 99-101 (*Cryptocephalus*; Australia); Lea 1904 : 333; Clavareau 1913 : 164; **comb. nov.**

†***microscopica*** Lea 1904 : 437-8 (*Loxopleurus*; Western Australia); Clavareau 1913 : 125; Britton and Stanbury 1980 : 272; **comb. nov.**

†***mitifica*** Lea 1904 : 436 (*Loxopleurus*; Newcastle, Gosford); Clavareau 1913 : 125; Britton and Stanbury 1980 : 273; **comb. nov.**

†***mixta*** Lea 1904 : 433-4 (*Loxopleurus*; King George Sound, Karridale, Vasse, Swan River, Geraldton); Clavareau 1913 : 125; Weise 1916 : 9; Britton and Stanbury 1980 : 273; **comb. nov.**

†***nigripennis*** Baly 1876 : 459 (*Idiocephala*; Rockhampton); Masters 1887 : 585 (*Cryptocephalus*); Lea 1904 : 341, 377, 393, 395 (*Idiocephala*); Clavareau 1913 : 203; Weise 1923 : 22; **comb. nov.**

†***nigrolineata*** Chapuis 1876 : 44 (*Loxopleurus*; Pine Mountain); Lea 1904 : 333; Clavareau 1913 : 125; **comb. nov.**

= †*castigatus* Lea 1904 : 439-440 (*Loxopleurus*; Sydney); Clavareau 1913 : 124; Britton and Stanbury 1980 : 252; **syn. nov.**

†***obscura*** Blackburn 1894 : 205-6 (*Rhombosternus*; Blue Mountains); Clavareau 1913 : 126; **comb. nov.**

†***obtusa*** Chapuis 1876 : 42 (*Loxopleurus*; Swan River); Masters 1887 : 590; Lea 1904 : 389, 395, 432, 437; Weise 1908 : 1; Clavareau 1913 : 125; **comb. nov.**

†***ornatipennis*** Lea 1904 : 422-3 (*Cryptocephalus*; Queensland, Endeavour River, Thursday Island); Clavareau 1913 : 170; **comb. nov.**

†***ornata*** Chapuis 1875 : 98 (*Cadmus*; Brisbane, Wide Bay); Masters 1887 : 581; Lea 1904 : 346, 356-7, 410, 414; Clavareau 1913 : 206; Goudie 1927 : 303; **comb. nov.**

†***pallens*** Lea 1904 : 408 (*Cryptocephalus*; South Australia); Clavareau 1913 : 170; Britton and Stanbury 1980 : 277; **comb. nov.**

†***pallidipes*** Lea 1904 : 431 (*Cryptocephalus*; *Loxopleurus*; Geraldton, Swan River); Clavareau 1913 : 125; **comb. nov.**

pallida Blackburn 1894 : 206-7 (*Rhombosternus*; Blue Mountains); Clavareau 1913 : 126; **comb. nov.**

†***palmerstoni*** Blackburn 1888 : 1473-4 (*Idiocephala*; Northern Territory); Clavareau 1913 : 203; **comb. nov.**

parens Clavareau 1913 : 171 (nom. nov. pro *sobrinus* Lea 1904, nec Jacoby 1904); **comb. nov.**

= †*sobrinus* Lea 1904 : 407 (*Cryptocephalus*; Queensland); Clavareau 1913 : 171 (preoc. by *sobrinus* Jacoby 1904, = *parens* Clavareau); Lea 1918 : 83 (valid name);

parenthetica Suffrian 1859 : 96-8 (*Cryptocephalus*; Australia); Chapuis 1879 : 77; Masters 1887 : 585; Lea 1904 : 338, 364, 400, 418; Clavareau 1913 : 171; Weise 1923 : 16 (*Idiocephala*); Shepard, Lawn and Schneider 1983 : 12 (host) [misdet.]; **comb. nov.**

= †*melanopa* Lea 1904 : 400 (*Cryptocephalus*; north-west Australia); Clavareau 1913 : 164; Weise 1916 : 9-10 (*Idiocephala*, var. of *parenthetica* Suffrian); Britton and Stanbury 1980 : 272; **syn. nov.**

†***paupercula*** Germar 1848 : 241-2 (*Cadmus*; Adelaide); Suffrian 1859 : 135-7 (*Loxopleurus*); Masters 1887 : 590; Lea 1904 : 358-9 (*Cadmus*); Clavareau 1913 : 172 (*Cryptocephalus*); **comb. nov.**

= †*rufescens* Boheman 1859 : 161 (*Loxopleurus*; Sydney, Malacca); Suffrian 1859 : 137-9; Baly 1865 : 77; Chapuis 1879 : 79; Masters 1887 : 591; Clavareau 1913 : 125; **syn. nov.**

pectoralis Chapuis 1879 : 79 (*Loxopleurus*; Rockhampton); Masters 1887 : 590; Clavareau 1913 : 125; **comb. nov.**

perparva Clavareau 1913 : 173 (nom. nov. pro *minusculus* Lea 1904, nec Fairmaire 1901); **comb. nov.**

= †*minusculus* Lea 1904 : 416-7 (*Cryptocephalus*; South Australia); Clavareau 1913 : 173 (preoc. by *minusculus* Fairmaire 1901, = *perparvus* Clavareau); Britton and Stanbury 1980 : 272;

†***piceitarsis*** Chapuis 1876 : 39 (*Loxopleurus*; Sydney); Masters 1887 : 590; Lea 1904 : 349, 391, 432-3, 436; Clavareau 1913 : 125; **comb. nov.**

plaginota Chapuis 1879 : 79 (*Loxopleurus*; Rockhampton); Masters 1887 : 590; Clavareau 1913 : 125; **comb. nov.**

†***poecilodermis*** Chapuis 1875 : 95 (*Cryptocephalus*; Port Denison); Chapuis 1879 : 77; Masters 1887 : 586; Lea 1904 : 366-7, 405-7; Clavareau 1913 : 174; Goudie 1927 : 304; Gressitt 1965 : 419, figs 4, 14 (subg. *Ochrosopsis*, *poeciloderma* [sic]); **comb. nov.**

†***pollux*** Lea 1904 : 435-6 (*Loxopleurus*; Karoola, Frankford, Huon River, Mount Wellington, Mount Victoria); Lea 1904 : 433; Clavareau 1913 : 125; Goudie 1927 : 304; Britton and Stanbury 1980 : 280; **comb. nov.**

†***proxima*** Weise 1923 : 22 (*Idiocephala*, Colosseum); **comb. nov.**

****pulchra*** Gressitt 1965 : 418-9 (*Cryptocephalus*, subg. *Mitocera*; New Guinea); **comb. nov.**

†***pulchella*** Saunders 1843 : 67 (Anodonta; New Holland); Saunders 1845 : 144 (*Idiocephala*); Masters 1887 : 586; Lea 1904 : 342, 375-6, 395, 399; Clavareau 1913 : 203; **comb. nov.**

†***pulchella*** Baly 1877 : 29 (type sp. of *Chariderma*; Western Australia); Masters 1887 : 582; Lea 1904 : 385-6, 424; Clavareau 1913 : 203; Brooks 1965 : 29 (host); **comb. nov.**

†***pura*** Blackburn 1888 : 1473 (*Idiocephala*; Northern Territory); Clavareau 1913 : 203; Hawkeswood 1988 : 98 (*Cryptocephalus*; host); **comb. nov.**

†***purpureotincta*** Lea 1904 : 398-9 (*Cryptocephalus*; Queensland, Kurrajong, Richmond River); Clavareau 1913 : 176; Weise 1923 : 20 (*Idiocephala*); Britton and Stanbury 1980 : 281; **comb. nov.**

†***quadratipennis*** Lea 1904 : 396-7 (*Cryptocephalus*; Tambourine); Clavareau 1913 : 177; Lea 1915 : 694; **comb. nov.**

†***ringens*** Chapuis 1875 : 99 (*Cadmus*; Australia); Masters 1887 : 581; Clavareau 1913 : 207; **comb. nov.**

= †*clypealis* Lea 1904 : 402-3 (*Cryptocephalus*; Swan River); Clavareau 1913 : 139; **syn. nov.**

†***rubicunda*** Lea 1904 : 403 (*Cryptocephalus*; South Australia); Lea 1904 : 416; Clavareau 1913 : 180; Britton and Stanbury 1980 : 283; **comb. nov.**

†***rufescens*** Saunders 1845 : 154 (*Ochrosopsis*; Van Diemen's Land); Chapuis 1876 : 343 (sen. syn. of *Cadmus subsulcatus* Suffrian); Masters 1887 : 586 (sen. syn. of *subsulcatus* Suffrian); Lea 1902 : 455 (*Cryptocephalus*); Lea 1904 : 346, 379; Clavareau 1913 : 204 (*Ochrosopsis*, sen. syn. of *subsulcatus* Suffrian); **comb. nov.**

= *subsulcatus* Suffrian 1859 : 116-8 (*Cryptocephalus*; Australia); Chapuis 1876 : 343 (jun. syn. of *rufescens* Saunders); Masters 1887 : 586 (jun. syn. of *Ochrosopsis rufescens*); Clavareau 1913 : 204 (jun. syn. of *rufescens* Saunders);

†***rufoterminalis*** Lea 1904 : 412 (*Cryptocephalus*; Uralla, Yass); Lea 1904 : 345, 411; Britton and Stanbury 1980 : 284; **comb. nov.**

†***rutilans*** Lea 1904 : 403-4 (*Cryptocephalus*; South Australia); Clavareau 1913 : 180; Britton and Stanbury 1980 : 284; **comb. nov.**

salebrosa Guérin-Meneville, in Duperrey 1832 : 143 (*Cryptocephalus*; Port Jackson); Blackburn 1890 : 138 (*Prionopleura*); Masters 1887 : 581 (*Cadmus*); Lea 1904 : 361 (*Cryptocephalus*, ? var. of *crucicollis* Boisduval); Clavareau 1913 : 207 (*Cadmus*, jun. syn. of *rugicollis* Gray); **comb. nov.**

†***saundersi*** Chapuis 1875 : 102 (*Rhombosternus*; Sydney); Masters 1887 : 588; Clavareau 1913 : 126; **comb. nov.**

†***scabiosa*** Lea 1904 : 419-420 (*Cryptocephalus*; South Australia); Clavareau 1913 : 183; Goudie 1927 : 304; Britton and Stanbury 1980 : 284; **comb. nov.**

scabrosa Olivier 1807 : 807-8, plate 5 fig. 74 (*Cryptocephalus*; New Holland); Suffrian 1859 : 112-5 (sen. syn. of *Idiocephala rugosa* Saunders); Chapuis 1879 : 77; Masters 1887 : 586 (sen. syn. *rugosus* Saunders); Lea 1904 : 337, 360 (sen. syn. of *Idiocephala rugosa* Saunders, *I. similis* Saunders, *C. rugifrons* Chapuis, *C. eximius* Chapuis), 365, 398: Froggatt 1907 : 202; Clavareau 1913 : 183 (sen. syn. of *eximius* Chapuis, *rugifrons* Chapuis, *rugosus* Saunders and *similis* Saunders); Hawkeswood 1988 : 98 (host); **comb. nov.**

= †*eximius* Chapuis 1875 : 93 (*Cryptocephalus*; Brisbane); Chapuis 1879 : 77; Lea 1904 : 333, 360 (jun. syn. of *scabrosus* Olivier); Clavareau 1913 : 183 (jun. syn. *scabrosus* Olivier);

= †*rugifrons* Chapuis 1875 : 93 (*Cryptocephalus*; Adelaide); Chapuis 1879 : 77; Masters 1887 : 586; Lea 1904 : 360 (jun. syn. of *scabrosus* Olivier); Clavareau 1913 : 183 (jun. syn. *scabrosus* Olivier);

= †*rugosa* Saunders 1843 : 67 (*Anodonta*; New Holland); Saunders 1845 : 146 (*Idiocephala*); Baly 1877 : 31; Masters 1887 : 586 (jun. syn. of *scabrosus* Olivier); Lea 1904 : 360 (jun. syn. of *Cryptocephalus scabrosus* Olivier); Clavareau 1913 : 183 (jun. syn. *scabrosus* Olivier);

= *similis* Saunders 1843 : 317 (*Idiocephala*; Sydney); Saunders 1845 : 147; Suffrain 1859 : 115-6 (*Cryptocephalus*); Masters 1887 : 586; Lea 1904 : 360 (jun. syn. of *Cryptocephalus scabrosus* Olivier); Clavareau 1913 : 183 (jun. syn. *scabrosus* Olivier);

[*scabrosus* Olivier is a variable species or species-complex which requires further study. I follow traditional synonymy]

†***sculptilis*** Chapuis 1875 : 99-100 (*Cadmus*; Clarence River, Brisbane); Masters 1887 : 582; Lea 1904 : 346-7, 347, 354, 407; Clavareau 1913 : 207; Brooks 1965 : 29 (host); Hawkeswood 1988 : 98 (*Cryptocephalus sculptus* [sic]; host); **comb. nov.**

†***scutata*** Chapuis 1875 : 99 (*Cadmus*; Swan River); Masters 1887 : 582; Lea 1904 : 346, 355, 455; Clavareau 1913 : 207; Weise 1916 : 11-2 (*maculatus* [lapsus] Chapuis); **comb. nov.**

semibrunnea Saunders 1843 : 317 (*Idiocephala*; near Sydney); Saunders 1845 : 148 (*subbrunnea* [sic]); Chapuis 1879 : 79 (*Loxopleurus*, *subbrunnea* [sic]); Masters 1887 : 589 (*subbrunneus* [sic], jun. syn. of *darwini* Saunders); Lea 1904 : 373, 433-4 (*Idiocephala, subbrunnea* [sic]); Clavareau 1913 : 126 (jun. syn. of *darwini* Saunders), 203 (valid [!], *subbrunnea* [sic]); **comb. nov.**

†***semicostata*** Chapuis 1876 : 43-4 (*Loxopleurus*; Queensland); Chapuis 1879 : 79; Masters 1887 : 591; Lea 1904 : 346, 389-390; Clavareau 1913 : 125; **comb. nov.**

†***serena*** Lea 1904 : 418-9 (*Cryptocephalus*; Geraldton); Lea 1904 : 433; Clavareau 1913 : 185; **comb. nov.**

†***socia*** Weise 1923 : 19-20 (*Idiocephala*; Alice River); **comb. nov.**

speciosa Boisduval 1835 : 587-8 (*Cryptocephalus*, New Holland); Guérin-Meneville, in Duperrey 1838 : 143; Baly 1877 : 31 (*Idiocephala*); Chapuis 1879 : 77 (*Cryptocephalus, speciosus* Guérin [sic]); Masters 1887 : 586 (*speciosus* Guérin [sic]); Lea 1904 : 364; Clavareau 1913 : 187 (*speciosus* Guérin [sic]); Weise 1923 : 17 (*Idiocephala, speciosus* Guérin [sic]); **comb. nov.**

†***stenocera*** Lea 1904 : 406-7 (*Cryptocephalus*; Rockhampton); Clavareau 1913 : 188; Britton and Stanbury 1980 : 287; **comb. nov.**

†***stictica*** Suffrian 1859 : 109-112 (*Cryptocephalus*; Port Philip, Melbourne, Sydney, Australia); Masters 1887 : 586; Clavareau 1913 : 185; **comb. nov.**

= *erosus* sensu Lea nec Saunders

†***stratiotica*** Chapuis 1875 : 99 (*Cadmus*; Brisbane, Melbourne); Masters 1887 : 582; Lea 1904 : 345, 347 (*stratiotinctus* [sic] Chapuis), 354; Clavareau 1913 : 207; **comb. nov.**

†***sturmii*** Chapuis 1876 : 37-8 (*Loxopleurus*; Australia); Masters 1887 : 591; Lea 1904 : 409; Clavareau 1913 : 125 (*sturmi* [sic]); **comb. nov.**

†***subfasciata*** Saunders 1845 : 153-4 (*Ochrosopsis*; New Holland); Masters 1887 : 586 (*Cryptocephalus*); Lea 1902 : 455 (*Cryptocephalus*, includes var. *melanocephalus* Saunders); Lea 1904 : 348, 378-9 (*Ochrosopsis, subfasciatus* [sic] Saunders, sen. [sic] syn. of *melanocephala* Saunders); Clavareau 1913 : 204 (jun. syn. of *melanocephalus* [sic] Saunders); **comb. nov. and stat. rev.**

†***subvirens*** Chapuis 1876 : 42 (*Loxopleurus*; Victoria); Masters 1887 : 591; Lea 1904 : 349, 390, 431; Clavareau 1913 : 125; **comb. nov.**

sulphuripennis Baly 1876 : 459-460 (*Rhombosternus*; Adelaide); Chapuis 1874 : 188 [*sulfuripennis, nom. nud.*]; Chapuis 1876 : plate 116, fig. 5; Lea 1904 : 346, 381; Clavareau 1913 : 126 (*sulfuripennis* [sic]); Jolivet 1957 : 94 (wing venation); **comb. nov.**

*†***suspecta*** Baly 1865 : 73-4, plate 3, fig. 4 (*Cryptocephalus*; Sarawak, Tringanee); Bryant 1923 : 137 (*Melinobius*); **comb. nov.**

†***sutor*** Suffrian 1859 : 143-5 (*Rhombosternus*; Australia); Masters 1887 : 588; Blackburn 1894 : 208; Clavareau 1913 : 126; **comb. nov.**

= †*sartor* Suffrian 1859 : 145-7 (*Rhombosternus*; Australia); Masters 1887 : 588; Blackburn 1894 : 208; Clavareau 1913 : 126; **syn. nov.** [*sartor* is the ♀ of *sutor*]

tasmanica Saunders 1843 : 317 (*Idiocephala*; Van Diemen's Land); Saunders 1845 : 148; Masters 1887 : 591 (*Loxopleurus*); Lea 1902 : 455 (*Loxopleurus*); Lea 1904 : 343, 372-3 (*Idiocephala*, sen. syn. of *Loxopleurus crassicostatus* Chapuis); Clavareau 1913 : 203 (sen. syn. of *crassicostata* Chapuis, possibly *impressicollis* Boheman); **comb. nov.**

= †*impressicollis* Boheman 1859 : 160 (*Loxopleurus*; Sydney); Suffrian 1859 : 139-141; Masters 1887 : 590; Lea 1904 : 372-3; Clavareau 1913 : 203 (possibly jun. syn. of *tasmanica* Saunders); **syn. nov.**

= *Loxopleurus crassicostatus* sensu Lea *nec* Chapuis

†***tenebricosa*** Lea 1904 : 410 (*Cryptocephalus*; Ipswich); Clavareau 1913 : 190; Britton and Stanbury 1980 : 289; **comb. nov.**

terminalis Chapuis 1879 : 78 (*Cryptocephalus*; Gayndah); Masters 1887 : 586; Lea 1904 : 336, 342, 367, 403; Clavareau 1913 : 190; **comb. nov.**

†***trilineata*** Lea 1904 : 427 (*Schizosternus*; New South Wales); Clavareau 1913 : 126; Britton and Stanbury 1980 : 290; **comb. nov.**

†***t-viride*** Lea 1904 : 417-8 (*Cryptocephalus t-viridis* [sic]; New South Wales); Clavareau 1913 : 193 (*t-viride*); **comb. nov.**

†***variipennis*** Lea 1904 : 401-2 (*Cryptocephalus*; South Australia, King George Sound, Swan River); Clavareau 1913 : 194; **comb. nov.**

vermicularis Saunders 1843 : 59 (*Ochrosopsis*; New Holland); Saunders 1845 : 152; Chapuis 1879 : 77 (*Cryptocephalus*); Masters 1887 : 586; Lea 1902 : 455; Lea 1904 : 377-8, 405 (*Ochrosopsis*); Clavareau 1913 : 204; **comb. nov.**

†***verticalis*** Chapuis 1876 : 38 (*Loxopleurus*; Australia); Masters 1887 : 591; Lea 1904 : 408, 434; Clavareau 1913 : 125; **comb. nov.**

†***vicaria*** Lea 1904 : 394-5 (*Cryptocephalus*; Port Denison, Gayndah); Clavareau 1913 : 195; Britton and Stanbury 1980 : 292; **comb. nov.**

†***virgata*** Lea 1904 : 441 (*Loxopleurus*; Rylestone, Forest Reefs); Lea 1904 : 443; Clavareau 1913 : 125; **comb. nov.**

†***viridinitens*** Chapuis 1875 : 94 (*Cryptocephalus*; Clarence River); Masters 1887 : 586; Lea 1904 : 365; Froggatt 1907 : 202; Clavareau 1913 : 195; Ohmart, Stewart and Thomas 1983 : 403 (host); **comb. nov.**

viridipennis Saunders 1842 : 70 (type sp. of *Mitocera*; Swan River); Saunders 1845 : 151, plate 9, fig. 5; Baly 1877 : 30 (*Ochrosopsis*, sen. syn. of *Cryptocephalus perlongus* Chapuis); Masters 1887 : 587 (*Mitocera*); Lea 1904 : 388 (*Mitocera*); Clavareau 1913 : 203 (sen. syn. of *perlonga* Chapuis); Weise 1923 : 17; Bryant : 928; Jolivet 1957 : 96 (wing venation); Gressitt 1965 : 418 (*Cryptocephalus*);

Hawkeswood 1988 : 98 (*C. viridipennis* Chapuis [sic, outside range of *viridipennis* Saunders]; host); **comb. nov.**

= †*perlongus* Chapuis 1875 : 94 (*Cadmus*; Port Essington, Tasmania); Baly 1877 : 30 (jun. syn. of *Mitocera viridipennis* Saunders); Masters 1887 : 585 (*Cryptocephalus*, valid sp.); Clavareau 1913 : 203 (jun. syn. of *viridipennis* Saunders);

= †*t-nigrum* Lea 1904 : 449-450 (*Cadmus t-niger* [sic]; Mount Kosciusko); Clavareau 1913 : 207 (*t-nigrum*); **syn. nov.**

[*viridipennis* shows clinal variation in rugosity and colour throughout its range from Tasmania to south Queensland. *t-nigrum* is the rugose, pale, northern form.]

†***viridis*** Saunders 1847 : 294, plate 15 fig 6 (type sp. of *Chloroplisma*; New South Wales); Masters 1887 : 587 (*Cryptocephalus*); Lea 1904 : 387-8 (sen. syn. of *Loxopleurus metallicus*, *L. corruscus* and *L. chalybaeus*); Clavareau 1913 : 205 (sen. syn. of *metallica* Chapuis, chalybaea Chapuis and *corusca* [sic] Chapuis); Jolivet 1957 : 96 (wing venation); **comb. nov.**

= †*aereus* Suffrian 1859 : 131-3 (*Loxopleurus*; Australia); Masters 1887 : 589; **syn. nov.**

= †*chalyboeus* Chapuis 1876 : 43 (*Loxopleurus*; Victoria); Masters 1887 : 589 (*chalybeus* [sic]); Lea 1904 : 387-8 (*chalybaeus* [sic] Chapuis, jun. syn. of *Chloroplisma viridis* Saunders); Clavareau 1913 : 205 (jun. syn. of *viridis* Saunders);

= †*corruscus* Chapuis 1876 : 40 (*Loxopleurus*; Australia); Masters 1887 : 589; Lea 1904 : 387-8 (jun. syn. of *Chloroplisma viridis* Saunders); Clavareau 1913 : 205 (*corusca* [sic], jun. syn. of *viridis* Saunders);

= †*metallicus* Chapuis 1876 : 40 (*Loxopleurus*; Melbourne); Masters 1887 : 590; Lea 1904 : 387-8 (jun. syn. of *Chloroplisma viridis* Saunders); Clavareau 1913 : 205 (jun. syn. of *viridis* Saunders);

****wallacei*** Baly 1865 : 74-5, plate 3, fig. 3 (*Cryptocephalus*; Timor); **comb. nov.**

2.4.4.1.2 Subgenus ***Diandichus*** Chapuis 1874 : 165-6 (in Pachybrachini); Baly 1877 : 25 (in Cryptocephalini); Lea 1904 : 330, 331, 444; Clavareau 1913 : 88 (in Pachybrachini); Jolivet 1957 : 90 (wing venation); Seeno and Wilcox 1982 : 37; **comb. nov.**

Type species : *Diandichus analis* Chapuis, by monotypy

†***absonus*** Lea 1904 : 443-4 (*Loxopleurus*; Kiama, Manly, Sydney, Galston); Clavareau 1913 : 124; Britton and Stanbury 1980 : 244;

analis Chapuis 1874 : 165 (Australia); Chapuis 1876 : plate 115 fig. 1; Masters 1887 : 591; Lea 1904 : 386, 426, plate 25 fig. 165; Clavareau 1913 : 88; Jolivet 1957 : 90 (wing venation); **comb. nov.**

= †*foveiventris* Lea 1904 : 425-6 (Geraldton); Clavareau 1913 : 88; **syn. nov.** [*Diandichus analis* as defined here is widespread throughout the southern half of Australia in various habitats. The differences between individuals in colour and length of pubescence have not been matched with any morphological constants, therefore this taxon is considered to be one species].

2.4.4.2 Genus ***Cadmus*** Erichson 1842 : 119; Chevrolat 1837 : 444 [*nom. nud.*]; Fairmaire 1843 : 14; Fogg 1859 : 333; Boheman 1859 : 155 (subg. of *Cryptocephalus* Geoffroy); Suffrian 1859 : 48-52, 88 (sen. syn. of *Odontoderes* Saunders, *Prionopleura* Saunders, *Brachycaulus* Fairmaire, *Onchosoma* Saunders); Chapuis 1874 : 159, 188-190 (sen. syn. of *Brachycaulus* Fairmaire, *Odontoderes* Saunders, *Prionopleura* Saunders, *Onchosoma* Saunders); Baly 1877 : 26-7 (sen. syn. of *Odontocerus* [sic] Saunders; Baly 1877 : 227; Lea 1904 : 330-2, 455; Froggatt 1907 : 201-2 (larva); Clavareau 1913 : 205 (sen. syn. of *Odonteres* Saunders, *Paracadmus* Baly and *Prionopleura* Saunders); Tillyard 1926 : 235; Monrós and Bechyné 1956 : 1124 (designation of type species for *Cadmus* Chevrolat, sen. syn. of *Cataplus* Gistel); Jolivet 1957 : 96 (wing venation); Gressitt 1965 : 419; Jolivet 1978 : 177 (hosts); Gressitt 1982 : 719 (distribution); Seeno and Wilcox 1982 : 39-40 (sen. syn. of *Cataplus* Gistel, *Odontoderes* Saunders, *Paracadmus* Baly, includes subgenera : *Prionopleura* Saunders, *Cyphodera* Baly); Ohmart, Stewart and Thomas 1983 : 403 (host)

2.4.4.2.1 Subgenus ***Cadmus*** s. str.

Type species : *Cryptocephalus australis* Boisduval, by subsequent reviser (Gressitt 1965); *Cryptocephalus gigas* Olivier (Monrós and Bechyné 1956).

[Designation of *C. gigas* as the type species is not accepted here because the inclusion or identity of this species was queried by Chevrolat (1837). All other names listed by Chevrolat are *nomina nuda*, therefore Chevrolat is rejected as the author of *Cadmus*.]

= ***Odontoderes*** Saunders 1846 : 202 (subg. of *Cryptocephalus*), nec Schoenherr in Sahlberg 1823 : 46 (Curculionidae); Chevrolat 1837 : 444 [*nom. nud.*]; Erichson

1842 : 119 [*nom. nud.*]; Fogg 1859 : 333; Chapuis 1874 : 188-9 (jun. syn. of *Cadmus* Erichson); Lea 1904 : 331; Clavareau 1913 : 205 (jun. syn. of *Cadmus*); Seeno and Wilcox 1982 : 40

Type species : *Cryptocephalus australis* Boisduval, by monotypy

= ***Prionopleura*** Saunders 1846 : 58 (subg. of *Cryptocephalus*); Saunders 1846 : 197; Chapuis 1874 : 188, 190 (jun. syn. of *Cadmus* Erichson); Baly 1877 : 27 (valid); Lea 1904 : 331; Clavareau 1913 : 207 (subgenus of *Cadmus*); Seeno and Wilcox 1982 : 40 (subg. of *Cadmus* Erichson)

Type species : *Cryptocephalus rugicollis* Gray, by original designation

= ***Cataplus*** Gistel 1847 : 404; Monrós and Bechyné 1956 : 1124 (jun. syn. of *Cadmus*); Seeno and Wilcox 1982 : 39 (jun. syn. of *Cadmus* Erichson)

Type species : *Cryptocephalus australis* Boisduval, by monotypy

= ***Paracadmus*** Baly 1877 : 227; Lea 1904 : 331; Clavareau 1913 : 205 (jun. syn. of *Cadmus*); Seeno and Wilcox 1982 : 40 (jun. syn. of *Cadmus* Erichson)

Type species : *Paracadmus lucifugus* Baly, by monotypy

†***alternans*** Chapuis 1875 : 101 (Gipsland); Masters 1887 : 579; Clavareau 1913 : 205;
australis Boisduval 1835 : 584-5, plate 8, fig. 15 (*Cryptocephalus*; Hobart); Saunders 1846 : 202-3, plate 15 fig. 2 (type species of *Odontoderes*); Suffrian 1859 : 52-55 (*Cryptocephalus*); Baly 1877 : 26 (*Cadmus*); Chapuis 1879 : 78; Masters 1887 : 579; Lea 1902 : 455; Lea 1904 : 353; Clavareau 1913 : 205; Jolivet 1957 : 96 (wing venation); Elliot and Delittle [1985] : 13 (host);
[*australis* Dejean, in Chevrolat 1837 : 444, nomen nudum (*Odontoderes* Chevrolat)];
†***cognatus*** Saunders 1846 : 201 (*Prionopleura*; Van Diemen's Land); Chapuis 1876 : 344 (*Cadmus*); Baly 1877 : 27 (*Prionopleura*); Chapuis 1879 : 78 (*Cadmus*); Masters 1887 : 579; Blackburn 1890 : 137 (sen. syn. of *quadrituberculatus* Suffrian); Lea 1902 : 455; Lea 1904 : 336, 382 (*Prionopleura*); Clavareau 1913 : 207 (*Cadmus*, sen. syn. of *quadrituberculatus* Suffrian); Jolivet 1957 : 97 (wing venation)

= *quadrituberculatus* Suffrian 1859 : 66-8 (*Cadmus*; Australia); Blackburn 1890 : 137 (*Prionopleura*, jun. syn. of *cognata* Saunders); Clavareau 1913 : 207 (*Cadmus*, jun. syn. of *cognatus* Saunders);

crucicollis Boisduval 1835 : 585 (*Cryptocephalus*; New Holland); Saunders 1846 : 58 (*Prionopleura*); Saunders 1846 : 198-9; Suffrian 1859 : 73-6 (*Cadmus*); Baly 1877 : 27; Masters 1887 : 579; Clavareau 1913 : 205; Blackburn 1890 : 136 (sen. syn. of *flavocincta* Saunders); Lea 1902 : 455; Lea 1904 : 355, 362 (*Cryptocephalus*, sen. syn. of *Prionopleura hopei* Saunders, *creek-nigra* [sic] Saunders, *flavocincta* Saunders, *cinnamomeus* Suffrian and *amplicollis* Chapuis), 451-2; Clavareau 1913 : 205-6 (includes vars *amplicollis* Chapuis, *cinnamomeus* Suffrian, *crux-nigra* Saunders, *flavocinctus* Saunders and *hopei* Saunders); Goudie 1927 : 303; Brooks 1965 : 29 (host); Morrow 1977 : 101 (host); Ohmart 1983 : 403 (host)

= †*amplicollis* Chapuis 1879 : 78 (*Cadmus*; Rockhampton); Masters 1887 : 579; Lea 1904 : 362 (jun. syn. of *crucicollis* Boisduval); Clavareau 1913 : 205 (var. of *crucicollis*);

= †*canaliculatus* Chapuis 1875 : 100 (Gipsland); Masters 1887 : 579; Clavareau 1913 : 205; **syn. nov.**

= *cinnamomeus* Suffrian 1859 : 76-8 (*Cadmus*; Australia, Sydney); Chapuis 1879 : 78; Masters 1887 : 580 (jun. syn. of *flavocinctus*); Blackburn 1890 : 136 (*Prionopleura*, jun. syn. of crucicollis Boisduval); Lea 1904 : 362; Clavareau 1913 : 206 (var. of *crucicollis*);

= †*cruxnigra* Saunders 1846 : 58-9 (*Prionopleura*; New Holland); Saunders 1846 : 199-200; Masters 1887 : 579 (var. of *crucicollis*); Lea 1904 : 362 (*creek-nigra* [sic] Saunders, var. of *Cryptocephalus crucicollis* Boisduval); Clavareau 1913 : 206 (var. of *crucicollis*);

= *hopei* Saunders 1846 : 58 (*Prionopleura*; Van Diemen's Land); Saunders 1846 : 199; Masters 1887 : 579 (var. of *crucicollis*); Lea 1904 : 362 (var. of *Cryptocephalus crucicollis* Boisduval); Clavareau 1913 : 206 (var. of *crucicollis*);

= †*flavocincta* Saunders 1846 : 59 (*Prionopleura*; New Holland); Saunders 1846 : 200; Suffrian 1859 : 78-81 (*Cadmus*); Baly 1877 : 27 (*Prionopleura*, *flavicinctus* [sic] Suffrian [sic]); Chapuis 1879 : 78 (*Cadmus*); Masters 1887 : 580 (sen. syn. of *cinnamomeus*); Blackburn 1890 : 136 (jun. syn. of *Cryptocephalus crucicollis* Boisduval); Froggatt 1895 : 334-5 (life history); Lea 1904 : 362 (var. of *Cryptocephalus crucicollis* Boisduval); Clavareau 1913 : 206 (var. of *crucicollis*);

= †*rugosus* Suffrian 1859 : 71-3 (Australia); Baly 1877 : 26 (*Brachycaulus*); Chapuis 1879 : 78 (*Cadmus*); Masters 1887 : 581; **syn. nov.**

[*Cadmus* "crucicollis" represents a species complex, which includes at least 6 species on aedeagal differences. The numerous colour forms have given rise to many species names but these may all be synonyms. Determination of validity of the species and synonyms in the complex would require a major study. I have therefore maintained previous synonymies, with the proviso that these are likely to be incorrect. *Cadmus canaliculatus* and *C. rugosus* also belong to this complex and are therefore included in synonymy.]

†***eruditus*** Blackburn 1890 : 136-7 (*Prionopleura*; South Australia); Lea 1904 : 343-4, 382; Clavareau 1913 : 208 (*Cadmus*);

†***excrementarius*** Suffrian 1859 : 57-9 (Australia); Baly 1877 : 27; Masters 1887 : 580; Lea 1904 : 353, 357, 374; Clavareau 1913 : 206; Goudie 1927 : 303; Brooks 1965 : 29 (host)

gigas Olivier 1807 : 785, plate 4 fig. 45 (*Cryptocephalus*; New Holland); Chapuis 1879 : 78; Boisduval 1835 : 587 (sen. syn. of *rubiginosus* Macleay); Suffrian 1859 : 62-6 (sen. syn. of *Cryptocephalus rugicollis* Gray, *Cryptocephalus rubiginosus* Boisduval); Masters 1887 : 580 (sen. syn. of *bifasciatus*); Lea 1904 : 352, 381-2; Clavareau 1913 : 206 (sen. syn. of *bifasciatus* Saunders); Monrós and Bechyné 1956 (designated as type species of *Cadmus* Chevrolat)

= *bifasciata* Saunders 1846 : 58 (*Prionopleura*; New Holland); Saunders 1846 : 198, plate 15, fig. 1; Baly 1877 : 27; Masters 1887 : 579, 580 (jun. syn. of *gigas*); Lea 1904 : 381-2 (good species); Clavareau 1913 : 206 (jun. syn. of *gigas* Olivier), 207 (valid sp.) [!];

= *rubiginosus* Boisduval 1835 : 587 (*Cryptocephalus*, jun. syn. of *gigas* Olivier [!]; New Holland); Masters 1887 : 581 (good species, sen. syn. of *gigas* sensu Suffrian nec Olivier and *rugicollis* Gray); Lea 1904 : 337, 352, 382 (jun. syn. of *rugicollis* Gray); Froggatt 1907 : 202; Clavareau 1913 : 207 (valid sp.); Morrow 1977 : 101 (host)

†***histrionicus*** Chapuis 1875 : 100 (Australia); Baly 1877 : 27 (*Prionopleura*); Masters 1887 : 580 (*histrionycus* [sic]); Blackburn 1890 : 137; Lea 1904 : 355 (*Cadmus*); Clavareau 1913 : 206; Goudie 1927 : 303;

lacertinus Chapuis 1879 : 78-9 (Rockhampton); Masters 1887 : 580; Lea 1904 : 447 (? *Brachycaulus*); Clavareau 1913 : 206 (*Cadmus*);

litigiosus Boheman 1859 : 155 (Sydney); Suffrian 1859 : 55-7; Baly 1877 : 27; Masters 1887 : 580; Lea 1904 : 352-3: Froggatt 1907 : 202; Clavareau 1913 : 206;

= †*vibrans* Suffrian 1859 : 59-62 (Port Philip); Baly 1877 : 27; Masters 1887 : 582; Clavareau 1913 : 207; **syn. nov.** [This species is based upon a teneral specimen of *C. litigiosus*.]

†***luctuosus*** Chapuis 1875 : 97-8 (Sydney, Port Curtis); Masters 1887 : 581; Blackburn 1890 : 135 (*Paracadmus*, sen. syn. of *P. lucifugus* Baly); Lea 1904 : 330, 336, 356 (sen. syn. of *lucifugus* Baly and *maculicollis* Chapuis), 413, 451; Clavareau 1913 : 206 (sen. syn. of *lucifugus* Baly and *maculicollis* Chapuis);

= †*maculicollis* Chapuis 1875 : 101-2 (Adelaide, Clarence River); Masters 1887 : 581; Lea 1904 : 356 (jun. syn. of *luctuosus* Chapuis); Clavareau 1913 : 206 (jun. syn. of *luctuosus*);

= †*lucifugus* Baly 1877 : 228-9 (*Paracadmus*; Australia); Baly 1877 : 227; Masters 1887 : 582; Blackburn 1890 : 135 (jun. syn. of *Cadmus luctuosus* Chapuis); Lea 1904 : 356 (jun. syn. of *luctuosus*); Clavareau 1913 : 206 (jun. syn. of *luctuosus*);

†***lutatus*** Chapuis 1876 : 343-4 (Sydney, Gipsland); Masters 1887 : 581; Clavareau 1913 : 206; Gressitt 1965 : 436

†***maculatus*** Blackburn 1891 : 135-6 (*Paracadmus*; Australia); Lea 1904 : 451; Clavareau 1913 : 206;

†***metallicus*** Lea 1904 : 414 (*Cryptocephalus*; Victoria); Clavareau 1913 : 164; Goudie 1927 : 304; Britton and Stanbury 1980 : 272; **comb. nov.**

monochrous Boisduval 1835 : 585-6, plate 8, fig. 16 (*Cryptocephalus*; King George Sound); Saunders 1846 : 201 (*Prionopleura*); Masters 1887 : 581 (*Cadmus*); [this poorly described species has not been recognised by any subsequent authors]

†***nothus*** Lea 1904 : 454-5 (Karridale); Lea 1904 : 336; Clavareau 1913 : 206;

[*pruinosus* Chevrolat 1837 : 444, *nomen nudum*];

†***purpurascens*** Chapuis 1875 : 101 (Sydney); Chapuis 1876 : plate 116, fig. 5; Baly 1877 : 27 (*Prionopleura*); Masters 1887 : 581 (*Cadmus*); Lea 1904 : 354 (*Cadmus*); Clavareau 1913 : 206;

†***quadrifasciatus*** Lea 1904 : 451-2 (Jenolan); Lea 1904 : 413; Clavareau 1913 : 206;

†***quadrivittis*** Chapuis 1879 : 78 (Rockhampton); Masters 1887 : 581 (*quadrivittatus* [sic]); Lea 1904 : 330, 336, 357 (*quadrivittatus* [sic] Chapuis); Clavareau 1913 : 206;

[*rubiginosus* Macleay, in Chevrolat 1837 : 444, *nomen nudum*];

rugicollis Gray, in Griffiths 1832 : 146, plate 67, fig. 5 (*Cryptocephalus*; New Holland); Guerin-Meneville, in Duperrey 1838 : 143; Saunders 1846 : 197, 201-2 (type sp. of *Prionopleura*); Baly 1877 : 27; Chapuis 1879 : 78 (*Cadmus*); Masters 1887 : 581 (jun. syn. of *rubiginosus* Boisduval); Blackburn 1890 : 137-8 (*Prionopleura*); Lea 1904 : 337, 352, 361 (*Cadmus*, sen. syn. of *rubiginosus* Boisduval and possibly *gigas* Olivier and *salebrosus* Guérin-Meneville); Clavareau 1913 : 207 (valid sp., sen. syn. of *salebrosus* Guérin);

= *rubiginosus* sensu auctt., nec Boisduval 1835. [the illustration of *rugicollis* is sufficient to show that this is the species *rubiginosus* of various authors but not of Boisduval, who described it as a junior synonym of *gigas* (q.v.)]

[*rugosus* Dejean, in Chevrolat 1837 : 444, *nomen nudum*];

†***sericeus*** Chapuis 1875 : 97 (Australia); Masters 1887 : 582; Clavareau 1913 : 207;

[***sexvittatus*** Chevrolat 1837 : 444, *nomen nudum* (*Odontoderes* Chevrolat)];

†***suturalis*** Blackburn 1890 : 137 (*Prionopleura*; Port Lincoln); Clavareau 1913 : 208 (*Cadmus*);

†***trispilus*** Chapuis 1875 : 101 (Port Denison); Baly 1877 : 27; Chapuis 1879 : 78; Masters 1887 : 582; Blackburn 1890 : 138 (*Prionopleura*); Lea 1904 : 357 (*Cadmus*); Clavareau 1913 : 207; Hawkeswood 1988 : 98 (*Cryptocephalus*; host).

2.4.4.2.2 Subgenus *Aorocarpon*, this work, subgen. nov.

Type species : *Brachycaulus posticalis* Lea, this work.

†***apicalis*** Saunders 1845 : 154 (*Ochrosopsis*; Van Diemen's Land); Chapuis 1879 : 78 (*Cryptocephalus*); Masters 1887 : 583; Lea 1902 : 455; Lea 1904 : 346, 379-380, 390 (*Ochrosopsis*); Clavareau 1913 : 204; Van den Berg 1982 : 52 (host); **comb. nov.**

†***cariosus*** Chapuis 1876 : 342-3 (*Cadmus*; Mount Victoria, New South Wales); Masters 1887 : 579; Lea 1904 : 330; Clavareau 1913 : 205; **comb. nov.**

= †*minor* Blackburn 1894 : 207-8 (*Rhombosternus*; Victorian Alps); Clavareau 1913 : 126; **syn. nov.**

†***pauxillus*** Chapuis 1876 : 43 (*Loxopleurus*; Hunter River, Queensland); Masters 1887 : 590; Clavareau 1913 : 125; **comb. nov.**

= †*perlatus* Lea 1904 : 454 (*Cadmus*; Sydney); Clavareau 1913 : 206; Britton and Stanbury 1980 : 279; **syn. nov.**

†***posticalis*** Lea 1904 : 446-7 (*Brachycaulus*, Glen Innes, Gosford); Oke 1932 : 167; **comb. nov.**

2.4.4.2.3 Subgenus *Brachycaulus* Fairmaire 1843 : 31; Fairmaire 1843 : 13-14; Chapuis 1874 : 188, 190 (jun. syn. of *Cadmus* Erichson); Baly 1877 : 26 (valid, sen. syn. of *Onchosoma* Saunders); Lea 1904 : 330-1; Clavareau 1913 : 208; Jolivet 1957 : 97 (wing venation); Karren 1972 : 894; Kasap and Crowson 1976 : 104, 110 (larva [misdet.], systematics); Jolivet 1978 : 177 (host); Seeno and Wilcox 1982 : 40; stat. rev.

Type species : *Brachycaulus ferrugineus* Fairmaire, by monotypy

= ***Onchosoma*** Saunders 1846 : 203-4 (subg. of *Cryptocephalus*); Chapuis 1874 : 188, 190 (jun. syn. of *Cadmus* Erichson); Baly 1877 : 26 (jun. syn. *Brachycaulus* Fairmaire); Lea 1904 : 331 (valid [!]); Seeno and Wilcox 1982 : 40 (jun. syn. of *Brachycaulus* Fairmaire)

Type species : *Onchosoma dorsalis* Saunders, by original designation

†***colossus*** Chapuis 1875 : 100 (*Cadmus*; Port Denison); Baly 1877 : 26 (*Brachycaulus*); Chapuis 1879 : 79 (*Cadmus*); Masters 1887 : 579; Lea 1904 : 358 (*Brachycaulus*); Clavareau 1913 : 208; Brooks 1965 : 29 (host);

†***crassicostatus*** Chapuis 1876 : 43 (*Loxopleurus*; Pine Mountain); Masters 1887 : 589; Lea 1904 : 372-3 (jun. syn. of *Idiocephala tasmanica* Saunders); **comb. nov. et stat. rev.**

ferrugineus Fairmaire 1843 : 14-5, plates 1-2, figs 7-9 (New Holland); Fairmaire 1843 : 31; Suffrian 1859 : 89-92 (*Cadmus*, sen. syn. of *Onchosoma foveocollis* [sic] Saunders); Masters 1887 : 580 (sen. syn. of *foveicollis*); Lea 1902 : 455; Lea 1904 : 383-4 (*Brachycaulus*, sen. syn. of *ewingi* Saunders, *dorsalis* Saunders, *tasmanica* Saunders, *foveicollis* Saunders, *rufescens* Saunders and *Cadmus verrucosus* Chapuis), 446; Clavareau 1913 : 208

= †*dorsalis* Saunders 1846 : 204-5, plate 15, fig. 3 (*Onchosoma*; New Holland); Baly 1877 : 26 (*Brachycaulus*); Masters 1887 : 580 (*Cadmus*); Lea 1902 : 455 (*Cadmus*); Lea 1904 : 383-4 (jun. syn. of *ferrugineus* Fairmaire); Clavareau 1913 : 208

= †*ewingii* Saunders 1846 : 204 (*Onchosoma*; Van Diemen's Land) Baly 1877 : 26 (*Brachycaulus*); Masters 1887 : 580 (*Cadmus*, var. of *dorsalis*); Lea 1902 : 455 (*Cadmus*, var. of *dorsalis* Saunders); Lea 1904 : 383-4 (jun. syn. of *ferrugineus* Fairmaire)

= †*foveicollis* Saunders 1846 : 206 (*Onchosoma*; Van Diemen's Land); Baly 1877 : 26 (*Brachycaulus*); Masters 1887 : 580 (*Cadmus*, jun. syn. of *ferrugineus*); Lea 1904 : 383-4 (jun. syn. of *ferrugineus* Fairmaire)

= †*rufescens* Saunders 1846 : 207 (*Onchosoma*; New Holland); Masters 1887 : 581 (*Cadmus*); Lea 1902 : 455 (*Cadmus*); Lea 1904 : 383-5 (jun. syn. of *ferrugineus* Fairmaire)

= †*tasmanica* Saunders 1846 : 205 (*Onchosoma*; Van Diemen's Land); Masters 1887 : 582 (*Cadmus*); Lea 1902 : 455 (*Cadmus*); Lea 1904 : 383-4 (jun. syn. of *ferrugineus* Fairmaire)

= †*verrucosus* Chapuis 1879 : 79 (*Cadmus*; Gayndah); Masters 1887 : 582; Lea 1904 : 383-4 (jun. syn. of *Brachycaulus ferrugineus* Fairmaire)
[*ferrugineus* is a very widespread and variable species. It is possible that it represents a species complex similar to *Cadmus crucicollis*, but for the present the traditional synonymy is maintained]

†***klugii*** Saunders 1846 : 206-7 (*Onchosoma*; New Holland); Baly 1877 : 26 (*Brachycaulus*); Masters 1887 : 580 (*Cadmus*); Lea 1904 : 446-7 (*Onchosoma*); Clavareau 1913 : 208 (*Brachycaulus klugi* [sic]); Oke 1932 : 167; Healy and Smithers 1971 : plate 46; Hawkeswood 1985 : 163 (host); Hawkeswood 1988 : 96 (host)

mamillatus Lea 1904 : 447 (*Cadmus*; Mount Tambourine); **comb. nov.**

†***minor*** Oke 1932 : 166-7 figs 19-20 (Inglewood, Sea Lake)

2.4.4.2.4 Subgenus ***Cadmoides***, this work, **subgen. nov.**

Type species : *Cadmus pacificus* Suffrian, this work.

†***comosus*** Lea 1904 : 421 (*Cryptocephalus*; Tambourine); Clavareau 1913 : 140; Weise 1923 : 17 (*Idiocephala*); **comb. nov.**

pacificus Suffrian 1859 : 68-71 (*Cadmus*, Australia); Chapuis 1879 : 78; Masters 1887 : 581; Lea 1902 : 455; Lea 1904 : 353-4 (host); Clavareau 1913 : 206; **comb. nov.**

†***strigillatus*** Chapuis 1875 : 98 (*Cadmus*, Victoria, Gipsland); Masters 1887 : 582; Lea 1902 : 455; Lea 1904 : 357; Clavareau 1913 : 207; **comb. nov.**

2.4.4.2.5 Subgenus ***Lachnabothra*** Saunders 1847 : 294-5 (subgenus of *Cryptocephalus*); Baly 1871 : 391-2; Chapuis 1874 : 191-2 (= *Chlamydicadmus* nom. nov. [!]); Lea 1904 : 330-1; Clavareau 1913 : 208 (sen. syn. of *Chlamydicadmus* Chapuis); Gressitt 1965 : 440 (subg. of *Cadmus* Erichson); Jolivet 1957 : 97 (wing venation); Karren 1972 : 894; Kasap and Crowson 1976 : 104 (larva ?); Seeno and Wilcox 1982 : 40 (valid, sen. syn. of *Chlamydicadmus* Chapuis)

Type species : *Lachnabothra hopei* Saunders, by monotypy.

= ***Chlamydicadmus*** Chapuis 1874 : 191-2 (nom. nov. [!] for *Lachnabothra* Saunders); Chapuis 1874 : 157, 159, 183; [no subsequent author has recognised this invalid name change]

adspersatus Chapuis 1876 : plate 116, fig. 6 [Australia, *nomen dubium*; type missing]

†***braccatus*** Klug 1824 : 159-160, plate 6, fig. 9 (*Chlamys*; unknown origin); Baly 1871 : 391-2 (*Lachnabothra*, *braceata* [sic] Klug); Chapuis 1874 : 192 (*Chlamydicadmus bracata* [sic] Klug); Masters 1887 : 569; Lea 1904 : 331, 350-1 (*Lachnabothra*, sen. syn. of *hopei* Saunders and *breweri* Baly); Clavareau 1913 : 209 (sen. syn. of *hopei* Saunders and var. *breweri* Baly); Jolivet 1957 : 97 (wing venation)

= †*hopei* Saunders 1847 : 295, plate 15 fig. 5 (New South Wales); Suffrian 1859 : 85-8 (*hopii* [sic], Cadmus); Baly 1871 : 392-3, 394-5; Chapuis 1874 : 192 (*Chlamydicadmus*); Masters 1887 : 569; Lea 1904 : 350-1 (*Lachnabothra*, jun. syn. of *braccata* Klug); Clavareau 1913 : 209 (jun. syn. of *braccata* Klug); Reid 1990 (in press; suppression of holotype, designation of neotype)

= †*saundersi* Baly 1871 : 397 (Australia); Baly 1871 : 398; Masters 1887 : 569; Lea 1902 : 454; Lea 1904 : 351; Clavareau 1913 : 209; Gressitt 1965 : 443; Morrow 1977 : 102 (host); Ohmart, Stewart and Thomas 1983 : 403 (host); **syn. nov.**

†***breweri*** Baly 1871 : 393-4 (Albany, King George Sound, Swan River); Masters 1887 : 569; Lea 1904 : 350-1 (jun. syn. of *Chlamys braccata* Klug); Clavareau 1913 : 209 (var. of *braccata* Klug);

= †*duboulai* Baly 1871 : 399 (Western Australia); Masters 1887 : 569 (*duboulayi* [sic]); Clavareau 1913 : 209 (*duboulayi* [sic]); **syn. nov.**

†***distinctus*** Baly 1871 : 398 (north-west Australia [sic, misreading of data label]); Masters 1887 : 569;

†***incoctus*** Lea 1904 : 420-1 (*Cryptocephalus*; Mackay); Britton and Stanbury 1980 : 264; **comb. nov.**

†***integer*** Baly 1871 : 394-5 (South Australia, Adelaide, Gawler Town); Masters 1887 : 569; Clavareau 1913 : 209;

†***waterhousei*** Baly 1871 : 396-7 (South Australia, Adelaide); Masters 1887 : 570; Lea 1904 : 350-1; Clavareau 1913 : 209;

†***wilsoni*** Baly 1871 : 395-6 (South Australia, Adelaide, Gawler Town); Chapuis 1879 : 79 (*Chlamydicadmus*); Masters 1887 : 570; Lea 1904 : 351 (*Lachnabothra*); Clavareau 1913 : 209; Goudie 1927 : 303

[**Cryptocephalus* Geoffroy in Müller 1764; Geoffroy 1762 : 231 (unavailable); Saunders 1842 : 11; Suffrian 1859 : 93, 98 (sen. syn. of *Dicenopsis* Saunders, *Idiocephala* Saunders, *Ochrosopsis* Saunders), Baly 1865 : 62; Chapuis 1874 : 155-6, 158-9, 161, 184-6, 187, 189 (sen. syn. of *Dicenopsis* Saunders, *Idiocephala* Saunders, *Mitocera* Saunders, *Ochrosopsis* Saunders, *Chloroplisma* Saunders); Baly 1877 : 30; Lea 1904 : 330-1; Jacoby 1908 : 192; Clavareau 1913 : 127 (sen. syn. of *Dicenopsis* Saunders, *Euphyma* Baly, *Idiocephala* Saunders); Tillyard 1926 : 235; Maulik1929 : 178; Crowson 1938 : 403 (metendosternite); Jolivet 1957 : 94 (wing venation); Morrow 1977 : 102 (host); Medvedev and Zaitsev 1978 : 136-145 (larvae); Silfverberg 1978 : 117-9 (nomenclature); Jolivet 1978 : 176 (host); Kimoto and Gressitt 1981 : 333-4; Gressitt 1982 : 719 (biogeography); Alegre and Petitpierre 1982 : 794-6 (chromosomes); Van den Berg 1982 : 53 (hosts); Seeno and Wilcox 1982 : 39 (sen. syn. of *Dicenopsis* Saunders, *Mitocera* Saunders, *Ochrosopsis* Saunders, *Anodonta* Saunders, *Idiocephala* Saunders, *Ochrosopus* Saunders, *Euphyma* Baly; includes 7 subgenera)

Type species : *Chrysomela sericea* Linnaeus 1758 (Latreille 1810; Silfverberg 1978); *Chrysomela decemmaculatus* Linnaeus 1758 (Gressitt and Kimoto 1961; Burlini 1969).

[Geoffroy's partially multinomial work was rejected as an available work (Opinion 228; 1961) therefore *Chrysomela decemmaculatus* L. cannot be the type and *Chrysomela sericea* L. as designated by Latreille (1810) is the type (Silfverberg 1978). Kerzhner (1981) showed that Müller (1764) copied directly from Geoffroy (1762) and that the generic names should be cited as Geoffroy *in* Müller. This neatly avoids the conflict of preserving Geoffroy's authorship with rejection of his original work and is similar to the treatment of Chevrolat's names in Dejean's catalogues. Silfverberg (1978, 1979) seems to misrepresent this issue. The ICZN has made no further ruling. Most modern works still cite Geoffroy 's (1762) authorship of *Cryptocephalus*, although the date for this authorship has been ruled against and Müller's work is the earliest available source for these names. Whether the type species is *sericea* L. or *decemmaculatus* L. does not materially affect the generic concept.

Subgenera (these are listed here for convenience but their status is not recognised):

Aryana Bert and Rapilly 1973 : (type sp. *davatchii* Berti and Rapilly, by monotypy); Berti and Rapilly 1979 : 241 (jun. syn. of *Cryptocephalus* s. str.)

Asiopus Lopatin 1965 : 452-3 (type sp. *flavicollis* F., by original designation), *nec* Sharp in Whymper 1891 : 43 (Coleoptera); Berti and Rapilly 1979 : 240 (jun. syn. of *Cryptocephalus* s. str.)

Burlinius Lopatin 1965 : 455 (type sp. *fulvus* Goeze, by original designation)

Cerodens Burlini 1969 : 539 (nom. nov. for *Ceropachys* Burlini nec Costa 1847; type sp. *emiliae* Burlini, by original designation)

Cryptodontus Burlini 1969 : 536 (type sp. *informis* Suffrian, by original designation), *nec* Mulsant and Rey 1865 : 36 (Hemiptera)

Disopus Stephens 1839 : 304 (type sp. *pini* L.)

Heterodactylus Medvedev 1963 : 38 (type sp. *tarsalis* Weise, by original designation), *nec* Spix 1825 : 25 (Reptilia), *nec* Guérin-Méneville 1841 : 213 (Coleoptera)

Jaxartiolus Jacobson 1922 : 517 (type sp. *baeckmannianus* Jacobson, by monotypy)

Lamellosus Tomov 1979 : 43 (type sp. *angorensis* Pic, by original designation)

Proctophysus Redtenbacher 1845 : 564 (type sp. *schaefferi* Schrank)

*†***billardierii*** Fabricius 1801 : 48 (New Cambria); Suffrian 1855 : 40; Suffrian 1859 : 93; Baly 1865 : 70. Suffrian (1859) introduced this species to the Australian fauna by confusing New Cambria with New South Wales, but he had already noted that this was a Javan species (1855). La Billardière, the naturalist on d'Entrecasteux's expedition (Carr and Carr 1976), only visited south-west Australia and Tasmania, therefore New Cambria is certainly not in New South Wales. La Billardière was in Java before and after his trip around Australia (Carr and Carr 1976) and I believe this is the true type locality. New Cambria was probably one of many names recorded on early expeditions which did not 'stick' (Carr and Carr 1976). The holotype is in good condition and is a species of *Cryptocephalus* (claws simple) similar to species found in south-east Asia including Java.

**laevicollis* Gebler 1830 : 205 and *laevicollis* var *viennensis* Weise 1882 : 159; Masters 1887 : 585 (var *arennensis* [sic]); Lea 1904 : 331 (var *arennensis* [sic]); an east European species with Austrian subspecies, there is no evidence for any association with Australia. The inclusion of *laevicollis* in the latter fauna may be due to confusion in catalogues between the names Austria and Australia.

All supposed Australian species of *Cryptocephalus* have been removed to other genera.]

2.4.4.3 Genus *Diachus* Leconte 1880 : 196; Clavareau 1913 : 200; Arnett 1971 : 906, 925; Seeno and Wilcox 1982 : 39; Reid 1988 : 6. [further refs in Clavareau 1913]

Type species : not known, apparently not designated.

auratus Fabricius 1801 : 57 (USA) [introduced]; Leconte 1880 : 197; Reid 1988 : 5-8 (hosts, distribution). [further references in Clavareau 1913]

2.4.4.4 Genus *Melatia*, this work, **gen. nov.**

Type species : *Cadmus glochidionis* Gressitt 1965, this work.

****acalyphae*** Gressitt 1965 : 430-1 (*Cadmus*, New Guinea); **comb. nov.**

****alternatus*** Gressitt 1965 : 431-2 (*Cadmus*, New Guinea); Gressitt 1965 : 433; **comb. nov.**

****aroanus*** Gressitt 1965 : 433-4 (*Cadmus*, New Guinea); **comb. nov.**

*†***bicolor*** Gressitt 1965 : 423-4 (*Cadmus*, New Guinea); **comb. nov.**

****cheesmanae*** Bryant 1943 : 569 (*Cryptocephalus*, New Guinea); Gressitt 1965 : 411; **comb. nov.**

*†***chlamyoides*** Baly 1865 : 66-7, plate 3 fig. 5 (*Cadmus*; Morty Island); Clavareau 1913 : 205; Gressitt 1965 : 424, 439, 442 (*chlamydoides* [sic]); **comb. nov.**

*†***chlamysinus*** Gressitt 1965 : 440-2 (*Cadmus*, subg. *Lachnabothra*; New Guinea); **comb. nov.**

****compactus*** Gressitt 1965 : 426 (*Cadmus*, New Guinea); **comb. nov.**

†***glochidionis*** Gressitt 1965 : 429-430 (*Cadmus*, New Guinea); Gressitt 1965 : 428; **comb. nov.**

****intermontanus*** Gressitt 1965 : 422-3 (*Cadmus*, New Guinea); **comb. nov.**

****karimui*** Gressitt 1965 : 410-411 (*Cryptocephalus*, New Guinea)

*†***lateralis*** Gressitt 1965 : 437-8 (*Cadmus*, New Guinea); **comb. nov.**

*†***latus*** Gressitt 1965 : 439-440 (*Cadmus*, New Guinea); **comb. nov.**

****macarangae*** Gressitt 1965 : 428 (*Cadmus*, New Guinea); **comb. nov.**

*†***metallicus*** Gressitt 1965 : 425 (*Cadmus*, New Guinea); Gressitt 1965 : 428, 432; **comb. nov.**

*†***multinodosus*** Gressitt 1965 : 442-3 (*Cadmus*, subg. *Lachnabothra*; New Guinea); **comb. nov.**

****nodosellus*** Gressitt 1965 : 426-8 (*Cadmus*, New Guinea); Gressitt 1965 : 426; **comb. nov.**

****nodosus*** Gressitt 1965 : 443 (*Cadmus*, subg. *Lachnabothra*; New Guinea); **comb. nov.**

*†***papuamontis*** Gressitt 1965 : 411-413 (*Cryptocephalus*, New Guinea); **comb. nov.**

papuanus* Bryant : 924-5 (*Cryptocephalus*; Papua); Bryant : 922; Gressitt 1965 : 423 (*Cadmus*), 425, 434, 437; **comb. nov.

pictellus* Gressitt 1965 : 432-3 (*Cadmus*, New Guinea); Gressitt 1965 : 430-1; **comb. nov.

*†**rusticus** Gressitt 1965 : 444-5 (*Cadmus*, subg. *Lachnabothra*; New Guinea); **comb. nov.**

sedlacekae* Gressitt 1965 : 413-414 (*Cryptocephalus*, New Guinea); **comb. nov.

solomonensis* Bryant 1943 : 568-9 (*Cadmus*, Solomon Islands); **comb. nov.

*†**squamulosus** Baly 1865 : 67-8, plate 3, fig. 2 (*Cadmus*; Batchian); Clavareau 1913 : 207; **comb. nov.**

strigatus* Gressitt 1965 : 438-9 (*Cadmus*, New Guinea); **comb. nov.

subcastaneus* Gressitt 1965 : 436-7 (*Cadmus*, New Guinea); **comb. nov.

*†**submetallescens** Baly 1865 : 68-9, plate 3 fig. 9 (*Cadmus*; Ternate); Clavareau 1913 : 207; **comb. nov.**

wauensis* Gressitt 1965 : 414-415 (*Cryptocephalus*, New Guinea); **comb. nov.

incertae sedis, described in *Cadmus* and *Cryptocephalus*, probably *Melatia.*
**fryi* Bryant 1943 : 570-1 (*Cryptocephalus*; Solomon Islands);
**gazellus* Gressitt 1965 : 415-416 (*Cryptocephalus*, New Guinea);
**kaindi* Gressitt 1965 : 434-6 (*Cadmus*, New Guinea);
**meraukensis* Gressitt 1965 : 416-417 (*Cryptocephalus*, New Guinea);

[**Melixanthus* Suffrian 1855 : 8; Reineck 1913 : 393-394;

Type species : *Melixanthus intermedius* Suffrian 1855, by monotypy.

= ***Anteriscus*** Weise 1906 : 39; Clavareau 1913 : 199 (subg. of *Melixanthus* Suffrian); Reineck 1913 : 393-394; Weise 1923 : 22 (jun. syn. of *Idiocephala* Saunders); Seeno and Wilcox 1982 : 39 (jun. syn. of *Melixanthus* Suffrian).

Type species : *Cryptocephalus erythromelas* Suffrian, this designation.

The synonymy of *Anteriscus* Weise and *Idiocephala* Saunders (Weise 1923) is rejected. There are no Australasian species of *Melixanthus*.]

[***Physicerus*** Chevrolat 1837 : 444, *nomen nudum*

speciosus d'Urville, in Chevrolat 1837 : 444, *nomen nudum*];

Appendix C : Original data matrices formatted for PAUP analyses

A key to the letter codes for taxa in the adult and larval matrices is given in Appendix A and in the figure captions on page 358.

pp. C2-C5 Larval and scatoshell data matrix. Sequence of characters is by row, i.e. the first row represents larval characters L1-L30. Numbers 1-80 and 89 are larval characters L1-L80 and L89, and numbers 81-88 are scatoshell characters E1-E8.

p. C6 Pupal data matrix. Each row represents characters P1-P14.

pp. C7 -C17 Adult data matrix. Sequence of characters is as in larval matrix. Numbers 1-228 represent characters A1-A228.

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EDUS 2 3 0 0 0 0 1 9 0 0 0 9 9 9 9 0 9 1 1 1 0 0 0 0 0 2 0 0 0 2
     0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 9 0 0 0 0 0 0 0 0 3 2 0 0 0 0
     0 0 0 0 9 9 0 9 9 0 9 9 0 9 1 0 0 9 0 9 0 9 9 9 9 9 9 9 0
SYNE 1 0 0 0 0 0 1 9 0 0 0 9 9 9 9 0 9 1 1 1 0 0 0 0 0 0 0 1 0 0
     0 9 0 0 0 9 9 1 9 9 9 9 9 9 9 9 9 9 0 9 9 0 0 0 3 2 0 9 1 0
     0 0 0 0 9 9 0 9 9 0 9 9 0 9 9 9 9 9 0 9 9 9 9 9 9 9 9 9 9
OOMO 2 3 1 0 2 1 1 0 0 1 0 9 9 9 9 0 9 1 1 1 0 0 0 1 0 0 0 0 0 0
     0 0 0 0 0 2 0 1 0 0 0 0 0 0 0 9 1 9 0 0 0 1 0 0 0 0 0 9 0 1
     0 0 0 0 0 0 0 0 0 1 0 0 1 9 1 0 1 0 0 9 1 0 0 0 9 9 0 1 0
CHMI 1 2 1 0 0 0 1 0 0 1 0 9 9 9 9 0 9 1 1 1 0 2 0 1 0 0 0 0 0 2
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     0 2 2 1 9 9 2 9 9 0 9 9 0 9 2 1 0 0 0 0 1 0 0 0 9 9 0 1 0
NEOC 1 2 1 0 0 0 1 0 0 1 0 9 9 9 9 0 9 1 1 9 0 0 0 1 0 0 0 0 0 0
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     1 2 2 1 9 9 2 9 9 9 9 9 9 9 2 9 1 9 0 9 1 0 0 0 9 9 0 1 0
LABI 1 2 1 0 0 0 1 0 0 1 0 9 9 9 9 0 9 1 2 0 0 1 0 1 0 1 0 0 1 1
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SMAR 1 2 1 0 0 0 1 0 0 1 0 9 9 9 9 0 9 1 2 0 0 1 0 1 0 0 1 1 0 2
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     1 0 0 0 1 1 0 1 1 0 0 0 1 9 2 0 1 1 0 0 2 1 9 0 9 9 9 9 0
PACH 9 9 9 9 9 9 1 9 9 1 0 9 9 9 9 9 9 9 9 9 0 1 0 1 1 0 0 0 2 0
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     0 0 0 0 0 9 0 0 1 9 0 0 9 9 2 9 1 9 0 0 2 1 9 1 9 1 9 2 0
STYL 9 9 9 9 9 9 9 9 9 1 0 9 9 1 9 1 1 0 0 0 0 1 0 1 1 0 0 0 1 0
     1 1 1 0 1 9 0 0 1 1 1 1 1 1 1 2 1 2 0 0 9 1 1 2 0 0 0 1 9 9
     9 0 0 0 1 9 0 0 1 9 0 0 9 0 3 0 9 9 0 0 9 9 9 9 9 9 9 9 0
PLAT 1 2 1 0 0 0 0 0 0 1 0 9 9 2 9 0 9 1 1 0 0 1 0 1 2 0 0 0 2 0
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AGMI 1 2 1 0 0 0 1 0 0 1 0 9 9 9 9 0 9 1 1 0 0 1 0 1 0 0 0 0 2 0
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AGTW 1 2 1 0 0 0 1 0 0 1 0 9 9 9 9 0 9 1 1 0 0 1 0 1 1 0 0 0 0 1
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     0 0 0 0 0 0 0 1 1 0 0 1 0 9 2 0 1 1 0 0 2 1 9 0 9 1 1 1 0
ATEN 1 2 1 0 0 0 1 0 0 1 0 9 9 9 9 0 0 1 1 0 0 2 0 1 1 0 0 0 1 0
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ARNO 2 3 1 0 0 0 1 0 0 1 2 0 1 1 0 1 1 0 0 0 0 1 0 1 2 0 0 0 2 0
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     0 1 0 0 1 0 0 2 1 1 0 0 2 9 2 1 1 1 0 0 2 1 9 0 9 1 1 1 0
SENO 2 3 1 0 0 0 1 0 0 1 1 9 9 1 9 2 0 1 1 0 0 1 0 1 2 0 0 1 2 0
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SEAC 2 3 1 0 0 0 1 0 0 1 3 0 0 1 0 1 1 0 0 0 0 1 0 1 2 0 2 1 2 0
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SEGC 2 3 1 0 0 0 1 0 0 1 1 9 9 1 9 1 0 1 1 0 0 1 0 1 2 0 0 1 2 0
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APIN 0 2 1 0 0 0 0 0 0 1 0 9 9 9 9 0 9 1 1 0 0 1 2 1 2 0 2 1 2 0
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DISE 1 0 0 1 1 0 1 9 0 1 0 9 9 9 9 0 9 1 1 0 0 1 0 1 0 0 1 0 1 1
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DIFI 1 0 0 1 1 1 1 9 0 1 0 9 9 9 9 0 9 1 1 0 0 1 0 1 0 0 1 0 1 1
     2 2 0 1 1 1 0 0 1 2 2 2 2 2 2 1 0 2 1 1 1 1 1 0 0 0 0 9 1 9
     9 1 1 1 0 1 0 0 1 0 1 1 0 9 2 1 1 1 0 0 9 9 9 9 9 9 9 9 0
NRPO 1 0 1 1 1 1 1 1 0 1 0 9 9 9 9 0 9 1 1 0 0 1 0 1 0 0 0 0 1 0
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PRSU 1 1 1 1 1 1 1 1 0 1 1 9 9 1 9 1 1 0 1 0 0 1 0 1 1 0 0 0 2 0
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     1 1 1 0 0 1 0 1 1 1 0 1 0 9 2 1 1 1 0 0 2 1 9 1 9 1 9 1 0
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ELON 1 1 1 1 1 1 1 1 0 1 0 9 9 9 9 0 9 1 1 0 0 1 0 1 0 0 0 0 1 0
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     1 1 1 0 0 1 0 0 0 0 0 1 0 9 2 1 1 1 0 0 2 0 1 9 9 9 0 0 0
DITS 1 0 1 1 1 1 1 1 0 1 0 9 9 0 9 1 1 1 1 0 0 1 0 1 1 0 0 0 1 0
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DICO 1 0 1 1 1 1 1 1 0 1 0 9 9 0 9 1 0 1 1 0 0 1 0 1 0 0 0 0 1 1
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PLEO 1 0 1 1 1 1 1 1 0 1 0 9 9 1 9 1 0 1 1 0 0 1 0 1 1 0 1 0 2 1
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MONA 1 1 1 1 1 1 1 1 1 1 2 1 1 1 0 1 1 1 0 0 0 1 0 1 2 0 0 0 2 0
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CRMO 1 2 1 0 0 0 1 0 0 1 1 9 9 1 9 1 1 1 2 0 0 1 0 1 2 0 0 0 2 0
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LOGR 1 2 1 0 0 0 1 0 0 1 3 0 0 1 1 1 1 2 2 0 2 1 2 1 2 0 2 1 2 0
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OCSU 1 2 1 0 0 0 1 0 0 1 1 9 9 1 9 1 1 1 1 0 0 1 0 1 2 0 2 1 2 0
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CHVI 1 2 1 0 0 0 1 0 0 1 1 9 9 1 9 2 9 1 1 0 0 1 1 1 2 0 2 1 2 0
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SCAL 1 2 1 0 0 0 1 0 0 1 1 9 9 0 9 1 1 1 1 0 0 1 1 1 2 0 2 9 2 0
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DIAN 1 2 1 0 0 0 1 0 0 1 1 9 9 1 9 1 1 1 1 0 1 1 1 1 2 0 2 1 2 0
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PALU 1 2 1 0 0 0 1 0 0 1 2 9 9 1 9 1 1 2 2 0 0 1 2 1 2 0 2 1 2 0
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CAPE 1 2 1 0 0 0 1 0 0 1 1 9 9 1 9 1 1 1 1 0 0 1 0 1 2 0 2 1 2 0
     2 2 1 1 1 3 0 0 1 2 2 2 2 2 2 2 2 1 2 0 0 1 1 1 0 0 0 1 1 1
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CAAU 1 2 1 0 0 0 1 0 0 1 1 9 9 1 9 1 1 1 1 0 0 1 1 1 1 0 1 1 2 0
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     0 1 1 0 1 1 0 2 1 0 0 1 0 1 1 0 1 1 0 0 2 2 9 9 1 1 1 1 0
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CALI 1 2 1 0 0 0 1 0 0 1 2 9 9 0 9 1 1 2 2 0 0 1 0 1 2 0 2 1 2 0
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CAPA 1 2 1 0 0 0 1 0 0 1 1 9 9 0 9 1 1 1 2 0 0 1 1 1 2 0 2 1 2 0
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Appendix D : Author's publications relevant to this study

1. Reid, C.A.M. (1988) *Diachus auratus* (F.) (Coleoptera: Chrysomelidae), a recent immigrant to the south-west Pacific region, on legumes. *General and applied Entomology* **20** : 5-8.

2. Reid, C.A.M. and Ohmart, C.P. (1989) Determination of the sex of pupae of *Paropsis atomaria* Olivier, and related Paropsina (Coleoptera: Chrysomelidae). *Journal of the Australian entomological Society* **28** : 29-30.

DIACHUS AURATUS (F.) (COLEOPTERA: CHRYSOMELIDAE), A RECENT IMMIGRANT TO THE SOUTH-WEST PACIFIC REGION, ON LEGUMES

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Communicated by P. Gullan

Summary

Diachus auratus (F.) originates from Central America, and is newly recorded from Vanuatu, New Caledonia and Australia. A brief diagnosis is given to separate *D. auratus* from other members of the Cryptocephalinae in this region. The species appears to have spread across the Pacific in association with cultivation of its subtropical legume hosts, particularly leucaena.

Introduction

Diachus auratus (F.) is native to Central America and the southern United States of America, occurring from Colombia to California and Florida (Jacoby 1892; Wilcox 1975). Its spread into the Pacific region was first noticed in Hawaii (Swezey 1915), and by 1978 it was also known from Tahiti, 5000 km to the south (Gourvès and Samuelson 1979). Recently I have examined the south-west Pacific Cryptocephalinae in the Bishop Museum, Hawaii, and many collections of Australian Cryptocephalinae. *Diachus auratus* is well represented in the south-west Pacific but is only known from one very recent specimen from Australia. This species feeds on leguminous trees but there is no evidence at present to suggest pest status.

Distribution

The distribution records for *D. auratus* in the Pacific region (Fig. 1) are as follows (all specimens in the Bishop Museum unless otherwise indicated): HAWAII: O'ahu I., on *Leucaena* (Swezey 1915); FRENCH POLYNESIA: Tahiti I., Papeete, on *Poinciana* (Gourvès and Samuelson 1979); VANUATU: 2, Efate I., Svivi, 50-150m, 27.ii.1970, N. L. H. Krauss; Erromango I.: 6, Navolou 13.iii.1978, N. L. H. Krauss; 8, Dillon's Bay, 0-100m, iii.1978, N. L. H. Krauss; 2, Dillon's Bay, 0-100m, i.1984, N. L. H. Krauss; 1, Tanna I., Lénakel, 0-100m, xi.1978, N. L. H. Krauss; 1, Vanua Lava I., Sola airport, 5m, 19.ix.1979; NEW CALEDONIA: 3, Noumea, v.1950, N. L. H. Krauss; 1, Noumea, Ile Marte, vii.1950, N. L. H. Krauss; 9 ("many more"), Noumea, Anse Vata, 30m, beating (2), grass, weedy legumes and *Leucaena* (1), Rubiaceae (1), 6-8.viii.1979, G. A. Samuelson; 3, Boulouparis, 40m, *Solidago altissima*, 30.iii.1968, J. L. Gressitt; AUSTRALIA: 1, Queensland, Kabra, on *Leucaena*, 26.x.1986, Elder (collection of Department of Primary Industry, Indooroopilly, Brisbane).

Diachus auratus has not previously been recorded from New Caledonia (Fauvel 1907), Vanuatu (Bryant 1936) or Australia (Lea 1904) and is therefore new to these countries. It is as yet unrecorded from the Solomon Islands (Bryant 1943), Micronesia (Gressitt 1955), Samoa (Gressitt 1956), Fiji (Bryant and Gressitt 1955) and New Guinea (Gressitt 1965; Kimoto, Ismay and Samuelson 1984) and is absent from more recent collections of cryptocephalines from these islands and Tonga.

Host plants

Nothing appears to be known of the host plants in the natural range of *D. auratus.* In the Pacific region it has usually been collected off leucaena (*Leucaena leucocephala* Lam. [= *glauca* (L.)]), but also *Delonix* (= *Poinciana*) *regia* (Boj. ex. Hook.) and *Solidago canadensis* L. var *scabra* (Muhl.) (= *altissima* L.). *Leucaena* Benth. and *Delonix* Raff. are leguminous trees, whereas *Solidago* L. belongs to the Asteraceae.

Leucaena leucocephala originates from Central America but has had a long history in the Pacific region, being introduced to the Philippines, Indonesia and Papua New

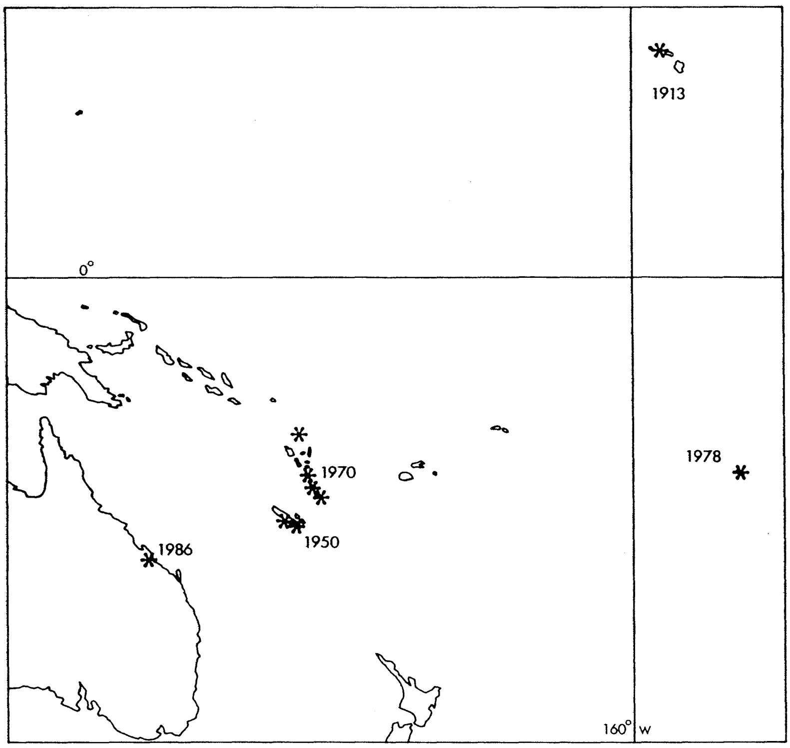


Fig. 1. South-west and central Pacific (Lambert zenithal equal area projection) showing distribution of *Diachus auratus* F. The earliest record for each island group is indicated. Small islands and atolls omitted.

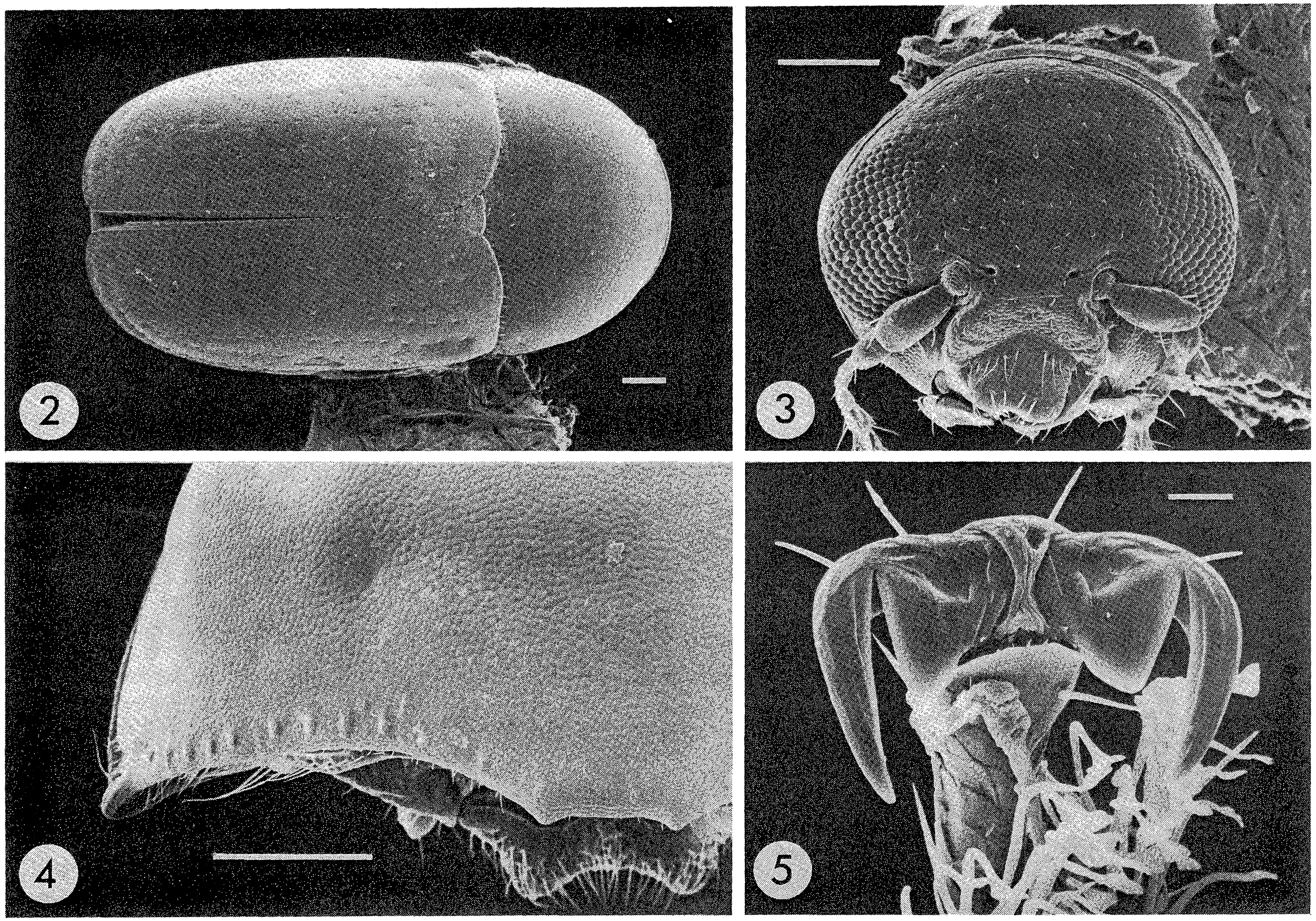
Guinea before 1800, and to Hawaii, Fiji and Australia before 1900 (Anon 1977). Although already having many applications in tropical agriculture, *leucaena* has lately been promoted as a "versatile legume whose full potential, thus far, is untapped" (Anon 1977, page iii). This tree appears to be the preferred host in the Pacific region, where both the flowers and leaves are eaten (Swezey 1915), and is probably the natural host in Central America.

Delonix regia is a widely grown tropical ornamental tree, originally from Madagascar (Allen and Allen 1981). Gourvès collected 20 specimens of *D. auratus* from this host in Tahiti (Gourvès and Samuelson 1979).

Solidago canadensis var *scabra* is native to eastern North America but is a cosmopolitan garden plant (Scoggan 1979). Gressitt's collection of *D. auratus* on this plant is probably an incidental host record as cryptocephaline beetles are not generally polyphagous (at least at the plant familial level).

Identification of *Diachus auratus*

Diachus Leconte was described to include eight North American Cryptocephalini (Leconte 1880). The tribe is well represented in Australia and New Guinea and is also recorded from the Solomon Islands (Bryant 1943) and Fiji (Bryant and Gressitt 1955). The Fijian species, which were placed in the Cryptocephalini by Bryant and Gressitt (1955), are definitely Monachulini and will not be discussed further. *Diachus* is therefore the only member of the Cryptocephalini east of the Solomon Islands. The Australasian genera are in considerable confusion, but I have seen most of the Australian species



Figs 2-5. *Diachus auratus* F. female. (2) dorsal; (3) face; (4) posterior of prothorax; (5) tarsal claw. Scales = 100μ (Figs 2-4) and 10μ (Fig. 5).

and good descriptions are available for the New Guinean species (Gressitt 1965). In south-east Asia *Diachus* is closest to *Melixanthus*, which is distributed from Africa to China, south to Borneo (Clavareau 1913).

For the purposes of identification, *D. auratus* may be easily distinguished from all other west Pacific Cryptocephalinae by the following combination of characters: small size, 1.7-2.5 mm; cylindrical body shape (Fig. 2); green with dull brassy-red pronotum; body entirely coarsely microreticulate; inner edge of eyes barely emarginate (Fig. 3); posterior edge of pronotum not margined but also not sharply crenulate (Fig. 4); pronotum with antebasal row of setose tubercles (Fig. 4); base of elytral suture slightly crenulate; scutellum triangular, flat; antennae short, 1.5 x width of head; prosternal process broad, apical margin concave and sides bordered (Fig. 4); claws sharply toothed (Fig. 5).

All of the 37 specimens available to me are females which suggests that the species may be parthenogenic. Parthenogenic cryptocephalines appear to be unknown (Smith and Virkki 1978) and the resolution of this problem will have to await a thorough study of specimens from the natural range of the species.

Acknowledgements

I particularly thank G. A. Samuelson for the loan of the unidentified south-west Pacific cryptocephaline material in the Bishop Museum, Hawaii, and Bryan Cantrell for access to the Department of Primary Industry collection, Brisbane, Australia. Penny Gullan made useful comments on the manuscript, and Kathy Pickerd advised on the SEM work.

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J. Aust. ent. Soc., 1989, **28**: 29-30

NOTE

DETERMINATION OF THE SEX OF PUPAE OF *PAROPSIS ATOMARIA* OLIVIER, AND RELATED PAROPSINA (COLEOPTERA: CHRYSOMELIDAE)

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Abstract

A simple method for sexing the pupae of *Paropsis* Olivier and related genera is described and illustrated. In *P. atomaria* Olivier, male pupae are generally smaller than female pupae.

Table 1. Characters used to sex pupae of *Paropsis atomaria*

Character	Male	Female
Hind margin sternite VIII	with a small median incision	with a deep median cleft to base
Lobes of sternite IX	ovate, separated by their diameter	transverse, contiguous

One of us (C.P.O.) needed to sex pupae of *Paropsis atomaria* Olivier for larval feeding trials but no descriptions of pupal sexual dimorphism in paropsines were available. The sex of pupae of *P. atomaria* was determined by rearing 20 pupae which had been separated into 2 morphologically recognisable groups using abdominal characters. The resultant adults were sexed by examination of fore and mid basitarsi, which in males have a uniform ventral disc of setae, but in females have a narrow glabrous median line (as do male hind basitarsi) (Baly 1862; Stork 1980). Fresh pupae of *P. atomaria* were prepared for SEM examination as described by Grodowitz *et al.* (1982).

The morphological differences between the sexes lie in the ventral part of the abdominal apex (Figs 1-2). The main points are given in Table 1. In detail they are: sternite VIII of ♂ with a small incision on posterior margin and 14-23 dark brown spinuliform setae each side of margin; sternite VIII of ♀ deeply cleft along midline from base to apex, with 11-15 dark brown marginal spinuliform setae each side; venter of tergite IX in both sexes represented by 2 brown sclerotised lobes with sinuate lateral margins, the lobes contiguous from base to apex, with many short setae; sternite IX divided, lobes ovate, separated by their diameter in ♂, lobes transverse, contiguous in ♀; sternite X divided, lobes ovate, contiguous in both sexes.

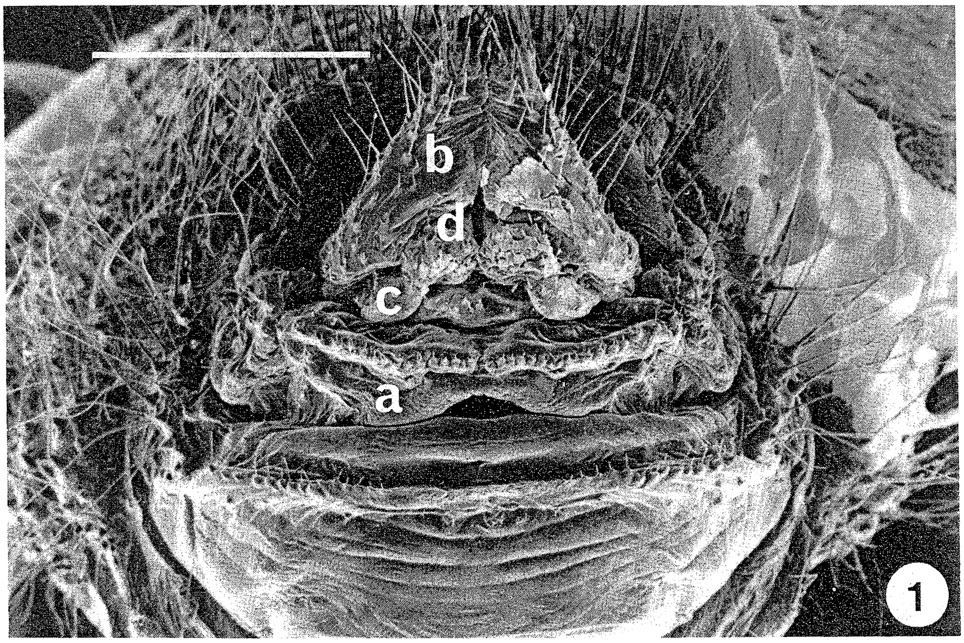

Fig. 1—*Paropsis atomaria*, male, apex of pupa, ventral. a, sternite VIII; b, tergite IX; c, lobe of sternite IX; d, lobe of sternite X. Scale line = 1 mm.

Male pupae are usually smaller than female pupae. Males: body length 13.2-15.3 mm (x = 13.9 ± 0.7), head width 2.8-3.3 mm (x = 3.0 ± 0.2), pronotal width 4.6-5.3 mm (x = 4.8 ± 0.2). Females: body length 13.4-16.3 mm (x = 15.0 ± 0.9), head width 3-3.6 mm (x = 3.3 ± 0.2), pronotal width 4.7-5.5 mm (x = 5.2 ± 0.3).

Pupae of 3 other species of *Paropsis* Olivier, 2 species of *Paropsisterna* Motschulsky and 1 species of *Chrysophtharta* Weise were examined and found to be essentially similar to *P. atomaria*, except that in *Chrysophtharta* sp. the spinuliform setae were considerably reduced and sternite VIII of the ♂ was simple. The important characters for differentiation of the sexes of these large paropsine pupae are the cleft sternite VIII of the ♀ and the separated lobes of sternite IX in the ♂.

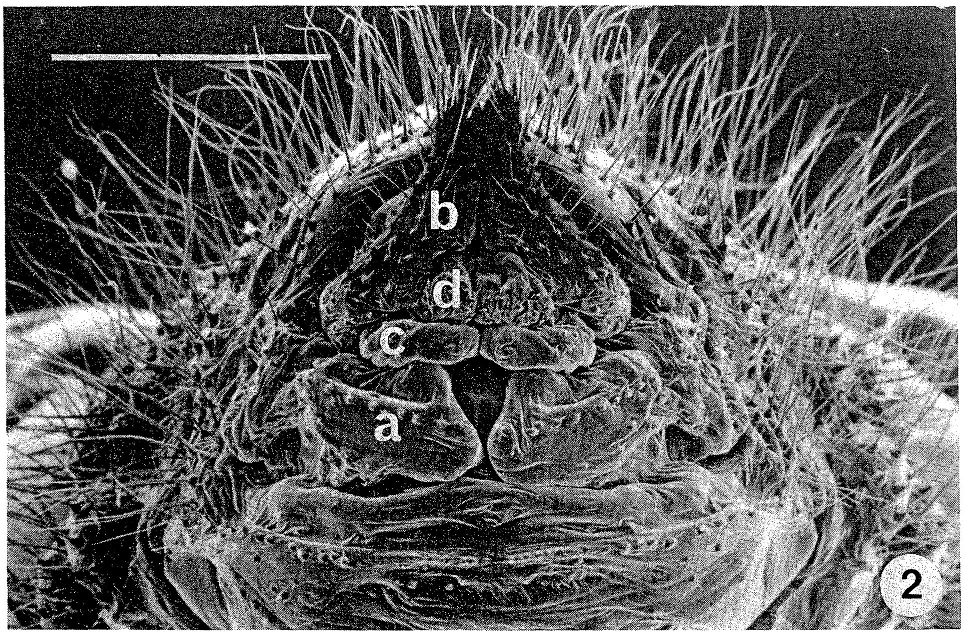

FIG. 2—*Paropsis atomaria*, female, apex of pupa, ventral. a, sternite VIII; b, tergite IX; c, lobe of sternite IX; d, lobe of sternite X. Scale line = 1 mm.

Acknowledgments

We thank Jeanette Thomas who helped rear *P. atomaria*, and Kathy Pickerd (CSIRO) for help with SEM.

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