THE CLASSIFICATION AND PHYLOGENY

OF THE

PSOCOPTERA

by

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I certify that the work included herein

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CONTENTS

SUMMARY

This work provides a phylogenetic classification of the insect order PSOCOPTERA.

Some of the problems involved, mainly arising from lack of adequate published data, are pointed out and work carried out to overcome them is indicated in a short introductory chapter (Chapter I). This consisted of accummulating data on the genera from published texts and illustrations, adding data from the study of fresh material or material held in collections and compiling generic definitions in adequate detail where possible.

Chapter II gives a general description of the Psocoptera together with brief background information on their biology.

As considerable changes are proposed in the classification of the order (in Chapter VII) the classification in use at present is set out for comparison to generic level and a brief history of systematic work on the order is given (Chapter III).

The data necessary for a discussion of the phylogeny is presented in the series of definitions of genera and suprageneric groups in Chapter IV. Data on fossil forms is given in Chapter V.

The principles of phylogenetic study are briefly discussed in Chapter VI and the important question of the relatively primitive or advanced condition of characters in the order is discussed. The monophyly of the order and the relationships between genera are established using Hennig's system and the results are set out in discussion and dendrogram. On the basis of the relationships so established a classification of the order is proposed which is considered to be practical and to reflect evolutionary history of the group. (Chapter VII).

Comments on the distribution of the Psocoptera are made in Chapter VIII and it is suggested that, despite inadequacy of data, a consideration of the distributions supports the proposed classification in general terms.

A general discussion follows and references and figures are included. An appendix provides a practical up-to-date key to the genera of the order.

ACKNOWLEDGEMENTS

This study of the Psocoptera really commenced with the collection, in 1950, of some Psocoptera in the vicinity of Grahamstown. Largely due to the encouragement of the staff of the Department of Zoology and Entomology of Rhodes University and particularly of Professor J. Omer-Cooper, I continued to collect specimens. Subsequent collecting and study over 18 years from several parts of Southern and Central Africa, Europe, Australia, New Zealand and Norfolk Island has provided much material. Material has been received on loan, by gift or exchange from collectors and colleagues engaged in the study of the Psocoptera from North and South America, Africa, Madagascar, Europe, Malaysia, Indonesia, Hawaii, several Pacific Islands, some Subantarctic Islands, Australia, New Guinea and New Zealand.

In 1964 and in 1968 opportunity arose to attend the XIIth and XIIIth International Congresses of Entomology held in London and Moscow respectively. Whilst journeying to and from these Congresses many institutions were visited where important collections of Psocoptera are held and special visits were made to centres where workers on the order reside who are not associated with institutions holding collections.

In 1964 collections at the following institutions were studied: Bernice P. Bishop Museum, Honolulu, Hawaii; California Academy of Sciences, San Francisco, California; United States National Museum, Washington, D.C.; Natural History Museum, New York; Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; British Museum (Natural History), London; Tring Museum, Tring; Leeds University, Leeds; Musee national d'Histoire naturelle, Paris; University of Hong Kong, Hong Kong.

In 1968 some of these institutions were revisited and visits to other collections not previously seen were included in my itinerary, namely: Bernice P. Bishop Museum; Normal State University, Normal, Illinois; Illinois State Natural History Survey, Urbana, Illinois; Royal Ontario Museum, Toronto, Canada; British Museum (Natural History); Tring Museum, Tring; Institut fur spezielle Zoologie, Humboldt Universitat, Berlin, D.D.R.; Rijksmuseum van Natuurlijke Historie, Leiden, Holland; Zoologisch Museum, Amsterdam, Holland; Naturhistorisches Museum, Vienna, Austria; Swedish Museum of Natural History, Stockholm, Sweden; Zoological Institute, University of Lund, Sweden; University of Moscow, U.S.S.R.; Palaeontological Institute, Moscow, U.S.S.R.; University of Singapore, Singapore.

Continuous access has been available to the collections of the several Australian State Museums and to the National Insect Collection, Canberra, Australian Capital Territory.

At the two International Congresses and at many of the institutions visited, current problems of psocid taxonomy and other aspects of psocid study were discussed with psocidologists.

I would like to thank the many colleagues in all these institutions who have helped me in so many ways. In particular I would like to thank Mr. J.V. Pearman, Professor A Badonnel and Professor E.L. Mockford for their helpful discussions on the Psocoptera; I have had the very helpful comments of Professor I.W.B. Thornton on a draft of this work.

In any present day studies we rest heavily on the work of our predecessors. I have been fortunate to have at my elbow, so to speak, the excellent library of the Australian Museum. Many of the references not in that library or in other Australian libraries, to all of which I have had free access, were seen in the libraries of the British Museum. As well as accumulating material, a deliberate attempt was made to compile a card index of references to the literature on the Psocoptera (Smithers, 1965d) and to the species of the World (Smithers, 1967).

From the study of my own collections, those of my generous colleagues, the institutions listed above and the literature have come the data used in the present study.

I would like to thank Mrs. Caroline Sinclair for patiently and carefully preparing the typescript and my wife for assistance in thefield, often under uncomfortable conditions, over many years.

Most of the laboratory work has been carried out in the Australian Museum.

Finally, I would like to express my appreciation of the guidance which I have had from Professor B.R. Allanson, Dr. G.B. Whitehead and Dr. E. McC. Callan whilst carrying out this work.

THE CLASSIFICATION AND PHYLOGENY OF THE PSOCOPTERA

CHAPTER I. INTRODUCTION

In the past two decades, there has been a considerable amount of discussion on questions of vital importance in relation to systematics, systematic theory and phylogenetic systematics. In the light of these developments, an attempt at reassessment of the classification of the insect Order PSOCOPTERA seemed worthwhile.

The aim of this work is to produce a classification of the Psocoptera which is reasonably practical as a working tool and also reflects the phylogeny of the members of the order. It was decided that as the scope was so large, that the problem be approached using the genus as the unit for consideration. Species within a genus not only exhibit many morphological features in common but they also have, in general, similarities in their biology, habitat requirements and behaviour and the genus can, therefore, be used as the unit in studies aimed at elucidating the relationships of groups of species.

The insect order Psocoptera (Psocids, Booklice, Barklice) is one of the so-called "minor" orders. It has, as is the case with many of the smaller orders, been somewhat neglected, not only in biological, physiological and ecological work but even where taxonomic studies are concerned. There are several reasons for this neglect. Psocids are small insects and usually at least some tedious dissection and preparation is needed before reliable determinations can be made; economically important species are few; until comparatively recently there were no faunal lists or bibliographies to guide the would-be student in his search for the remarkably scattered references to these insects. With so little in the way of background help there has been little incentive for new students to embark on their study. There has, nevertheless, always been a small number of workers publishing on the order.

Where a small number of scattered workers investigates a group of insects over a period of time, working on limited parts of the group or within set geographical limits there result small changes in classification of parts of the group. Sooner or later it becomes apparent that an overall reassessment of the classification in general use is advisable to assist in speeding an increase in knowledge of the systematics of the group as a whole. The phylogenetic system of reasoning put forward by Hennig (1966) makes it possible to establish the relationships of groups and results in the groups being arranged in a hierarchy. For such a system to be applied to an order of insects it is first necessary to have a fairly extensive knowledge of the order. In some cases it is possible to obtain adequate information from the literature where up-to-date works are available dealing with distinct faunal areas or where there are revisionary works at specific or generic level on a worldwide basis. Such works, however, are few on the Psocoptera and any attempt to reassess the classification of this order needs considerable prior descriptive work at the generic level, if not at the species level.

The first task was to obtain adequate information on the morphology and biology of the genera. This has, of course, been a large and somewhat tedious one. The literature was searched for information on each genus; where this has been inadequate attempts were made to obtain fresh material so that missing data could be included. Two hundred and fifteen genera of Psocoptera have been described. I have seen material of one hundred and thirty eight of these, in many cases several species have been available. Of the remaining genera fifty one can be considered adequately described and figured in the literature. This leaves twenty six genera. Many of these are based on single specimens and have not been collected since their first description or are genera known from very limited amber material; additional information on these is not therefore available to me.

In assembling information on the genera material in collections at my disposal have been examined; where possible dissections have been carried out. Material of other genera has been borrowed or obtained from colleagues and simiarly dealt with. Of many genera whole or dissected material has been seen in the collections of other institutions or individuals. In some cases material was available for inspection but not for dissection; this applies particularly to many type specimens preserved dry. It has been possible to provide adequate definitions for the most important of the described genera. At the same time illustrative material of most of the genera has been accumulated, either from published work, my own previously published material or by preparing fresh illustrations. Having thus accumulated data on morphology, biology and distribution of the Recent genera, it was considered necessary to have also some information on fossil forms for comparison. The process of data accumulation was then also carried out for fossil genera as for Recent forms. In this connection material in the Australian Museum and the opportunity of seeing the important collections in the Palaeontological Institute in Moscow have proved invaluable.

With data on Recent and fossil genera and with definitions fuller than have previously been available, the classification of the group, from a phylogenetic point of view, has been considered and a modified classification arrived at. The principles of Hennig have here been applied to the Psocoptera using ecological and biological data when available, as well as morphological data on Recent and fossil forms. The classification proposed in Chapter VII differs considerably from that now in general use and is considered to reflect phylogenetic relationships as well as being a classification which can be used for practical purposes.

CHAPTER II. GENERAL COMMENTS ON THE PSOCOPTERA

1. INTRODUCTION

The Psocoptera constitute an order of about 1,700 described species arranged at present in 215 genera. They are found in all regions. They range from less than 1 to almost 10 mm. in length, and have a characteristic appearance due, mainly, to their having a round, mobile head, long antennae, enlarged ptero-thorax and the wings held roofwise over the abdomen. Most species are winged as adults, but alary polymorphism occurs and brachyptery or aptery in one or both sexes is common. Their relationships are not clear, but their nearest living relatives appear to be the Phthiraptera-Mallophaga. Both groups have a hypopharynx of peculiar form, but fossil evidence to link them is lacking. The Psocoptera would seem to have been derived from primitive hemipteroid stock. Publications on the order up to 1964 have been listed and annotated by Smithers (1965c).

2. GENERAL DESCRIPTION OF ADULTS

Head. (Figs. 2.1, 2.2). Large and mobile, with distinct epicranial suture; clypeus divided into narrow transverse anteclypeus and characteristically bulbous postclypeus; frons small. Compound eyes usually strongly convex, sometimes reduced to groups of ommatidia (e.g. Liposcelis); 3 ocelli present in winged forms (usually absent in apterous forms), grouped in most families on a tubercle, widely separated in some (e.g. Lepidopsocidae). Antennae filiform, usually 13-segmented, segments sometimes very numerous (e.g. Lepidopsocidae, Trogiidae); scape and pedicel short, remaining segments elongate. Labrum simple. Mandibles asymmetrical, with large, ridged molar area and a toothed incisor edge (fig. 2.3). Maxillae (fig. 2.4) without differentiated cardo; stipes with a broad, fleshy galea strengthened by complex sclerotizations; lacinia modified into an elongate, strongly sclerotized rod, proximally sunken well into head capsule, apically variously toothed; palpi

4-segmented. Labium with sclerotized mentum; prementum divided; paraglossae membranous, flanking minute glossa; palpi reduced, 1- or 2-segmented. Hypopharynx with extremity of lingua bearing two superlinguae; lingua partially thickened ventrally into two oval lingual sclerites, each connected to a median sitophore sclerite by a fine filament.

Thorax. Prothorax reduced in winged forms; pterothorax well developed, the terga divided into a scutum and scutellum, behind which lies the postnotum. In apterous forms terga of meso- and metathorax sometimes fused, without subdivision. Pleura developed in accordance with powers of flight, reduced in flattened apterous forms. Sterna reduced in winged forms, broad in flattened apterous forms. Normally two pairs of spiracles.

Legs. Usually slender, similar; in *Liposcelis* the femora are strongly dilated. Hind coxae in many families bear on their inner surfaces a supposed stridulatory organ (Pearman's organ) (fig. 2.5) consisting of a small rugose dome and an adjacent membranous area of integument (tympan or mirror). Trochanters without movable articulation with femur. Tibiae long, cylindrical, apically spurred, carrying ctenidiobothria. Tarsi 2- or 3-segmented; at least 1st segment usually with row of ctenidiobothria; pretarsus with 2 apical claws, toothed or not, and a variously formed pulvillus (fig. 2.6); empodia lacking.

Wings. (Fig. 2.7). Membranous, hind wings smaller than fore wings, both often reduced or absent; at rest usually held roofwise over the body with the hind margins uppermost; coupled both in flight and at rest. Membrane usually bare, except for pterostigma, in some families scaled (e.g. Lepidopsocidae); veins and margins bare or setose. Venation of fore wing reduced; Sc reduced; pterostigma present, bounded behind by R_1; R and M usually 3-branched; M fused with Rs for a length, meeting it at a point, or joined to it by a cross-vein; M and Cu_1 fused in basal part of wing; Cu_1 usually forked distally, the cell between the branches (areola postica) being a characteristic feature of the psocopteran wing; M frequently fused with apex of areola postica, or joined to it by a cross-vein, or meeting it in a point (closed discoidal cell). Cu_2 (analis of Enderlein) usually finer than other veins, less often setose, runs free to margin in primitive forms, meets margin at same point (nodulus) as IA in advanced forms; only one anal vein (axillaris of Enderlein) present, except in Amphientomidae, Ptiloneuridae and extinct families. Hind wing with venation further reduced; M and Cu_1 usually not branched. Venational aberrations are frequent, and departures from the basic plan occur in some families, either by loss (especially of Cu_{1a}) or additional branching. The Lower Permian Psocoptera had a more generalized venation and other primitive features.

Abdomen. Nine-segmented, terminating in a dorsal epiproct and a pair of lateral paraprocts (fig. 2.8); paraprocts of winged forms usually each with a field of sensory setae (trichobothria) Cerci never present. Usually 8 pairs of spiracles. Sternum 9 of male (hypandrium) (fig. 2.9) well-developed, lying ventral to the phallosome, usually simple, sometimes complexly ornamented with sclerotized structures (e.g. Psocidae). The phallosome (fig. 2.10) consists of two "parameres" ("external parameres" of some authors), which are sclerotized and free distally, joined basally, and flank the aedeagus ("internal parameres" of some authors). Within the framework so formed lies the expanded and eversible end of the ejaculatory duct (penial bulb) of which the walls may be sclerotized in a complex manner (e.g. Peripsocidae). Sternum 7 of female forms well-developed subgenital plate (fig. 2.11). Ovipositor (fig. 2.12) of 3 pairs of valves: the gonapophyses of segment 8 (ventral valves) which are usually elongate and pointed; two pairs of appendages of segment 9, the dorsal valves, usually long and broader than the ventral valves, and the external valves, which are usually short, broad, and setose. Reduction of some or all of the valves occurs in varying degree, and they may be absent (some Archipsocus spp.).

Internal anatomy. Oesophagus elongate; midgut wide, convoluted, leading into short hind gut; 4 Malpighian tubes. A pair of long, tubular, ventral labial glands function as salivary glands, and a pair of variously formed dorsal glands as silk glands. Nerous system concentrated; meso- and metathoracic ganglia fused, and a single small abdominal ganglion adjacent to that in the pterothorax. Two large nerves and their branches from the abdominal ganglion serve the abdomen, except for segment 1 which is served by a pair of small nerves. Testes usually 3-lobed, sometimes spherical or fusiform; vasa deferentia lead to large, complex seminal vesicles which secrete spermatophore material; ejaculatory duct short, but broadens distally to form penial bulb of phallosome. Ovaries of 3-5 polytrophic ovarioles opening into common median duct via short transverse oviducts; gonopore behind sternum 7; a spermatheca opens on sternum 9 by a duct of variable length, the opening sometimes having characteristic adjacent sclerotizations.

3. IMMATURE STAGES

The eggs are ellipsoidal, ovoid, or oblong and the chorion may be sculptured or smooth. Development of the embryo has been followed in only a few species. Hatching is achieved with the aid of an egg-burster on the frontal region of the embryonic cuticle, which is immediately shed. On hatching, the nymph is generally like the adult, but always has 2-segmented tarsi, relatively shorter antennae, lacks ocelli and has equal thoracic segments. There are normally 6 nymphal instars, but the number may vary, especially in polymorphic species. Wing-bud development is apparent from the 2nd instar; rudiments of the external genitalia may be discernible in the final nymphal instar.

4. BIOLOGY

Psocids are found on the foliage or branches of trees and shrubs, on or under bark, on fences and walls, in leaf litter, under stones, on rocks, in caves, in human habitations, and in stored products. One species may occur in several habitats. They feed on unicellular algae, lichens, fungal hyphae, spores, and fragments of plant or insect tissue; Liposcelis bostrychophilus Bad. has been reared on yeast media.

Various degrees of intraspecific association are found, some species occurring in loose groups of adults and nymphs apparently brought into proximity of each other because of attraction to food source or other environmental factors. In other cases nymphs remain in close physical contact, the groups reassembling after forced dispersal of the members; the adults of such species are usually solitary. Small groups of nymphs or adults are sometimes found under communal webs, the size of web depending on the species; in Archipsocus the webs may be of spectacular proportions covering the trunks and branches of large trees. Nymphs are sometimes rendered inconspicuous by means of particles of debris adhering to glandular body hairs; other nymphs and adults may resemble their backgrounds by virtue of colour pattern.

The coxal (Pearman's) organ is presumably stridulatory in function. The ticking noise frequently described, however, is caused by the underside of the apex of the abdomen being struck against the surface on which the insect is standing.

Polymorphism is fairly common in some families, the usual form involving loss or reduction of wings in the female, but loss of wings in the male alone and equal reduction in both sexes are also known. Control of polymorphism appears in some species to be at least in part environmental and loss or reduction of wings is frequently associated with loss of ocelli, trichobothria and coxal organ, and retention of duplex setae in the adult.

Copulation is usually preceded by a prenuptial dance, the male facing the female or approaching from behind, after which he intrudes himself backwards under her, from in front. Spermatozoa are transferred in a spermatophore which may be of complex form (e.g. *Lepinotus*). Eggs are laid singly or in groups on or under bark, or on leaves, usually on the lower surface and frequently adjacent to a vein. They may also be laid on other substrata. They may be covered with silk or an encrustation of debris. Viviparity occurs in *Archipsocus*, and obligatory parthenogenesis is frequent. Males are rare in some species and species are known which are parthenogenetic in some parts of their range but not in others; facultative parthenogenesis also occurs.

5. NATURAL ENEMIES

Psocids are preyed upon by spiders, pseudoscorpions, neuropterous larvae, ants, reduviids, wasps and thrips. They are attacked by parasitic nematodes and entomophagous fungi; the gut usually contains protozoa. Mymarid parasites (*Alaptus* spp., Hymenoptera) and capsid predators (Hemiptera) have been recorded as destroying eggs.

6. ECONOMIC SIGNIFICANCE

Psocids are not of great economic importance although species associated with stored products sometimes develop enormous populations. Their occurrence seems usually to be secondary, poor storage and infestation by pests rendering conditions suitable for them (Champ and Smithers, 1965) but there is some evidence that they may cause damage to whole grain. They occasionally occur in large numbers in houses, where they are a nuisance rather than destructive. Neglected insect collections may be ruined by psocids (usually *Liposcelis* spp.).

CHAPTER III. PRESENT CLASSIFICATION OF THE PSOCOPTERA

1. BRIEF HISTORY OF THE CLASSIFICATION OF THE PSOCOPTERA

The classification put forward in Chapter VII is a result of a reassessment of that in use by most present-day authors. There have been changes in the past and in order to put the latest suggested changes into perspective a brief history of the classification of the order is given here.

Latreille (1794) was the first author to separate off the insects today included in the Psocoptera as a distinct group. He united them under the generic name Psocus and included them in the Neuroptera.

Leach (1815) considered the psocids as a tribe (Psocides) of the order Neuroptera and divided them into two families, the winged Psocida and the wingless Atropida. The term Neuroptera still covered very diverse insect forms such as the present Odonata, Ephemeroptera, Plecoptera and Isoptera.

Curtis (1837) used the family name Psocidae and made use of venational characters in his generic diagnoses of winged forms.

Burmeister (1839) used the name Corrodentia to cover the present Isoptera, Embioptera, Coniopterygidae and Psocoptera. Venational and tarsal characters were used in his generic diagnoses and he grouped all the known species into three genera within one family, Psocina.

Hagen (1854) included the Isoptera, Embioptera, Psocoptera, Plecoptera, Ephemeroptera, Phasmida and Odonata in the Pseudoneuroptera. The same author (Hagen, 1866b) later published a synonymic synopsis in which he grouped the 136 known species in 21 genera. These he included in the single family Psocina and set out their characteristics in a key, using ocellar, tarsal and wing characters. This work forms the starting point for any serious work at the species level and was the first adequate synopsis of the known species.

Kolbe (1880b) reclassified his family Psocidae into five tribes, mainly on the basis of wing and tarsal characters and attempted to interpret the various forms as an evolutionary sequence. He retained the family in the Pseudoneuroptera. Kolbe's system was not generally accepted and Leach's arrangement continued to be used by most authors.

Enderlein (1903e) used the name Copeognatha as a subordinal name for the Psocidae and in another paper (Enderlein, 1903a) reclassified the group with a basic dichotomy determined by tarsal segmentation. Eleven families, divided into many subfamilies, were recognised and although wing characters were considered of prime importance in classification, other features, such as antennae, mouthparts, ocelli and, occasionally, genitalia, were used. Other authors (e.g. Ribaga, 1905b) also introduced such features in their descriptions at about that time.

Shipley (1904) regarded the psocids as a distinct order and employed the term Psocoptera.

Enderlein (1911b) extended his previous classification (Enderlein, 1903a) including forms which had been described from amber. He still maintained a basic dichotomy based on the number of tarsal segments and he proposed a detailed nomenclature to cover a complex set of dichotomies devised in an attempt to express his opinions on the phylogeny of the group (Enderlein, 1911b, Pl. XXVII).

Tillyard (1926a) also suggested a division of the order into two, using the subordinal names Parapsocida and Eupsocida for these. His division into suborders, however, was based on antennal, wing and prothoracic characters and cut across the primary divisions proposed by Enderlein.

Banks (1929) considered the group as of superfamily status, the Psocoidea, and added a second superfamily, the Zorotypoidea (for Zorotypus), placing them both in the order Corrodentia. The Psocoidea he divided into six families, using tarsal, thoracic, and antennal characters. In his many other papers Banks used wing venation extensively as a taxonomic character.

Karny (1930) proposed a classification in which he included fossil forms, dividing the group into four, using mainly wing, antennal and tarsal features. His classification included a detailed listing of families, subfamilies, tribes and genera.

Prior to Pearman's work (Pearman, 1936a) classifications were based mainly on fairly obvious, easily seen features. The differences in the classifications can be largely accounted for by the differing emphasis put on the various features by the authors in a somewhat arbitrary fashion.

Pearman (1936a) adopted a new approach and investigated a wide range of morphological features, including genitalia, as a result of which he proposed a new grouping of the order into 26 families plus a small group of unplaceable genera. He united genera which shared groups of characters and thus bore overall resemblance to one another. Unfortunately, he did not provide definitions of his new family divisions but merely mentioned one or two genera in each. The families he grouped into seven main categories to which he "would ascribe a status somewhat superior to that of a super-family". An eighth family group (the Homilopsocidea) was erected to accommodate nine families which could not be fitted into his other seven family groups. In addition to morphological features he mentioned the types of egg-laying habits found in each family. A full treatment of the subject was promised (Pearman, 1936a, p. 58) but has not yet appeared.

Roesler (1944) provided a key to the then-known genera. He arranged these in seventeen families grouped into three suborders. He retained the family groups of Pearman but redistributed the families in Pearman's Homilopsocidea. At the same time he grouped some of Pearman's families and split others. A wide range of morphological characters was used by Roesler.

Badonnel (1951) used a combination of the classifications of Pearman and Roesler in that he retained Pearman's family groups (including the Homilopsocidea) but superimposed Roesler's subordinal grouping of the families. Badonnel's classification is at present the most widely used arrangement.

The works mentioned above are the main steps via which the currently accepted classification of the Psocoptera has been reached. There have been, in addition, papers in which changes of a more minor or more transient nature have been made (e.g. Roesler, 1940a, 1940b, 1940c, 1943; Badonnel, 1955; Smithers, 1964e, 1967a).

Pearman's work (1936a) made it clear that all previously suggested arrangements, based as they were on a few morphological characters, were "artificial" in the sense that not even the initial division of the group indicated relationships and that genera which would be considered closely related on venational evidence alone were, in fact, found to be much less closely related when a wider range of morphological features was considered. Pearman's classification was an attempt to indicate natural relationships and this aim was to some extent achieved but its shortcoming were recognised by the setting up of the Homilopsocidea for those families of which the relationships were thought not to be clear mainly because sufficient data were not available. Also, later study has indicated that some other groups, e.g. Calopsocidae, which were thought to be well placed also needed reconsideration. Roesler (1944) attempted to eliminate the Homilopsocidea. This he achieved by suggesting that Pearman's homilopsocidean families with 2-segmented tarsi be united into one family (Pseudocaeciliidae sens. Roesler) and those with 3-segmented tarsi into another (Mesopsocidae sens. Roesler). The Hemipsocidae he placed in the Psocidae. Whilst this arrangement clearly has much to recommend it, it does include some anomalies, particularly in that the Pseudocaeciliidae (sens. Roesler) became a heterogeneous group to some extent owing to the inclusion of the Lachesillidae, Peripsocidae and some genera which were generally accepted as belonging to the Elipsocidae. There are several minor anomalies in Roesler's scheme e.g. the inclusion of Chaetopsocus in the Trichopsocidae (Trichopsocinae of Roesler); Chaetopsocus is a synonym of Ectopsocus. On the whole, however, Roesler's classification represents an advance on Pearman's in so far as at least some indication of the relationships of some of the homilopsocidean families are indicated by his grouping.

Badonnel (1951) has made a compromise between Pearman's and Roesler's classifications. He retained the Homilopsocidea but grouped the families with 2 or 3-segmented tarsi under non-commital headings.

Table 1 indicates the relations which the classifications of Pearman (1936a), Badonnel (1951) and Roesler (1944) bear to each other.

Table 2 is a synopsis of the family arrangements in general use, that is, it is virtually the classification of Badonnel (1951) incorporating the several subsequent changes of varying magnitude which have been suggested in later literature.

TABLE 1. RELATIONSHIPS BETWEEN RECENT CLASSIFICATIONS

Pearman 1936a	Badonnel 1951	Roesler 1944
PSOCOPTERA	PSOCOPTERA	COPEOGNATHA
	TROGIOMORPHA	TROGIOMORPHA
ATROPETAE	ATROPETAE	ATROPETAE
Lepidopsocidae	Lepidopsocidae	Lepidopsocidae
Atropidae	Trogiidae)	Trogiidae
Psoquillidae	Psoquillidae)	
PSOCATROPETAE	PSOCATROPETAE	PSOCATROPETAE
Psocatropidae	Psyllipsocidae)	Psyllipsocidae
Scoliopsyllopsidae	Prionoglaridae)	
	TROCTOMORPHA	TROCTOMORPHA
AMPHIENTOMETAE	AMPHIENTOMETAE	AMPHIENTOMETAE
Amphientomidae	Amphientomidae	Amphientomidae
	Plaumannidae	Plaumannidae
NANOPSOCETAE	NANOPSOCETAE	NANOPSOCETAE
Liposcelidae	Liposcelidae	Liposcelidae
Pachytroctidae	Pachytroctidae	Pachytroctidae
	PSOCOMORPHA	EUPSOCIDA
CAECILIETAE	CAECILIETAE	CAECILIETAE
Calopsocidae	Calopsocidae	Neurosemidae
Caeciliidae	Caeciliidae)	
Amphipsocidae	Amphipsocidae)	Polypsocidae
Stenopsocidae	Stenopsocidae)	
Polypsocidae	Polypsocidae)	
EPIPSOCETAE	EPIPSOCETAE	EPIPSOCETAE
Epipsocidae	Epipsocidae	Epipsocidae
	Ptiloneuridae	Ptiloneuridae
	Callistopteridae	Callistopteridae
	Psilopsocidae	Psilopsocidae
PSOCETAE	PSOCETAE	PSOCETAE
Myopsocidae	Myopsocidae	Myopsocidae
Thyrsophoridae	Thyrsophoridae)	
Psocidae	Psocidae)	
	)	Psocidae
HOMILOPSOCIDEA	HOMILOPSOCIDEA)	
Hemipsocidae	Hemipsocidae)	
Elipsocidae	Elipsocidae)	
Philotarsidae	Philotarsidae)	Mesopsocidae
Mesopsocidae	Mesopsocidae)	
Pterodelidae	Lachesillidae)	
Peripsocidae	Peripsocidae)	
Pseudocaeciliidae	Pseudocaeciliidae)	Pseudocaeciliidae
Trichopsocidae	Trichopsocidae)	
Archipsocidae	Archipsocidae)	
PSOCIDA AGNOTA		

Allopsocus, Valenzuela etc.

TABLE 2. PRESENT ARRANGEMENT OF FAMILIES

Order PSOCOPTERA

Suborder TROGIOMORPHA

Atropetae
- Lepidopsocidae
- Trogiidae
- Psoquillidae

Psocatropetae
- Psyllipsocidae
- Prionoglaridae

Suborder TROCTOMORPHA

Amphientometae
- Amphientomidae
- Musapsocidae
- Troctopsocidae
- Manicapsocidae
- Compsocidae

Nanopsocetae
- Liposcelidae
- Pachytroctidae
- Sphaeropsocidae

Suborder PSOCOMORPHA

Epipsocetae
- Epipsocidae
- Ptiloneuridae
- Callistopteridae

Caecilietae
- Caeciliidae
- Stenopsocidae
- Amphipsocidae
- Polypsocidae

Homilopsocidea
- Lachesillidae
- Peripsocidae
- Hemipsocidae
- Calopsocidae
- Pseudocaeciliidae
- Trichopsocidae
- Archipsocidae
- Elipsocidae
- Psoculidae
- Philotarsidae
- Mesopsocidae

Psocetae
- Psocidae
- Thyrsophoridae
- Psilopsocidae
- Myopsocidae

Psocida Agnota

2. PRESENT ARRANGEMENT OF GENERA

Given below is the arrangement of genera used by most present day authors. This is intended as a reference list; details of characters and discussion of proposed changes in this classification, both at generic and at higher levels, are dealt with more appropriately in other parts of this work. Genera which include species from amber are marked with an asterisk (*). Fossil genera are dealt with separately later.

Order PSOCOPTERA

Suborder TROGIOMORPHA

Group ATROPETAE

Family LEPIDOPSOCIDAE

Subfamily THYLACELLINAE

* Thylacella Enderlein, * Thylax Hagen.

Subfamily PERIENTOMINAE

Lepium Enderlein, * Nepticulomima Enderlein, Notolepium Enderlein, Parasoa Thornton, * Perientomum Hagen, Proentomum Badonnel, Soa Enderlein.

Subfamily LEPIDOPSOCINAE

Cyptophania Banks, Echinopsocus Enderlein, * Echmepteryx Aaron, Lepidopsocus Enderlein, Pteroxanium Enderlein, Scolopama Enderlein.

Subfamily LEPOLEPIDINAE

Lepolepis Enderlein.

Family TROGIIDAE

Subfamily EMPHERIINAE

* Empheria Hagen, * Trichempheria Enderlein.

Subfamily TROGIINAE

Anomocopeus Badonnel, Cerobasis Kolbe, Lepinotus Heyden, Myrmicodipnella Enderlein, Trogium Illiger.

Family PSOQUILLIDAE

Balliella Badonnel, Eosilla Ribaga, Psoquilla Hagen, Rhyopsocus Hagen.

Group PSOCATROPETAE

Family PSYLLIPSOCIDAE

Dolopteryx Smithers, Dorypteryx Aaron, Psocatropos Ribaga, * Psyllipsocus Selys-Longchamps, Speleketor Gurney.

Family PRIONOGLARIDAE

Prionoglaris Enderlein.

Suborder TROCTOMORPHA

Group AMPHIENTOMETAE

Family AMPHIENTOMIDAE

Subfamily ELECTRENTOMINAE

* Electrentomum Enderlein, * Parelectrentomum Roesler.

Subfamily TINEOMORPHINAE

Cymatopsocus Enderlein, Tineomorpha Enderlein.

Subfamily AMPHIENTOMINAE

* Amphientomum Pictet, Hemiseopsis Enderlein, Marcenendius Navas, Nephax Pearman, Paramphientomum Enderlein, Pseudoseopsis Badonnel, Seopsis Enderlein, Seopsocus Roesler, Stigmatopathus Enderlein, Stimulopalpus Enderlein, Syllysis Hagen.

Family MUSAPSOCIDAE

Musapsocus Mockford.

Family TROCTOPSOCIDAE

Protroctopsocus Mockford, Troctopsocopsis Mockford, Troctopsoculus Mockford, Troctopsocus Mockford.

Family MANICAPSOCIDAE

Epitroctes Mockford, Manicapsocus Smithers, Nothoentomum Badonnel, Phallopsocus Badonnel.

Family COMPSOCIDAE

Compsocus Banks, Electrentomopsis Mockford.

Group NANOPSOCETAE

Family LIPOSCELIDAE

Subfamily EMBIDOPSOCINAE

Belapha Enderlein, Belaphopsocus Badonnel, Belaphotroctes Roesler, Embidopsocus Hagen, Troctulus Badonnel.

Subfamily LIPOSCELINAE

* Liposcelis Motschulsky.

Family PACHYTROCTIDAE

Subfamily TAPINELLINAE

* Psylloneura Enderlein, Tapinella Enderlein.

Subfamily PACHYTROCTINAE

Antilopsocus Gurney, Pachytroctes Enderlein.

Family SPHAEROPSOCIDAE

Badonnelia Pearman, Sphaeropsocopsis Badonnel, * Sphaeropsocus Hagen.

Suborder PSOCOMORPHA

Group EPIPSOCETAE

Family EPIPSOCIDAE

Subfamily GOJINAE

Goja Navas.

Subfamily NEUROSTIGMINAE

Neurostigma Enderlein.

Subfamily EPIPSOCINAE

Epipsocopsis Badonnel, * Epipsocus Hagen.

Family PTILONEURIDAE

Cladiopsocus Roesler, Euplocania Enderlein, Ptiloneura Enderlein, Ptiloneuropsis Roesler, Triplocania Roesler.

Family CALLISTOPTERIDAE

Callistoptera Enderlein.

Group CAECILIETAE

Family CAECILIIDAE

Subfamily DYPSOCINAE

Coryphosmila Enderlein, Dypsocus Hagen, Isophanes Banks.

Subfamily CAECILIINAE

Asiopsocus Gunther, * Caecilius Curtis, Dasydemella Enderlein, Enderleinella Badonnel, Eocaecilius Badonnel, Fulleborniella

Enderlein, Lacroixiella Badonnel, Maoripsocus Tillyard, Mepleres Enderlein, Paracaecilius Badonnel, * Ptenolasia Enderlein, Ptenopsila Enderlein, Tagalopsocus Banks, Teliapsocus Chapman, Ypsiloneura Pearman.

Subfamily SCHIZOPECHINAE

Schizopechus Pearman.

Family STENOPSOCIDAE

Epikodamaius Kuwayama, Graphopsocus Kolbe, Kodamaius Okamoto, Matsumuraiella Enderlein, Stenopsocus Hagen, Taeniostigma Enderlein.

Family AMPHIPSOCIDAE

Subfamily AMPHIPSOCINAE

Amphipsocopsis Smithers, Amphipsocus McLachlan, Harpezoneura Enderlein, Pentathyrsus Enderlein, Xenopsocus Kolbe.

Subfamily KOLBEINAE

Dasypsocus Enderlein, * Kolbea Enderlein.

Family POLYPSOCIDAE

Monocladellus Enderlein, Polypsocus Hagen.

Group HOMILOPSOCIDEA

Family LACHESILLIDAE

Eolachesilla Badonnel, Lachesilla Westwood.

Family PERIPSOCIDAE

Subfamily ECTOPSOCINAE

Ectopsocopsis Badonnel, Ectopsocus McLachlan, Interpsocus Edwards.

Subfamily PERIPSOCINAE

Kaestneriella Roesler, Notiopsocus Banks, Peripsocus Hagen.

Subfamily (?)

Anomopsocus Roesler.

Family HEMIPSOCIDAE

Anopistoscena Enderlein, Hemipsocus Selys-Longchamp.

Family CALOPSOCIDAE

Calopsocus Hagen, Dirla Navas, Neurosema McLachlan.

Family PSEUDOCAECILIIDAE

Subfamily PSEUDOCAECILIINAE

Allocaecilius Lee and Thornton, Cladioneura Enderlein, Heterocaecilius Lee and Thornton, Lobocaecilius Lee and Thornton, Mesocaecilius Okamoto, Pseudocaecilius Enderlein, Ophiodopelma Enderlein, Phallocaecilius Lee and Thornton, Pseudoscottiella Badonnel, Scottiella Enderlein, Scytopsocopsis Lee and Thornton, Trichocaecilius Badonnel, Scytopsocus Roesler.

Subfamily ELECTROPSOCINAE

* Electropsocus Roesler.

Family TRICHOPSOCIDAE

* Palaeopsocus Kolbe, Trichopsocus Kolbe.

Family ARCHIPSOCIDAE

Archipsocopsis Badonnel, * Archipsocus Hagen.

Family ELIPSOCIDAE

Subfamily ELIPSOCINAE

Cuneopalpus Badonnel, Drymopsocus Smithers, * Elipsocus Hagen, Hemineura Tetens, Kilauella Enderlein, Palistreptus Enderlein.

Subfamily PSEUDOPSOCINAE

Palmicola Mockford, Pseudopsocus Kolbe, Reuterella Enderlein.

Subfamily PROPSOCINAE

Antarctopsocus Badonnel, Pentacladus Enderlein, * Propsocus McLachlan, Spilopsocus Smithers.

Subfamily NEPIOMORPHINAE

Nepiomorpha Pearman, Nothopsocus Badonnel, Paedomorpha Smithers, Roesleria Badonnel.

Subfamily LESNEIINAE

Lesneia Badonnel, Graphocaecilius Enderlein, Hemicaecilius Enderlein, Lenkoella Machado-Allison and Papavero.

Family PSOCULIDAE

Psoculus Roesler.

Family PHILOTARSIDAE

Aaroniella Mockford, Austropsocus Smithers, Haplophallus Thornton, Philotarsopsis Tillyard, * Philotarsus Kolbe, Zelandopsocus Tillyard.

Family MESOPSOCIDAE

Hexacyrtoma Enderlein, Labocoria Enderlein, Mesopsocus Enderlein.

Group PSOCETAE

Family PSOCIDAE

Subfamily AMPHIGERONTIINAE

Amphigerontia Kolbe, Blaste Kolbe, Blastopsocidus Badonnel, Elaphopsocus Roesler, Neoblaste Thornton, Neopsocopsis Badonnel.

Subfamily ANTIPSOCINAE

Antipsocus Roesler.

Subfamily CERASTIPSOCINAE

Tribe CERASTIPSOCINI

Cerastipsocus Kolbe, Eremopsocus McLachlan, Psococerastis Pearman, Scaphopsocus Smithers.

Tribe METYLOPHORINI

Brachinodiscus Enderlein, Diplacanthoda Enderlein, Metylophorus Pearman, Pilipsocus Badonnel.

Tribe CYCETINI

Cycetes Enderlein.

Subfamily PSOCINAE

Atlantopsocus Badonnel, Camelopsocus Mockford, Copostigma Enderlein, Ghesquierella Badonnel, Hyalopsocus Roesler, Neopsocus Kolbe, Oreopsocus Roesler, Pearmania Badonnel, * Psocidus Pearman, Psocus Latreille, Ptycta Enderlein, Steleops Enderlein, * Trichadenotecnum Enderlein.

Family THYRSOPHORIDAE

Dictyopsocus Enderlein, Thyrsophorus Burmeister, Thyrsopsocus Enderlein.

Family PSILOPSOCIDAE

Psilopsocus Enderlein.

Family MYOPSOCIDAE

Lophopterygella Enderlein, Myopsocus Hagen, Phlotodes Enderlein.

PSOCIDA AGNOTA

Allopsocus Banks, Valenzuela Navas.

CHAPTER IV. DEFINITIONS OF GENERA AND SUPRAGENERIC CATEGORIES

Although several attempts at a comprehensive classification of the Psocoptera have been made, in most of the earlier attempts the characters used have been limited; they seldom included other than wing, tarsal, antennal, mouthpart or ocellar features. Pearman (1936a), Roesler (1944) and Badonnel (1951) have been the main authors responsible for attempting comprehensive classifications using a wider range of morphological and, occasionally, other features. Any attempts at classification in the past, however, have suffered from one great drawback; a great many genera have been described very sketchily and the original generic descriptions, as well as those of any subsequently included species, have contained reference to a very limited (in some case only one or two) morphological features. As a result of this, the placing of many genera was largely guesswork, using a somewhat intuitive method based on broad experience of the order. Thus, for example, the Calopsocidae came to be placed in the group Epipsocetae; study of fresh material paying attention to a wider range of features, including genitalia, than had hitherto been used resulted in the realisation that the family is very similar to the Pseudocaeciliidae in most features, but happens to differ in some conspicuous, significant ways (Smithers, 1967a).

Further examples of the difficulties arising from lack of knowledge of the detailed morphology of genera will not be given here, although this is of frequent occurrence in the Psocoptera and many such cases will become immediately apparent in the rearrangements of genera suggested later in this work. Many genera have been so poorly described in the literature that any logical discussion of them has been impracticable. Clearly, in order to remove this major obstacle, it was necessary to assemble the basic data to make such discussion possible. To fulfil this need, an attempt has been made to provide adequate descriptions for as many genera of the order as possible. This has been a considerable task and the definitions arrived at by the expansion of the published descriptions through additional investigation are given below. The manner in which the information has been assembled was mentioned in Chapter I.

Even now, however, some genera remain which cannot be compared with others because of lack of material. Some genera were erected on the basis of a single, inadequately described specimen; in a few cases it is likely that even this one specimen has been destroyed by war, revolution or neglect of collections. It is felt, however, that the more comprehensive descriptions given here reduce the number of inadequately described genera to a level such that adequate knowledge of the morphology of enough of the genera has now been assembled to make a reasonable discussion of classification and phylogeny possible.

In order that the grouping and relationships of the genera and higher groups which have been accepted in the past and those which are proposed later can be discussed it is necessary to have a clear statement of the limits of these generic and suprageneric categories. There is given here, therefore, a set of definitions of the genera and suprageneric groups which form part of the basis for later discussion of classification, phylogeny and zoogeography.

In the definitions of the suprageneric categories the characters given do not always occur in all genera in the group although they occur in the majority. Characters mentioned in the definitions are not mentioned again in the definitions of subsidiary groups without special reason for doing so. Some characters conditions, such as brachyptery or aptery, occur in many groups and although the suprageneric definition may contain reference to a condition some genera may not have that character condition.

(Note: In the definitions which follow, groups which include species from amber are marked with an asterisk (*)).

DEFINITION OF THE PSOCOPTERA

A brief general account of the main features of the order has already been given; detailed generic definitions follow. A concise definition of the order is as follows:

Small, free-living, exopterygote Neoptera, with large, mobile head, filiform antennae and bulbous postclypeus; mandibles asymmetrical; maxillae with rod-shaped lacinia; labial palpi reduced; wings membranous, usually held roofwise over abdomen, venation reduced and specialized; brachyptery and aptery frequent; tarsi 2- or 3-segmented in adults, 2-segmented in nymphs; cerci absent.

CHARACTERS OF THE SUBORDER TROGIOMORPHA

Antennae of more than 20 segments, without secondary annulations. Adults with 3-segmented tarsi. Labial palps 2-segmented. Paraprocts usually with a strong posterior spine. In winged forms pterostigma not thickened. Hypopharynx with chitinous filaments separated for whole length. Stigmapophysis and coupling apparatus at nodulus in form of separate hooks.

CHARACTERS OF THE GROUP ATROPETAE

Head short and broad. Inner side of second segment of maxillary palp with conical sensillum. Antennae never with secondary annulations. Fore wings without nodulus; brachyptery and aptery common. Hind tibia and tarsus together shorter than abdomen. Body and wings sometimes clothed with scales. Gonapophyses of females reduced. Eggs sculptured, laid singly, without any form of covering.

CHARACTERS OF THE LEPIDOPSOCIDAE

Belonging to the Trogiomorpha. Antennae of numerous segments (more than twenty sometimes as many as fifty) without secondary annulation; ocelli widely separated, not grouped on a tubercle. Lacinia apically divided with a few teeth, usually with one tooth shorter than the others. Maxillary palps with a sensillum on the inner side of the second segment. Labial palp 2-segmented. Fore wings usually acuminate, clothed with scales, as are the legs and body. Pterostigma not thickened. Sc frequently well developed, distal section relatively long. R - Rs crossvein usually present. Rs and M usually fused for a length with M branching near separation from Rs. Bifurcation of Cu_1 relatively near wing base giving a long areola postica. Cu_2 and IA end separately at wing margin, that is, no nodulus. In hind wing R_1 relatively long. M with two branches arising separately. There is a general tendency for vein branching to result in strongly acute angles at the bifurcations so that the veins tend to run a course more nearly parallel to the wing axis than is usual in the order. Stigmapophysis and coupling at nodulus in form of a series of hooks. Tarsi 3-segmented. Claws with strong apical curvature and with at least one strong preapical tooth, sometimes more than one, with or without smaller teeth. Pulvillus long, fairly fine, pointed or expanded at tip. Coxal rasp present. Paraproct with strong posterior spine. Trichobothrial field absent but some setae with basal rosettes may be present. Female gonapophyses reduced to a small, frequently lightly sclerotized dorsal valve and a large, elongate-ovoid setose, external valve. Dorsal valve sometimes absent. Male phallosome with anteriorly diverging parameres and more or less complex median aedeagus. Eggs with sculptured chorion, layed singly, not covered with silk nor encrusted with debris.

GENERA INCLUDED IN THE LEPIDOPSOCIDAE

Thylacellinae:

Thylacella Enderlein, 1911
Thylax Hagen, 1866

Perientominae:

Lepium Enderlein, 1906
Nepticulomina Enderlein, 1906
Notolepium Enderlein, 1910
Parasoa Thornton, 1962
Perientomum Hagen, 1865
Proentomum Badonnel, 1949
Soa Enderlein, 1904

Lepidopsocinae:

Cyptophania Banks, 1931
Echinopsocus Enderlein, 1903
Echmepteryx Aaron, 1886
Lepidopsocus Enderlein, 1903
Pteroxanium Enderlein, 1922
Scolopama Enderlein, 1906

Lepolepidinae:

Lepolepis Enderlein, 1906

Subfamily THYLACELLINAE

* *Thylacella* Enderlein (13 species)

Thylacella Enderlein, 1911. *Palaeontographica* 58: 439.
Type species: *T. eversiana* Enderlein.

Median epicranial suture sometimes with distinct anterior arms (figs. 4.1, 4.2). Vertex strongly arched, strongly setose. Frons large, postclypeus fairly flat; setae more dispersed than on upper part of head. Genae sometimes with a few setae. Antennae long, with up to about forty segments, eyes usually large, reaching level of vertex, setose. Ocelli widely spaced, anterior ocellus tending to be reduced in size. Lacinia (fig. 4.3) usually fairly simply divided at apex. Fourth segment of maxillary palp broadened, somewhat hatchet-shaped. Fore wings (fig. 4.4) narrow, elongate usually pointed, sometimes slightly thickened. Basal section of Sc evanescent, distal section well developed. Pterostigmal area long and fairly flat. R - Rs crossvein short. Rs and M fusion long. Rs divided at end of long stem. M_3 arising near separation of M from Rs and Cu_1. IA frequently evanscent. Anal area slightly angled. Wings setose on membrane as well as elsewhere, but not scaly; margin with long, dense hairs. Hind wing (fig. 4.5) pointed, elongate, narrow. Sc usually evanescent. R_1 arises proximal of M_2. A closed basal cell is present M + Cu being separate from R basally, M joining R in a long fusion after separation from Cu_1. Branches of Rs ending on either side of wing apex. M 2-branched, the branches arising from a oommon stem or separately. Veins and membrane, especially in distal part of wing, setose, margin long hairy. Claws (fig. 4.11) with two preapical teeth; pulvillus fairly broad, expanded apically. Paraproct (fig. 4.6) usually ovoid, with a strong posterior spine and scattered setae. A small group of trichobothria may occur, not grouped into a field, with an adjacent normal seta. Subgenital plate simple. Gonapophyses (fig. 4.7) reduced to an elongate, tapering, round-ended setose external valve with or without a remnant of a dorsal valve. Sclerification of valves very variable, generally slight. Hypandrium simple. Phallosome (figs. 4.8 - 4.10) consisting of two anteriorly diverging external parameres which are expanded posteriorly into strongly developed lobes; parameres joined by transverse sclerite near base of posterior expansions.

Habitat: Leaf litter, bird's nests. (One species in Copal from Zanzibar).

Distribution: Zanzibar (Copal), "East Africa", Congo, Nigeria, Angola, Rhodesia, Tanganyika, Mozambique, Madagascar.

* Thylax Hagen (1 species)

Thylax Hagen, 1866. Ent. mon. Mag. 2: 172.
Type species: T. fimbriatum Hagen.

Hagen (1866): "In some degree resembling Empheria, but differs as follows. The ocelli are more separated; antennae 40-jointed, but shorter, and the two basal joints stouter. Prothorax forming a transverse ring slightly narrower than the head. Wings rather long, very narrow, lanceolate; the posterior margin appears angulated before the middle; reticulation analogous, but the median vein and the subcosta are united by a transverse vein before the pterostigma, so that there is an elongated hexagonal areola below it; the simple branch of the superior fork broken at the base, so as to form a short transverse vein from below. Inferior wings much more acute, the anterior margin excised at the apex; neuration as in A. paradoxum".

Habitat: Unknown.

Distribution: Zanzibar (Copal).

Note: The above description is quoted from Hagen (1866). There is no mention made of scales on the wings or body and from the little information given it seems that this genus is similar to Thylacella. Until further material is forthcoming the most that can be done is to allow the genus to stand and consider it as being related to Thylacella.

Subfamily PERIENTOMINAE

Lepium Enderlein (3 species)

Lepium Enderlein, 1906. *Spolia zeylan*. 4: 81.
Type species: *L. chrysochlorum* Enderlein.

Epicranium steep with fairly sharp vertex. Frons and postclypeus fairly flat. Eyes large, prominent, closely and finely pubescent. Ocelli widely spaced, anterior ocellus smaller than lateral ocelli which are near the eyes. Lacinia (fig. 4.12) with trifid apex, one tooth being smaller and at an angle divergent to the others. Fourth segment of maxillary palp hatchet-shaped. Claws (fig. 4.13) very long and narrow with small preapical tooth. Pulvillus long and fine. Fore wings (fig. 4.14) fairly broad, pointed. Setae occur between the scales. Hind margin hairy as far as Cu_2. Area between subcosta and costa thickened, bearing setae but not scales. Sc well developed in basal section and distal section of Sc long. R_1 - Rs crossvein present. Venation similar in other respects to *Thylacella*. Stigmapophysis in form of series of hooks. Hind wing (fig. 4.15) with margin, except costal margin of costal cell, strongly setose. Basal part of costa with short hairs. Veins in distal part of wing with more than one row of setae; membrane in distal half sparsely setose. Narrow basal cell present. Sc basal section present; distal section absent. M_2 arises separately from M_1 and basad of R_1. IA distinct.

The genital structures of this genus are not known.

Habitat: On house walls, in leaf litter and under bark of dead trees.

Distribution: Ceylon, Formosa, India.

* Nepticulomima Enderlein (13 species)

Nepticulomima Enderlein, 1906. Spolia zeylan. 4: 95.

Type species: N. sakuntala Enderlein.

Wings and body with scales. Vertex setose, hair long. Antennae fairly long, thin; at most 24-segmented. Segments much longer than wide. Eyes large; pubescence relatively long and stout. Ocelli wide apart, anterior ocellus tending to be smaller than others. Lacinia (fig. 4.16) apically divided into two, one tooth showing signs of further subdivision. Claws (fig. 4.17) slender, apically strongly curved; one or two preapical teeth (variable feature). Fore wings (fig. 4.18) with pointed apex. Venation similar to that of Lepium, Sc evanescent basally. R_1 long, joined to Rs by a short crossvein or fused with it for a length. Hind wing with closed basal cell. R_1 arises distad of M_1. Paraproct with strong posterior spine and some trichobothria not grouped into a field. Subgenital plate simple. Gonapophyses (fig. 4.19) reduced to elongate, ovoid, setose external valve. Hypandrium simple. Phallosome (figs. 4.20, 4.21) with well developed parameres and complex aedeagus.

Habitat: On rotten wood, on walls of houses, on bark in rain forest.

Distribution: Zanzibar (Copal), Cameroons, Ivory Coast, Congo, Seychelles, Ceylon, Malaya, Java, Bismarck Archipelago, New Guinea, Queensland, Samoa, Brazil, England (in stored products).

Notolepium Enderlein (1 species)

Notolepium Enderlein, 1910. S.B. Ges. naturf. Fr. Berl. 1910: 74.

Type species: N. paraguayense Enderlein.

Characters similar to Perientomum. Fore and hind wings strongly acuminate. Antennae at most 24-segmented. Segments about four times as long as wide. Eyes large; pubescence sparse and short. Fore wing without IA, R_1 and Rs connected by a cross-vein. Hind wing with basal cell. R_1 arises proximad of M_2. Claws with one preapical tooth.

Habitat: Under bark.

Distribution: Paraguay.

Note: This genus was described from a single female and has not been recorded since its original description.

Parasoa Thornton (1 species)

Parasoa Thornton, 1962. Pacific Ins. 4: 449.
Type species: P. haploneura Thornton.

No scales on known specimens.

Median epicranial suture distinct, anterior arms not so. Lacinia (fig. 4.22) trifid at apex. Claws (fig. 4.23) with a preapical tooth and some fine processes basad of the tooth. Eyes pubescent, hairs fine and short. Antennae fewer than 30-segmented, segments about five times as long as wide. Three ocelli present, widely spaced. Fore and hind wings (figs. 4.24, 4.25) with reduced venation, lanceolate, setose with long marginal setae, especially near base. In fore wing Cu_2 and another vein (R + M?) only visible. Hind wing similar in shape and venation to fore wings. Subgenital plate simple with four noticeably stronger setae on hind margin. Paraproct (fig. 4.26) with strong posterior spine and a small dorso-basal sclerotized ridge. Two trichobothria and other setae present. Gonapophyses (fig. 4.27) reduced to external setose valves only.

Brachypterous forms known in which the wings are reduced to small vestiges, lacking ocelli.

Habitat: In caves.

Distribution: Malaya.

* Perientomum Hagen (12 species)

Perientomum Hagen, 1865. Ent. mon. Mag. 2: 151.
Type species: Amphientomum paradoxum Hagen.

Median epicranial suture distinct; anterior arms absent. Epicranium strongly setose, hairs long. Antennae at most 24-segmented, thin, segments at least four times as long as broad. Antennae fairly short, only about half length of fore wing. Eyes large, with short, relatively stout pubescence. Three ocelli, widely spaced, the anterior ocellus tending to be nearly in line with the other two. Lacinia (fig. 4.28) with trifid apex. Claws with a preapical tooth. Pulvillus fairly broad, apically expanded. Fore wing (fig. 4.29) acuminate. Basal section of Sc present, ending free in costal area. Distal section well-developed. R_1 long. IA present. R_1 and Rs meet in a point or are fused for a short length. In hind wing (fig. 4.30) a basal cell is present. R_1 arises proximad of M_1 but distad of M_2. Paraproct with some trichobothria and otherwise setose. Subgenital plate simple with four longer, posterior marginal setae. Gonapophyses (fig. 4.31) elongate, reduced to setose external valve with remnant of membranous dorsal valve sometimes discernible.

Habitat: On walls of houses, indoors and out; on bark, on bamboo stems, under bark.

Distribution: Ceylon, Queensland, Canary Islands, Zanzibar? (Copal).

Note: Males of this genus do not appear to have been taken. The Zanzibar record is somewhat dubious as the source of the Copal is not definitely known.

Proentomum Badonnel (1 species)

Proentomum Badonnel, 1949. Rev. franc. Ent. 16: 23.
Type species: P. personatum Badonnel.

Characters similar to those of Perientomum. Maxillary palp with fourth segment hatchet shaped. Fore wings (fig. 4.32) acuminate. Sc present, ending in R_1. Rs and M meeting in a point. In the hind wings (fig. 4.33) branches of M arise from a common fork. Lacinia (fig. 4.34) bifid, with one tooth with indications of further subdivision. Claw (fig. 4.35) with two preapical teeth. Pulvillus fine, slightly expanded apically. Paraproct (fig. 4.36) with a small group of trichobothria and a single normal seta in addition to other seta. Posterior spine well developed. Gonapophyses (fig. 4.37) consisting of a reduced but sclerotized dorsal valve and a broad, tapering, round-ended setose external valve.

Habitat: Unknown.

Distribution: Ivory Coast.

Soa Enderlein (3 species)

Soa Enderlein, 1904. Zool. Jb. Abt. Syst. 20: 109.
Type species: S. dahliana Enderlein.

Epicranium sharp. Frons and postclypeus flattened. Head sparsely setose. Antennae fine, segments long in relation to width. Lacinia (fig. 4.38) with apex divided into two very unequal apical teeth, the larger with indications of being bifid. Fourth maxillary palp segment somewhat hatchet-shaped (fig. 4.39). Eyes with short fine pubescence. Three ocelli fairly close together, anterior ocellus very small. Claws (fig. 4.40) with two preapical teeth. Pulvillus fine. Fore wings (fig. 4.41, 4.45) not as acuminate as in Perientomum, with Sc ending in R_1. Hind wing (fig. 4.43) with basal cell. R_1 arises distad of M_1. Gonapophyses (fig. 4.44) with dorsal and external valve remaining.

Habitat: Leaf litter, on walls of houses.

Distribution: Angola, Bismarck Archipelago, Ceylon, Sierra Leone, Java, Seychelles, Tahiti, Germany, Ivory Coast, Belgian Congo, England (in stored products), Brazil, Madagascar, Australia (ex ship's hold).

Note: All the above records except the first two are of one species, S. flaviterminata Enderlein, which is sometimes associated with stored products and is, therefore, easily spread by man.

Subfamily LEPIDOPSOCINAE

Cyptophania Banks (2 species)

Cyptophania Banks, 1931. Proc. Hawaii ent. Soc. 7: 440.
Type species: C. hirsuta Banks.

Characters of the family but with fore wings (fig. 4.45) thickened, shortened and elytriform with indistinct venation. Hind wings absent. Antenna more than 30-segmented, the segments relatively short, Rs in fore wing branched. Media 2-branched. Ocelli absent.

Habitat: On sugar cane, in leaf litter.

Distribution: Hawaii, Samoa, Laysan Island, Seychelles.

Echinopsocus Enderlein (1 species)

Echinopsocus Enderlein, 1903. Ann. hist.-nat. Mus. hung. 1: 331.
Type species: E. erinaoeus Enderlein.

Characters of the family. Epicranium sharp. Antennae with very short segments, more than 40-segmented. Eyes small, densely setose, setae fine. Ocelli absent. Lacinia broad towards apex, trifid. Claws long and straight with apex curved; two preapical teeth. Fore wing (fig. 4.46) pointed, well clothed with hairs in addition to scales. Sc evanescent as is the basal section of R and R_1. Distal section of Sc long as is R_1 thus giving a deeply triangular pterostigmal area. Rs, which has lost is basal section, arises thus from M and is simple. M 2-branched, M_{1+2} ending at wing tip. Cu_1 divides near separation from M. Cu_2 and IA fine. Hind wings absent.

Distribution: New Guinea.

Note: This genus was described from a single specimen and has not been recorded since.

* Echmepteryx Aaron (37 species)

Echmepteryx Aaron, 1866. Proc. Acad. nat. Sci. Philad. 38: 17.
Type species: Amphientomum hageni Packard.

Antennae fairly long, of numerous short segments. Eyes pubescent, hairs fine and short. Ocelli (fig. 4.49) far apart, anterior ocellus almost in line with lateral ocelli. Lacinia (fig. 4.47) trifid with each tooth fairly short and stout. Fourth segment of maxillary palp hatchet-shaped. Claw (fig. 4.48) with one strong and usually one, or more, very small preapical tooth. Pulvillus fine, pointed. Fore wings (fig. 4.50) acuminate. Basal section of Sc present or evanescent; distal section long. R_1 and Rs joined by a short crossvein. Rs branched. IA sometimes evanescent. Hind wing (fig. 4.51) acuminate. Sc present or evanescent. No basal cell. M 2-branched, the branches arising independantly or from a common stem. Length of stem of Rs relative to fork-length variable. Paraproct (fig. 4.52) with strong posterior spine and at least a few trichobothria with an associated normal seta. Hypandrium and subgenital plates simple. Gonapophyses (fig. 4.53) reduced to an elongate, spindle-shaped, setose external valve. Sometimes a membranous remnant of what may be the remains of a dorsal valve can be detected but the gonapophyses can be considered as virtually reduced to the external valve. Phallosome (figs. 4.54 - 4.56) with parameres broadened apically and with a median aedeagal structure consisting of a symmetrical pair of sclerites incorporating the end of the sperm duct.

<u>Habitat</u>: On foliage and stems of shrubs and trees, in birds nests, on bark, on mosses and epiphytes.

<u>Distribution</u>: Ivory Coast, East Africa, Angola, Madagascar, Seychelles, Ceylon, Java, Australia, New Zealand, Samoa, Chile, Paraguay, Cuba, North America, Germany (introduced in hot house)

<u>Lepidopsocus</u> Enderlein (8 species)

<u>Lepidopsocus</u> Enderlein, 1903. <u>Ann. hist.-nat. Mus. hung</u>. 1: 328.
Type species: <u>L. nepticulides</u> Enderlein.

Epicranium fairly sharp. Anterior arms of median epicranial suture present. Head hairy. Eyes large, setose.

Antennae long, as long as fore wing; segments short; about 45-segmented. Ocelli wide apart, forming a very flat triangle, that is, median ocellus not far in advance of lateral ocelli. Lacinia with apex trifid. Fourth segment of maxillary palp strongly broadened towards apex. Claws long and narrow with one preapical tooth. Fore wing (fig. 4.57) apically narrowed but not sharply pointed. No basal section of Sc. Basal section of R evanescent or absent. Distal section of Sc well developed. R_1 long. R_1 and Rs fused for a length. Hind wing (fig. 4.58) with a small basal section of Sc. No distal section. R_1 often ending free before wing margin, arising near origin of Cu_1. Cu_1 strong and sinuous. No closed basal cell. M 2-branched, the branches arising from a common stem or separately. Apical abdominal structures little known.

Habitat: Mainly leaf litter dwellers.

Distribution: Seychelles, Singapore, Samoa, Hawaii.

Pteroxanium Enderlein (2 species)

Pteroxanium Enderlein, 1922. Ent. mon. Mag. 58: 102.
Type species: P. squamosum Enderlein.

Epicranium rounded. Anterior arms of epicranial suture present. Antennae about 24-segmented. Eyes large, with long pubescence. Three ocelli fairly close together, small. Lacinia (fig. 4.59) trifid, the lateral teeth somewhat divergent. Maxillary palp with fourth segment hatchet-shaped. Claws long with preapical tooth behind which may occur a few smaller serrations. Pulvillus fine. Fore wing (fig. 4.60) scale-like, elytriform, nearly reaching apex of abdomen, broad narrowing to rounded apex. Sc absent or present only in distal section. Rs arising from R_1 in basal part of wing - Rs simple. R and M not united anywhere. M

2-branched. Cu_1 simple or branched. IA weak. Hind wings absent. Paraprocts as usual in the family. Gonapophyses reduced to elongate, setose, external valves. Phallosome (fig. 4.61) very similar to phallosome of Echmepteryx.

Habitat: On bark, under stones.

Distribution: Chile, Europe, North America, Tasmania, New Zealand, Argentina.

Note: The above records except for that from Chile, all refer to Pteroxanium kelloggi (Ribaga) a species which appears to have been transported by man.

Scolopama Enderlein (1 species)

Scolopama Enderlein, 1906. Spolia zeylan. 4: 110.
Type species: S. halterata Enderlein.

Epicranium with long setae. Antennae with very short segments, more than 30-segmented. Eyes pubescent. Three ocelli, close together. Claws slender with curved apex, three small and one large preapical setae. Pulvillus fine. Fore wing (fig. 4.62) strongly acuminate. Sc basal section absent, distal section very long. R_1 long. Rs simple, meeting M in a point in basal part of wing. M 3-branched, M_1 ending at wing apex. No crossvein from R to Rs. Hind wing reduced to veinless rudiment. Structure of apex of abdomen unknown.

Habitat: Leaf litter.

Distribution: Ceylon.

Note: This genus is known from one specimen only.

Subfamily LEPOLEPIDINAE

Lepolepis Enderlein (3 species)

Lepolepis Enderlein, 1906. Spolia zeylan. 4: 112.
Type species: L. ceylonica Enderlein.

Anterior arms of epicranial suture distinct. Postclypeus strongly bulbous. Antennae fairly long, segments only about twice as long as wide, more than 50-segmented. Eyes pubescent. Ocelli absent. Lacinia trifid (fig. 4.63). Fourth segment of maxillary palp hatchet-shaped. Claws with preapical tooth; pulvillus fine. Fore wings reduced to small scale-like lobes, as long as wide, rounded apically; wings extend only part way along abdomen. No indication of veins, elytriform. Hind wings absent. In long-winged forms fore wing (fig. 4.65) with Rs arising from M_1 i.e. basal section of R absent. Sc evanescent. M 3-branched. Cu_1 simple. Cu_2 and IA evanescent. In hind wing (fig. 4.66) Sc present in basal section. R_1 simple. Basal cell present; Rs simple. M 2-branched. Cu_2 and IA present. Paraproct (fig. 4.64) with two trichobothria and two other setae; posterior spine well developed. Gonapophyses reduced to elongate, setose external valves. Phallosome (fig. 4.67) with broadened parameres and complex aedeagus. One species polymorphic.

Habitat: Leaf litter, stored products (1 specimen in England), in houses (Ceylon).

Distribution: England (in West African ground nuts), Iles Glorieuse, Ceylon, Formosa, Eastern North America.

CHARACTERS OF THE TROGIIDAE

Belonging to the Trogiomorpha. Antennae of many segments, without secondary annulation. Ocelli absent. Lacinia with apex divided into a few large teeth. Maxillary palp with sensillum on second segment. Labial palps 2-segmented. Wings absent or rudimentary. Body and wings not scaly. Tarsi 3-segmented. Claws without preapical tooth. Pulvillus fine. Coxal organ sometimes present, represented by rasp. Paraproct with strong apical spine, without trichobothria. Female gonapophyses reduced to an elongate external valve with or without a small dorsal valve remnant. Spermatheca with accessory bodies. Male phallosome with anteriorly diverging parameres and median complex aedeagus. Eggs laid singly, sculptured, bare.

GENERA INCLUDED IN THE TROGIIDAE

Trogiinae:

Trogium Illiger, 1798
Lepinotus Heyden, 1850
Cerobasis Kolbe, 1882
Myrmicodipnella Enderlein, 1909
Anomocopeus Badonnel, 1967

Empheriinae:

Empheria Hagen, 1856
Trichempheria Enderlein, 1911

Subfamily EMPHERIINAE

* *Empheria* Hagen (2 species)

Empheria Hagen, 1856. *Die im Bernstein befindlichen organischen Reste* 2 (1): 64.
Type species: *E. reticulata* Hagen.

Median epicranial suture distinct, anterior arms faint.

Antennae about as long as wings, 23-segmented, thin, the segments relatively short. Eyes large, without setae. Three ocelli present, close together. Lacinia fine, apically without teeth. Fourth segment of maxillary palp (fig. 4.68) elongate, not hatchet-shaped. Claws small, without preapical tooth. Fore wing (fig. 4.69) oval, costal thickening continues around wing. Basal Sc long, ending on R_1; distal Sc well developed. R_1 - Rs crossvein present. R, M and Cu_1 arising from common basal stem. Rs branched. M 3-branched. Cu_{1a} sinuous, long. Veins, except Cu_2 and margin setose. Costal and subcostal cells broad. Basal section of Rs absent. Membrane not setose except for cells Cu_2 and IA. Hind wing (fig. 4.70). Sc present as a basal spur ending free in costal cell. Rs branched. M 2-branched, arising from a common stem. R_1 arises between M and Cu. Hind wing glabrous. Gonapophyses reduced to elongate, setose, external valve.

Habitat: Unknown.

Distribution: East Prussia (in amber).

Note: In Empheria (Bebiosis) pertinens (Enderlein) the fourth segment of the maxillary palp is hatchet-shaped and the fore wing membrane glabrous, even in cells Cu_2 and IA. It would seem that a case could be made out for retaining this latter species in a genus (Bebiosis) separate from Empheria reticulata.

* Trichempheria Enderlein (1 species)

Trichempheria Enderlein, 1911. Palaeontographica 58: 345.

Type species: Empheria villosa Hagen.

This genus is very similar to Empheria, differing in having the fore wing membrane (fig. 4.71), except for the costal and subcostal cells, setose and the fourth segment of the maxillary palp broadened (fig. 4.72).

Habitat: Unknown.

Distribution: East Prussia (in amber).

Subfamily TROGIINAE

Anomocopeus Badonnel (1 species)

Anomocopeus Badonnel, 1967. *Biol. l'Amerique austr.* 3: 549.
Type species: *A. nasutus* Badonnel.

Median epicranial suture evanescent; anterior arms absent. Vertex rounded. Postclypeus strongly bulbous. Eyes large, pubescent. Ocelli absent. Lacinia (fig. 4.73) apically trifid; asymmetrical, the left lacinia being considerably reduced. Fourth segment of maxillary palp hatchet-shaped. Claws without preapical tooth. Pulvillus fine. Metathorax somewhat more developed than mesothorax, the former divided by a transverse groove. Apterous. Epiproct with two lateral fields of five setae each. Paraprocts hairy, without trichobothria, with fine posterior spines. Hypandrium (fig. 4.74) somewhat extended posteriorly into a small median lobe with an apical fringe of setae. No abdominal brush. Phallosome (fig. 4.75) with parameres anteriorly and posteriorly free, connected by a transverse band near posterior end; aedeagal structures not very complex. Females unknown.

Habitat: In grass heads.

Distribution: Chile.

Cerobasis Kolbe (9 species)

Cerobasis Kolbe, 1882. *Ent. Nachr.* 8: 212.
Type species: *C. muraria* Kolbe.

Median epicranial suture and anterior arms distinct. Antennae more than 20-segmented; segments short. Eyes large, pubescent. Ocelli absent. Lacinia (fig. 4.75) trifid. Fourth maxillary palp segment broad. Fore wings reduced to setose flaps or absent. Coxal rasp present. One or two spurs on hind tibiae in addition to apical spurs. Paraproct with strong posterior spine, without trichobothria. Gonapophyses reduced to an elongate, setose external valve with a remnant which may represent a dorsal valve. Spermatheca with accessory bodies. Phallosome (fig. 4.76) with parameres anteriorly separated and with aedeagal sclerifications. Males with abdominal brush.

Habitat: In human habitation, on lichens, on bark, in stored products, on rocks, under stones.

Distribution: Europe, Canary Islands, Morocco, St. Paul Island, North America, Angola, South Africa, Australia, Argentina, Chile.

Lepinotus Heyden (7 species)

Lepinotus Heyden, 1850. Stettin. ent. Ztg. 11: 84.
Type species: L. inquilinus Heyden.

Similar to Cerobasis but with fourth maxillary palp segment elongate; coxal rasp absent and lacking tibial spines other than apically. Male with abdominal brush. Spermatheca with accessory bodies.

Habitat: In leaf litter, on bark, under stones, in human habitation, in stored products.

Distribution: Widespread owing to association with man. Non-domestic species found in South Africa, Angola and Tanganyika.

Myrmecodipnella Enderlein (1 species)

Myrmecodipnella Enderlein, 1908. Boll. Lab. zool. Portici 3: 329.
Type species: M. aptera Enderlein.

Similar to Cerobasis but apterous. Gonapophyses (fig. 4.77) with fairly well developed dorsal valve as well as elongate, setose, external valve. Three spurs present on hind tibiae in addition to apical spurs.

Habitat: In ant's nest.

Distribution: California.

Note: This genus was described from a single female and has not been recorded since.

Trogium Illiger (1 species)

Trogium Illiger, 1798. Kugelann Verzeichniss der Kafer preussens p. 500.
Type species: Termes pulsatorium Linnaeus.

Similar to the other genera of the family but characterized by: fore wings represented by rudimentary flaps; fourth maxillary palp segment broad; posterior tibiae without spines other than apical ones. Antennae up to 29-segmented. Median and anterior arms of epicranial suture distinct. Eyes pubescent. Lacinia trifid.

Habitat: In human habitation, in nests of wasps and bees; on trees.

Distribution: Almost cosmopolitan, transported by man.

CHARACTERS OF THE PSOQUILLIDAE

Belonging to the Trogiomorpha. Antennae with many segments, not secondarily annulated. Ocelli not grouped on a tubercle. Lacinia narrow with apex divided into two teeth. Maxillary palp with sensillum on second segment. Labial palp 2-segmented. Fore wing with rounded apex. Wings and body without scales; wing margin with fringe of well-developed setae. Pterostigmal area not thickened. Basal section of Sc fairly long. M_3 arises in basal half of wing with M_1 and M_2 arising from a relatively long common stem. M_3 arising basad of separation of Rs + M. Cu_1 divides relatively near wing base giving a long triangular areola postica. Cu_2 and IA end separately at wing margin. There is a tendency for the angles of the bifurcating veins to be acute, resulting in the veins being more nearly parallel with the wing axis than is usual in the order. Hind wing with M branched. Tarsi 3-segmented. Claws without preapical tooth. Pulvillus moderately broad with expanded tip. Paraproct with strong spine; some setae with basal "rosettes" but these are not grouped into a definite trichobothrial field. Subgenital plate usually simple. Female gonapophyses reduced to at most a small dorsal valve and an elongate external valve. Females with characteristic accessory bodies associated with the spermatheca; spermatheca with some sclerification. Male phallosome with anteriorly diverging parameres and a complex median aedeagus. Some species brachypterous. Eggs laid singly, sculptured, bare.

GENERA INCLUDED IN THE PSOQUILLIDAE

Psoquilla Hagen, 1865

Rhyopsocus Hagen, 1876

Eosilla Ribaga, 1908

Balliella Badonnel, 1949

Balliella Badonnel (1 species)

Balliella Badonnel, 1949. Bull. Inst. sci. nat. Belg. 25: 9.
Type species: B. ealensis Badonnel.

Antennal segments relatively short. Eyes large. Ocelli wide apart. Lacinia (fig. 4.78) gently tapering towards apex, ending in three poorly defined teeth. Claws fine, gently curved at apex, without preapical tooth. Fore wing (fig. 4.79) rounded. Venation reduced. Sc absent, both basally and distally so that the pterostigmal area is not closed proximally. R simple or branching immediately before wing margin to give a small fork. M 2-branched. Cu_1 simple, that is, areola postica absent. R, M and Cu fused basally for a length. A long Rs-M crossvein present. Veins (except Cu_2) and margin setose. Hind wing (fig. 4.80) with a short basal Sc. R_1 absent. Rs branched. M simple. A small basal cell present, that is, M and Rs fused for a length after separation of M and Cu. Epiproct with few setae, in specialized positions and paraproct without trichobothria and with only few normal setae (fig. 4.81). Subgenital plate simple. Gonapophyses reduced to the elongate, setose external valve. Spermatheca with mushroom-shaped accessory bodies. Males unknown.

Habitat: On leaves and bark.

Distribution: Congo.

Eosilla Ribaga (2 species)

Eosilla Ribaga, 1908. Redia 5: 20.
Type species: E. jacobsoni Ribaga.

Eyes with only a single dorso-lateral seta. Ocelli far apart. Lacinia (fig. 4.82) with bifid apex. Fourth segment of maxillary palp broad. Claws without preapical tooth, pulvillus fairly broad, a little expanded apically (fig. 4.83). Fore wing (fig. 4.84) with rounded apex. Venation difficult to see, and the membrane slightly thickened; the wing, therefore somewhat elytriform, membrane and margin setose. Sc present in basal section. A faint R_1 - Rs crossvein; basal section of Rs evanescent. M 3-branched, Cu_1 branching very near wing base giving a very long areola postica. Hind wing (fig. 4.85) membranous. Sc present basally, ending free in wing membrane. R_1 absent. M simple. Cu_1 simple. Hypandrium simple. Phallosome (fig. 4.86) with separate parameres, complex posteriorly, connected by a broad V-shaped transverse sclerite. Females unknown.

Habitat: Dead leaves.

Distribution: Java, Seychelles.

Psoquilla Hagen (2 species)

Psoquilla Hagen, 1865. Ent. mon. Mag. 2: 123.
Type species: P. marginepunctata Hagen.

Characters similar to other genera of the family. Fore wing (fig. 4.87) not thickened, with setose margin and veins. Veins distinct; M_3 arises proximad of Rs. In hind wing R_1 present. Polymorphism occurs in this genus; brachyptery and microptery frequent in Psoquilla marginepunctata.

Habitat: In birds' nest, on bark, under bark in stored products.

Distribution: Paraguay, Brazil, Bermuda, Malaya, Europe, Congo, Ivory Coast, Gold Coast, Angola, Australia, North America, Hawaii. Easily distributed by man in stored products.

Rhyopsocus Hagen (11 species)

Rhyopsocus Hagen, 1876. Bull. U.S. nat. Mus. 1 (3): 55.
Type species: R. eclipticus Hagen.

Brachyptery common. Median epicranial suture distinct. Antennae 22-segmented. Eyes large. Ocelli present in macropterous forms, reduced or absent in brachypterous forms. Lacinia (fig. 4.88) bifid. Fourth maxillary palp expanded. Claws without preapical tooth. Fore wing (fig. 4.89) rounded, not thickened. Basal part of Sc fairly short; distal section short. R_1 long, giving a long, flat, pterostigmal area. R_1 - Rs crossvein present. Basal part of Rs absent, Rs apparently arising from M. M 3-branched, M_3 arising basad of apparent origin of Rs. Cu_1 branches near wing base, giving very long areola postica. Veins (except Cu_2) with a single row of setae. Hind wing (fig. 4.90) with basal Sc ending free in wing membrane. R_1 present. M simple. Wing glabrous. Epiproct with few specially placed setae; paraproct with a few trichobothria and a single strong seta (fig. 4.91). Hypandrium sometimes slightly asymmetrical. Phallosome with free parameres connected by an aedeagal sclerite; broad, V-shaped. Gonapophyses (fig. 4.92) reduced to remnant of dorsal valve and elongate, setose, external valve.

Habitat: On trees, dry leaves, in human habitation, in stored products, in bird's nest.

Distribution: Congo, Ivory Coast, Angola, South Africa, Tanganyika, Britain (in stored products), Kerguelen Island, Peru, North America.

CHARACTERS OF THE GROUP PSOCATROPETAE

Head long, vertical. Inner side of second maxillary palp segment without sensillum. Antennae with some segments secondarily annulated. Fore wing with nodulus; in brachypterous forms at least recognizable remnants of veins present. Hind tibia and tarsus together longer than abdomen. Scales never present. Gonapophyses reduced, but with external valve in form of a broad membranous, setose, lobe. Eggs sculptured, layed singly, without any covering.

CHARACTERS OF THE PSYLLIPSOCIDAE

Belonging to the Trogiomorpha. Head somewhat elongate, genae long. Antennae long, of many segments, without secondary annulations. Ocelli not grouped together on a tubercle. Lacinia narrow, apically divided into a few large teeth. Maxillary palps without sensillum on second segment although some species have a strong seta in the equivalent position. Labial palps 2-segmented. Fore wings with pterostigmal area not thickened. Sometimes a cross-vein from R_1 - Rs. Areola postica long but Cu_{1b} much shorter than Cu_{1a}. Cu_2 and IA meet together at the wing margin (nodulus). Hind wing with M 2-branched. Tarsi 3-segmented. Claws without preapical tooth; pulvillus narrow. Female gonapophyses reduced; ventral valve rudimentary, dorsal valve small and usually membranous, external valve membranous, broad, setose. Paraproct with strong posterior spine; some setae with basal "rosettes" but without a definite trichobothrial field. Male phallosome with anteriorly diverging parameres and complex median aedeagus. Polymorphism known. Eggs laid singly, sculptured, with small papillae, not covered with silk nor encrusted with debris.

GENERA INCLUDED IN THE PSYLLIPSOCIDAE

Psyllipsocus Selys-Longchamps, 1872
Dorypteryx Aaron, 1883
Psocatropos Ribaga, 1899
Speleketor Gurney, 1943
Dolopteryx Smithers, 1958

Dolopteryx Smithers (1 species)

Dolopteryx Smithers, 1958. *J. ent. Soc. S. Afr.* 21: 113.
Type species: *D. domestica* Smithers

Fore wings (fig. 4.93) reduced, narrowing towards apex, the veins and margin bearing long setae. Venation reduced with only five veins approaching or reaching the margin. Hind wings rudimentary but distinct. Lacinia (fig. 4.94) with four diverging terminal teeth of various sizes. Claws with strong preapical tooth, pulvillus fine. Gonapophyses (fig. 4.95) reduced to dorsal and external valves the latter broad and bearing some especially stout setae. Paraprocts with apical spine. Fourth maxillary palp segment hatchet-shaped, but elongate. Median and anterior arms of epicranial suture indistinct but present. Antennae at least 26-segmented. Eyes small, of comparatively few facets. Ocelli rudimentary. Prothorax with notum divided into four lobes. Subgenital plate simple. Phallosome consisting of two parameres diverging strongly anteriorly united by transverse sclerites in posterior region.

Habitat: In human habitation (probably a cave dweller).

Distribution: Southern Rhodesia.

Dorypteryx Aaron (3 species)

Dorypteryx Aaron, 1883. Trans. Amer. ent. Soc. 11: 37.
Type species: D. pallida Aaron.

Wings narrow, reduced (fig. 4.96), with pointed apex, the margin and veins setose. Only two veins present. Hind wings absent. Lacinia (fig. 4.97) with four apical teeth. Maxillary palp with fourth segment (fig. 4.98) very long, hatchet-shaped. Claws with preapical tooth with a comb of small chitinous processes basad of the tooth, pulvillus fine. Gonapophyses (fig. 4.99) reduced to the external valve bearing three large macrosetae and other long hairs, remnant of dorsal valve present. Paraprocts with posterior spine. Antennae at least 24-segmented, from the eighth segment secondarily annulated. Ocelli absent.

Habitat: In human habitation, in caves.

Distribution: Argentina, North America, Europe.

Psocatropos Ribaga (6 species)

Psocatropos Ribaga, 1909. Riv. Pat. veg. Padova 8: 156.
Type species: P. lachlani Ribaga.

Polymorphic species. Fore wings reduced (figs. 4.100, 4.101) and with venation reduced and variable in accord with wing reduction. M 2- or 3-branched. Cu_1 simple. Sc usually absent basally, Rs frequently simple. Hind wings much reduced with aberrant venation. Gonapophyses reduced to dorsal and external valves (fig. 4.102) the latter with one preapical seta larger than the others. Paraprocts (fig. 4.103) with a few trichobothria and a few setae. Phallosome (figs. 4.104, 4.105) with parameres bent in middle and connected by aedeagal sclerites. Lacinia (figs. 4.106, 4.107) trifid.

Habitat: In human habitation, in stored products, in termites nests.

Distribution: Europe, North America, Cameroons, Mozambique, Congo, East Africa, Seychelles, Java, Formosa, India, New Guinea, Hawaii, Peru.

Note: Easily spread by man in stored products and merchandise.

* Psyllipsocus Selys-Longchamps (14 species)

Psyllipsocus Selys-Longchamps, 1872. Ent. mon. Mag. 9: 145.
Type species: P. ramburii Selys-Longchamps.

Polymorphic, long-winged forms with eyes and ocelli occurring in the same species as forms which are micropterous or apterous and in which the eyes are reduced and ocelli absent. Vertex rounded. Antennae more than 22-segmented. Lacinia (fig. 4.108) with apex trifid. Maxillary palp with fourth segment long, but not quite cylindrical (fig. 4.109). Claws with small preapical tooth (fig. 4.110) and a "brush" of fine processes basad of the tooth. Fore wings (figs. 4.111, 4.112) of various degrees of development. Venational aberration common with reduction of wing size (fig. 4.113). Fore wings rounded apically. Sc not reaching R. Distal section of Sc present, R_1 curved or straight to wing margin to give triangular pterostigmal area. R_1 - Rs crossvein sometimes present. Rs and M fused for a length. M 3-branched. Cu_{1b} short in relation to Cu_{1a} giving a low areola postica. Cu_2 and IA meeting wing margin at nodulus. Veins sparsely setose, margin glabrous. Hind wing (figs. 4.114, 4.115) without Sc. R_1 present. Rs branched, fused with M for a length. M 2-branched. Basal cell present formed by separation of M from Cu_1 and fusion with Rs. Venation aberrant in brachypterous forms (fig. 4.116). Paraproct (fig. 4.117) with trichobothria and without spine in macropterous forms; without trichobothria and with tendency to retain posterior spine in brachypterous forms (fig. 4.118). Subgenital plate simple. Gonapophyses reduced to a membranous dorsal valve supported by a median chitinized rod and a large, setose, membranous external valve (fig. 4.119); sometimes the remnant of a ventral lobe may be detected (fig. 4.120). Phallosome (fig. 4.121) with anteriorly divergent, fine parameres, linked posteriorly by aedeagal sclerifications.

<u>Habitat</u>: In caves, leaf litter, in habitations, in mines, under stones.

<u>Distribution</u>: Burma (in amber), North America, Mexico, Argentina, Europe, Congo, Angola, Algeria, India, Afghanistan, Malaya, Formosa, Japan, Australia, Guam, Hawaii.

Note: Psyllipsocus ramburii S. - L. is a widespread species associated with man.

Speleketor Gurney (1 species)

Speleketor Gurney, 1943. Ann. ent. Soc. Amer. 36: 197.
Type species: S. flocki Gurney.

Vertex smoothly rounded. Antennae long, without setae, segments from third to apex annulated. Eyes moderately large, placed laterally. Ocelli present, far apart. Lacinia (fig. 4.122) with truncate apex one side of which is shorter than the other. Maxillary palp very fine and long; fourth segment very long, cylindrical. Claw without preapical tooth; reduced "brush". Legs very long and slender. Fore wing (fig. 4.123) with Sc curving to meet R. Distal section of Sc strong. R_1 - Rs crossvein present. Rs and M fused for a length. M 3-branched. Cu_{1a} strongly curved, Cu_{1b} fairly short. Hind wing (fig. 4.124) with Sc ending free. Rs and M fused for a length. M 2-branched. Cu_2 and IA fused basally. Wings glabrous. Subgenital plate emarginate posteriorly. Gonapophyses reduced to a remnant of a dorsal valve and a broad, setose external valve bearing two strong posterior setae (fig. 4.125). Hypandrium simple. Phallosome (fig. 4.126) of peculiar form; parameres joined anteriorly diverging posteriorly, joined by a small aedeagal sclerite.

Habitat: In cave.

Distribution: Arizona.

CHARACTERS OF THE PRIONOGLARIDAE

Belonging to the Trogiomorpha. Antennae long, without secondary annulations. Head relatively long. Ocelli not grouped on a tubercle. In adults mandibles (fig. 4.127) with exceptionally strong incisor tooth, strongly curved, apically pointed with fine serrations along the internal margin. Nymphal mandibles normal. Lacinia absent in adults. In nymphs lacinia a little broadened towards apex which is divided into a short series of large teeth (fig. 4.128). Maxillary palp without sensillum on second segment. Labial palpi 2-segmented. Hypopharynx peculiar in having the glossa membranous; the chitinous filaments are strong and rigid (the filaments and the ovoid sclerites are absent from the nymphs). Fore wing (fig. 4.129) without thickened pterostigma. Basal section of Sc well developed, curving to meet R. M + Cu strongly curved. Crossvein from R_1 - Rs. Cu_{1a} fairly long. Cu_2 and IA meeting wing margin together at nodulus. In hind wing (fig. 4.130) M 2-branched. Cu_2 strongly sinuous in basal third. IA and 2A fused basally, dividing near margin with IA strongly sinuous. Tarsi 3-segmented. Claw with preapical tooth (sometimes small). Anterior claws with basal hair, posterior claws without. (Paraproct characters of adult unknown). Phallosome (fig. 4.131) consisting of a plate bearing a distal, dorsally curving spatulate process flanked by two palp-like organs. The homologies of the parts of the phallosome cannot be established. Female gonapophyses unknown.

GENERA INCLUDED IN THE PRIONOGLARIDAE

Prionoglaris Enderlein, 1909

Prionoglaris Enderlein (2 species)

Prionoglaris Enderlein, 1909. *Arch. zool. exp. gen.* 1: 533.

Type species: *P. stygia* Enderlein.

Characters of genus as for family.

Habitat: Caves.

Distribution: France, Belgium, Portugal, Balkans, Afghanistan.

CHARACTERS OF THE SUBORDER TROCTOMORPHA

Labial palps 1- or 2-segmented. Antennae 11- to 17-segmented, the flagellar segments from the fifth onwards usually secondarily annulated. Adults with 3-segmented tarsi. Pterostigma not thickened. Winged forms, if not bearing scales, lack ctenidiobothria. Pearman's organ, if present at all, in the form of a hyaline, hemispherical capsule. Subgenital plate large and broad, usually with T-shaped internal sclerite. Gonapophyses complete, glabrous. Second maxillary palp segment sometimes with sensillum on inner side. Hypopharynx with chitinous filaments separated at distal extremity.

CHARACTERS OF THE GROUP AMPHIENTOMETAE

Head long. Antennae 11- to 15-segmented. Maxillary palp sensillum present. Wings usually present, seldom brachypterous. Nodulus present. Body and wings usually clothed with scales. Meso- and metanotum never fused. Femora of fore legs sometimes with comb. Wings carried roof-wise over abdomen. Tarsi 3-segmented. Claws variously toothed. Labial palps 1- or 2-segmented. Ocelli widely separated. Gonapophyses complete, glabrous. Eggs smooth, encrusted with debris.

CHARACTERS OF THE AMPHIENTOMIDAE

Belonging to the Troctomorpha. Antennae 15-segmented, secondarily annulated. Ocelli separated. Sensillum sometimes on second maxillary palp segment. Lacinia with apex divided into a small median and broad tooth. Labial palps 1- or 2-segmented. Fore wings with pterostigmal area not thickened, small. Hook of nodulus and stigmapophysis made up of small hooks. Rs connected to M by a cross-vein. Areola postica usually long. Cu_2 and IA end in nodulus. Two anal veins present. Hind wing with basal section of Rs frequently absent. M not branched. Wings and body scaly. Pearman's organ reduced. Tarsi 3-segmented. Claws long, with one or more preapical teeth. Fore legs with comb. Subgenital plate broad and rounded, usually with a small internal T-shaped sclerite. Gonapophyses complete, ventral and dorsal valves pointed, external valve broad, large, without setae, frequently divided into two or more lobes. Spermathecal opening with sclerifications. Phallosome with parameres posteriorly diverging from a small median anterior plate. Aedeagus distally open with membranous sheets arising from the inner margin of the diverging halves, the sheets sometimes meeting medially. The homologies of the parts of the phallosome are not clear. Eggs covered with an encrustation.

GENERA INCLUDED IN THE AMPHIENTOMIDAE

Electrentominae:

Electrentomum Enderlein, 1911

Parelectrentomum Roesler, 1940

Tineomorphinae:

Cymatopsocus Enderlein, 1903

Tineomorpha Enderlein, 1906

Amphientominae:

Amphientomum Hagen, 1856

Hemiseopsis Enderlein, 1906

Marcenendius Navas, 1913

Nephax Pearman, 1935

Paramphientomum Enderlein, 1906

Pseudoseopsis Badonnel, 1955

Seopsis Enderlein, 1906

Seopsocus Roesler, 1940

Stigmatopathus Enderlein, 1903

Stimulopalpus Enderlein, 1906

Syllysis Hagen, 1865

Subfamily ELECTRENTOMINAE

* Electrentomum Enderlein (1 species)

Electrentomum Enderlein, 1911. Palaeontographica 58: 337.

Type species: E. klebsianum Enderlein.

Vertex fairly steep but rounded. Anterior arms of epicranial suture absent. Antennae fine, 13-segmented, flagellar segments elongate. Eyes large, not pubescent. Three small ocelli in close triangle. Lacinia with a lateral cusp curved outward and a few indistinct, rounded denticles (fig. 4.132). Maxillary palp with fourth segment elongate, parallel sided with rounded apex. Claw with preapical tooth. Ctenidiobothria absent. Fore wing rounded (fig. 4.133) without scales. Margin and veins glabrous. Basal Sc short, ending in R. R_1 distally curved to give a rounded hind margin to pterostigmal area. Rs-M crossvein present. M 3-branched, branches arising close together. Areola postica low. 2A fusing with IA about half way along IA. Hind wing (fig. 4.134) with basal Sc ending free in membrane. Basal section of Rs absent. M not branched.

Habitat: Unknown.

Distribution: East Prussia (in amber).

* Parelectrentomum Roesler (1 species)

Parelectrentomum Roesler, 1940. Zool. Anz. 129: 228.
Type species: P. priscum Roesler.

This genus differs from Electrentomum only in the presence of a basal section of Rs in the hind wing.

Habitat: Unknown.

Distribution: East Prussia (in amber).

Subfamily TINEOMORPHINAE

Cymatopsocus Enderlein (1 species)

Cymatopsocus Enderlein, 1903. Ann. hist. -nat. Mus. hung. 1: 314.
Type species: C. opalinus Enderlein.

Vertex fairly flat. Median and anterior arms of epicranial suture present. Antennae very fine, shorter than fore wing; 13-segmented. Eyes large, flatly applied to sides of head. Two ocelli, small, widely spaced, lying near compound eyes. Lacinia (fig. 4.135) with inner denticle and a series of outer denticles. Claw with one or two preapical teeth; claw fairly straight with small apical curvature. Fore wing (fig. 4.136) elongate, with pointed apex and irregular hind margin. Basal Sc ends free. Stem of Rs short, fork long. Rs - M crossvein long. M 3-branched. Cu_1 branches near margin giving small areola postica. In hind wing (fig. 4.137) basal Sc short, ending free. R_1 long. No basal section of Rs. M 2-branched. Hind margin somewhat irregular. Body and wings clothed with scales. Genitalic features unknown.

Habitat: Unknown.

Distribution: Malaya (Kuala Lumpur).

<u>Note</u>: This genus has not been recorded since its first description and a subsequent figuring from the same author.

<u>Tineomorpha</u> Enderlein (3 species)

<u>Tineomorpha</u> Enderlein, 1906. <u>Spolia zeylan</u>. 4: 49.
Type species: <u>T</u>. <u>greeniana</u> Enderlein.

Vertex fairly tall but rounded. Anterior arms of median epicranial suture distinct. Antennae fairly short, 13-segmented. Eyes with short pubescence. Two ocelli, relatively large, close to compound eyes. Lacinia (fig. 4.138) with median denticle and a large lateral denticle subdivided into many small irregularities. Claw (fig. 4.139) with preapical teeth, one small and one large, basad of which is a sparse "brush". Fore wings (fig. 4.140) with rather pointed apex. Venation similar to <u>Cymatopsocus</u>. Margin of wing entire. Hind wing (fig. 4.141) as in <u>Cymatopsocus</u>. Subgenital plate simple without T-shaped sclerite. Gonapophyses (fig. 4.142) well developed. External valve not setose, divided into lobes. Spermathecal opening with surrounding sclerification (fig. 4.143). Epiproct setose. Paraproct with trichobothria in a poorly delimited field together with additional setae. Surface of paraproct generally setose in addition to specialized marginal and ventral setae.

<u>Habitat</u>: Under bark, on bark.

<u>Distribution</u>: Angola, Ceylon, Java.

Subfamily AMPHIENTOMINAE

* <u>Amphientomum</u> Pictet (15 species)

<u>Amphientomum</u> Pictet, 1854. <u>Traite de Palaeontologie</u> 2: 376.
Type species: <u>A</u>. <u>paradoxum</u> Pictet.

Vertex rounded. Anterior arms of epicranial suture evanescent. Antennae 15-segmented with secondary annulation. Three ocelli, well spaced. Eyes large, with or without pubescence. Maxillary palps with sensillum. Lacinia (fig. 4.144) with apex divided into a small internal tooth and a broad external one with indications of subdivision; lacinia curved towards apex. Tibia of fore legs with a row of fixed teeth. Claws (fig. 4.145) with one or two preapical teeth, as well as a few spinules basad of the teeth; preapical teeth variable in size. Fore wings (figs. 4.146 - 4.148) with basal Sc evanescent. Rs and M joined by a crossvein. M 3-branched, the branches arising fairly close together. Cu_1 branching fairly close to wing margin; areola postica with sharp apex directed towards wing base. 2A present. Hind wing (fig. 4.149) with Sc evanescent. Basal section of Rs absent. Rs forked. M not branched. Wings and body with scales. Subgenital plate usually with T-shaped sclerite. Gonopophyses (figs. 4.150, 4.151) with ventral valve pointed. Dorsal valve pointed. External valve lobed, not setose. Spermathecal opening with sclerifications of various forms (figs. 4.152, 4.153). Hypandrium usually simple. Phallosome consisting of a pair of parameres arising from an anterior plate; the distal ends of the parameres flattened and bearing pores, membranous, the membranes meeting in the midline. Aedeagal sclerification usually not evident (figs. 4.154 - 4.156).

<u>Habitat</u>: On rocks, on bark.

<u>Distribution</u>: East Prussia (in amber), Congo, Angola, Madagascar.

<u>Hemiseopsis</u> Enderlein (2 species)

<u>Hemiseopsis</u> Enderlein, 1906. <u>Spolia zeylan</u>. 4: 73.

Type species: <u>Amphientomum</u> <u>fulleborni</u> Enderlein.

Very similar to Amphientomum. No sensillum on second segment of maxillary palp, claw with one preapical tooth and a series of spinules (fig. 4.157). Distal section of Sc absent in fore wing (fig. 4.158) and IA ending in membrane in hind wing (fig. 4.159). Gonapophyses (fig. 4.160) similar to Amphientomum and spermathecal opening with sclerification (fig. 4.161).

Habitat: On leaves, under rocks, in termite nest.

Distribution: East Africa, Congo, Angola.

Marcenendius Navas (2 species)

Marcenendius Navas, 1913. Rev. Acad. Madr. 12: 334.
Type species: M. nostras Navas.

This genus cannot be recognized from the descriptions other than that it is probably an Amphientomid. Its relegation to the category of "Psocida Agnota" is prevented only by this probability.

Nephax Pearman (3 species)

Nephax Pearman, 1935. Stylops 4: 134.
Type species: N. sofadanus Pearman.

Vertex rounded. Median and anterior arms of epicranial suture present. Antennae secondarily annulated. Eyes pubescent. Two or three ocelli, wide apart, lateral ocelli close to eyes. Lacinia (fig. 4.162) with complex apex or divided into a small internal tooth and a large, external one as in other Amphientomid genera. Claws with one preapical tooth (fig. 4.163) and a series of basal spinules. Fore wings (fig. 4.164) reduced, with pointed apex. Stigmapophysis absent. Distal segment of Sc present or absent. Cu_1 forked or not. Rs and M meeting in a point or fused for a short length. Hind wings reduced to small veinless flaps. Gonapophyses (fig. 4.165) as in Amphientomum. Subgenital plate with rudiment of T-shaped sclerite. Spermathecal opening (fig. 4.167) sclerified. Hypandrium simple. Phallosome (fig. 4.166) of form usual in Amphientomum.

Habitat: Under stones.

Distribution: Angola, South Africa, Palestine.

Paramphientomum Enderlein (4 species)

Paramphientomum Enderlein, 1906. Spolia zeylan. 4: 63.
Type species: P. nietneri Enderlein.

Very similar to Amphientomum but in hind wing R_1 ends in membrane, not reaching wing margin and distal section of Sc absent.

Habitat: On stones, on moist walls.

Distribution: Ceylon, Java, Formosa, Japan.

Pseudoseopsis Badonnel (2 species)

Pseudoseopsis Badonnel, 1955. Pub. cult. Cia. Diamant Angola 26: 46.
Type species: P. vilhenai Badonnel

Very similar to Seopsis Enderlein but claws with one preapical tooth and spinules basad of tooth (fig. 4.168). Differs from Seopsis in not having a sensillum on second maxillary palp segment, in having a sclerified process on subgenital plate, in not having spermathecal opening sclerifications and in having a complex spermatheca (fig. 4.169). Gonopophyses (fig. 4.170) similar to Amphientomum.

Habitat: On rocky outcrop, under bark.

Distribution: Angola, Texas.

Seopsis Enderlein (8 species)

Seopsis Enderlein, 1906. Spolia zeylan. 4: 67.
Type species: S. vasantasena Enderlein.

Very similar to Amphientomum but with R_1 in hind wing ending in membrane and with only one preapical tooth on claw. Lacinia (fig. 4.171). Gonapophyses (fig. 4.172). Sclerification of spermathecal opening (fig. 4.173). Phallosome (fig. 4.174).

Habitat: On walls, on bark, on rocks, under stones, in termite nest.

Distribution: Angola, Ceylon, Philippines.

Seopsocus Roesler (3 species)

Seopsocus Roesler, 1940. Zool. Anz. 129: 229.
Type species: S. acuminatus Roesler.

Head flat. Eyes large, pubescent. Three ocelli, close together. Antennae 12-segmented, secondarily annulated. Lacinia curving, apically divided as usual in the family. Fourth segment of maxillary palp with sensillum. Males macropterous, females brachypterous. Male fore wing (fig. 4.175) with stem of Rs very short or even with R_{2+3} and R_{4+5} arising separately from the Rs - M crossvein (fig. 4.176). Basal section of Sc ending in R. Distal section present. Areola postica long, low, triangular. Cu_2 and IA ending near each other on wing margin but not together. 2A present. In hind wing (fig. 4.177) Rs more or less evanescent basally. Fore wing in females (fig. 4.178) reduced. Sc and M reduced. Coxal organ present as hemispherical hyaline structure in both sexes. Claw with two preapical teeth as well as spinules. Hypandrium simple, with a weakly developed T-shaped sclerite. Gonapophyses as in *Amphientomum*. Hypandrium simple. Phallosome as in *Amphientomum*.

Habitat: On bark.

Distribution: Brazil, Argentina.

Stigmatopathus Enderlein (1 species)

Stigmatopathus Enderlein, 1903. *Ann. hist. -nat. Mus. hung.* 1: 312.
Type species: *S. horvarthi* Enderlein.

Similar to *Amphientomum* but in fore wing distal section of Sc and R_1 lying very close together and parallel (fig. 4.179). 2A absent. In hind wing (fig. 4.180) R_1 absent, basal section of Rs present but broken at position of bifurcation of R. Claw with one preapical tooth. Ocelli absent.

Habitat: Not recorded.

Distribution: Malaya, Java.

Stimulopalpus Enderlein (3 species)

Stimulopalpus Enderlein, 1906. *Spolia zeylan.* 4: 65.
Type species: *S. japonicus* Enderlein.

Very similar to Seopsis but without comb of spines on fore femora. Distal section of Sc in fore wing absent (fig. 4.181). Two ocelli.

Habitat: On rocks.

Distribution: East Africa, Angola, Rhodesia, Natal, Transvaal, Ivory Coast, Japan.

Syllysis Hagen (5 species)

Syllysis Hagen, 1865. Ent. mon. Mag. 2: 151.
Type species: Amphientomum caudatum Hagen.

Vertex sharp. Three ocelli placed relatively close together. Sensillum present. Claws with two preapical teeth. Border of fore wing (fig. 4.182) produced between M_1 and M_2. Distal section of Sc absent. 2A present. In hind wing (fig. 4.183) Sc ends in membrane. R_1 absent, i.e. R stops before origin of Rs. Basal section of Rs absent.

Habitat: On bark.

Distribution: Ceylon, Java, Paraguay.

CHARACTERS OF THE MUSAPSOCIDAE

Belonging to the Troctomorpha. Antennae 12-segmented. Frontal sutures absent. Lacinia (figs. 4.184, 4.185) with apex of three tines composed of a median cusp, the tip of the lateral cusp and a subapical denticle of the lateral cusp. Tarsi 2-segmented. Pretarsal claws (fig. 4.186) of each foot unlike, the anterior claw broadened by a membranous covering or cowl, the posterior claw without a cowl and bearing a preapical tooth. Without scales. Fore wing (fig. 4.187). Pterostigma open basally, i.e. distal section of Sc missing. In fore wing 2A joining IA or ending freely without reaching wing margin. Basal section of Rs in hind wing (fig. 4.188) missing but the two ends of the vein sometimes present. Subgenital plate (fig. 4.189) with a broad internal sclerite. External valve of ovipositor (fig. 4.190) not divided into lobes, without setae. Phallosome with parameres apically crossing each other medially; aedeagus divided distally, membranous sheets connect the two arms thus formed (figs. 4.191, 4.192).

GENERA INCLUDED IN THE MUSAPSOCIDAE

Musapsocus Mockford, 1967

Musapsocus Mockford (5 species)

Musapsocus Mockford, 1967. *Psyche* 74: 122.
Type species: *M. huastecanus* Mockford.

Characters as for family.

Habitat: Dried leaves.

Distribution: Mexico, Venezuela, Costa Rica, Trinidad.

CHARACTERS OF THE TROCTOPSOCIDAE

Belonging to the Troctomorpha. Antennae 11-, 13- or 15-segmented. Frontal sutures absent. Lacinia tip with median cusp divided, lateral cusp with two or more prominent preapical denticles. Tarsi 3-segmented. No scales. Pterostigma open or closed basally. Sc meeting R. Fore wing with 2A running from its origin a short length along wing margin then joining IA. Basal segments of Rs present or absent. Subgenital plate sometimes with a T-shaped sclerite. Female gonapophyses with external valve bilobed, without setae. Phallosome without external parameres, posterior ends of phallosome arms separated and connected by membrane.

GENERA INCLUDED IN THE TROCTOPSOCIDAE

Troctopsocus Mockford, 1967 (= *Plaumannia* Roesler, 1940)
Protroctopsocus Mockford, 1967
Troctopsocopsis Mockford, 1967
Troctopsoculus Mockford, 1967

Protroctopsocus Mockford (1 species)

Protroctopsocus Mockford, 1967. *Psyche* 74: 131.
Type species: *T. enigmaticus* Mockford.

Antennae 15-segmented. Fore wing (fig. 4.193) with pterostigma closed basally. Basal section of Rs present in hind wing (fig. 4.194). Females polymorphic, occurring in macropterous and brachypterous forms, the latter with fore wings a little shortened and elytriform. Macropterous forms with ocelli, ocelli poorly developed in brachypterous forms. Frons longer than postclypeus in anterior view. Claw with two preapical teeth. Fourth segment of maxillary palp a little swollen near tip. Lacinia (fig. 4.195) with median cusp bidentate having a small inner denticle and a larger outer denticle; lateral cusp with apex undivided. Three denticles before apex, two basal ones arising at same level, much smaller than more distal one. First femur with row of spines. Subgenital plate (fig. 4.196) with thickened apex, bearing some stout setae. Gonapophyses (fig. 4.197). Brachypterous females with fore wings in which heavy veins mark out depressed cells. Hind wings very short, venation greatly reduced.

Habitat: Leaf litter.

Distribution: Mexico.

Troctopsocopsis Mockford (3 species)

Troctopsocopsis Mockford, 1967. Psyche 74: 135.
Type species: T. martinicus Mockford.

Antennae 13-segmented. Fore wing (fig. 4.198) with pterostigma open basally. Hind wing (fig. 4.199) with basal segment of Rs present in hind wing. Anterior arms of epicranial suture absent. Frons longer than postclypeus in front view. Anterior claw of each foot with cowl and without preapical tooth; posterior claw without cowl, without tooth and with a long basal seta bent near its apex. Subgenital plate (fig. 4.200) without T-shaped sclerite, with four setae in middle of hind margin. Phallosome (fig. 4.201) a simple Y-shaped structure. Clunium with posterior comb (fig. 4.202). Lacinia (fig. 4.203). Paraprocts with trichobothria. Gonapophyses (fig. 4.204).

Habitat: Dead fern leaves, club-mosses.

Distribution: Martinique, Dominica, St. Lucia.

Troctopsoculus Mockford (1 species)

Troctopsoculus Mockford, 1967. *Psyche* 74: 133.
Type species: *T. morenus* Mockford.

Antennae 11-segmented. Fore wing (fig. 4.205) with pterostigma open basally. Hind wing (fig. 4.206) without basal section of Rs. Anterior arms of median epicranial sutures indistinct. Claw with two preapical teeth. Lacinia (fig. 4.207). Subgenital plate (fig. 4.208.) without stout marginal setae. T-shaped sclerite present. Gonapophyses (fig. 4.209).

Habitat: Low shrubs.

Distribution: Mexico.

Troctopsocus Mockford (3 species)

Troctopsocus Mockford, 1967. *Psyche* 74: 139.
Type species: *Plaumannia separata* Roesler.

Antennae 13-segmented. Fore wing (fig. 4.210), with pterostigma open basally. Hind wing (fig. 4.211) with basal section of Rs present. Claws as in *Troctopsocopsis*. Fore wing with M - Cu crossvein. Subgenital plate (fig. 4.212) with tapering posterior margin, with four stout setae in middle, with T-shaped sclerite. Phallosome (fig. 4.213) a simple Y-shaped structure. Gonapophyses (fig. 4.214). Posterior margin of clunium bordering epiproct slightly thickened and with slightly scalloped edge, interrupted by smooth edge in the middle. Lacinia (fig. 4.215).

Habitat: Dry fern leaves, foliage.

Distribution: Venezuela, Brazil, Trinidad, Mexico.

CHARACTERS OF THE MANICAPSOCIDAE

Belonging to the Troctomorpha. Antennae 15-segmented. Frontal sutures absent. Lacinia tip with lateral cusp curved outwards and bearing a few indistinct, rounded denticles. No row of denticles on anterior carina of first femur. Tarsi 3-segmented. Claws each with one preapical tooth. Without scales. Pterostigma closed basally. Fore wing with 2A joining wing margin or joining IA. Basal section of Rs absent in hind wing. Gonapophyses with external valve only slightly divided. Subgenital plate with T-shaped sclerite. Male phallosome with median divided aedeagus and with parameres curving towards each other posteriorly arising from a long anterior sclerotized extension.

GENERA INCLUDED IN THE MANICAPSOCIDAE

Manicapsocus Smithers, 1966
Nothoentomum Badonnel, 1967 (= *Epitroctes* Mockford, 1967).
Phallopsocus Badonnel, 1967

Manicapsocus Smithers (1 species)

Manicapsocus Smithers, 1966. *J. ent. Soc. S. Afr*. 28: 46.
Type species: *M. alettae* Smithers

Fore wing (fig. 4.216) with 2A joining wing margin. Antenna with first flagellar segment curved. R_1 greatly expanded near wing margin. Epicranial plates raised into knobs mesad of eyes. Three ocelli almost in a straight line across head. Lacinia (fig. 4.217). Claw with preapical tooth. Pulvillus short and thick. Sc curved to meet R. Rs and M joined by a crossvein. Hind wing with Sc short, ending free. Basal section of Rs absent. Subgenital plate (fig. 4.218). Gonapophyses (fig. 4.219).

Habitat: Dead branches

Distribution: Southern Rhodesia.

Nothoentomum Badonnel (3 species)

Nothoentomum Badonnel, 1967. Biol. l'Amer. austr. 3: 551.
Type species: N. palpalis Badonnel.

Epitroctes Mockford, 1967. Psyche 74: 144.
Type species: E. tuxtlarum Mockford. Syn. nov.

Appearance that of a nymph with very large eyes. Postclypeus very bulbous. No ocelli. Maxillary palps thin, very long in males (fig. 4.221). Lacinia clearly trifid (fig. 4.222). Antennae 15-segmented. No scales. Dorsal thoracic lobes simple. Wings reduced in males (fig. 4.223), with a single vein; very small in females. Coxal organ absent. Claws without preapical tooth and without pulvillus (fig. 4.224). Hypandrium simple. Phallosome (figs. 4.225, 4.220) of a median bifurcated rod to which are laterally attached the parameres surrounding a membranous bulb. On the membrane connecting the phallosome to the hypandrium are two sclerotized patches. Subgenital plate (fig. 4.226) simple with a transverse hind border, well sclerotized. T-shaped sclerite present; gonapophyses (fig. 4.227). No trichobothria.

Habitat: On rocks, on bark.

Distribution: Mexico, Chile.

Note: Badonnel (1967a) described Nothoentomum palpalis from Chile. Later that year Mockford (1967a) described Epitroctes tuxtlarum from Mexico. For each of these species a new genus was raised. It is clear that these species, with a third mentioned but not described by Mockford, are congeneric and the generic name Nothoentomum should be used for them. Epitroctes is synomymous with Nothoentomum (syn. nov.).

Phallopsocus Badonnel (1 species)

Phallopsocus Badonnel, 1967. Biol. l'Amer. austr. 3: 554.
Type species: P. carminatus Badonnel.

Appearance of a nymph with large eyes. Postclypeus little bulbous. No ocelli. Eyes not pubescent. Lacinia (fig. 4.228) with strongly curved apex with teeth hardly prominent. Maxillary palp normal for Amphientometae (fig. 4.229). Antennae 15-segmented. Thoracic tergites short, subequal. Both sexes totally apterous. Tarsi 3-segmented. Coxal organ rudimentary. Claw with strong preapical tooth and a small supplementary tooth. Hypandrium simple. Phallosome (fig. 4.230) complex. Subgenital plate (fig. 4.231) with somewhat sclerotized border, with small T-shaped sclerite. Gonapophyses (fig. 4.232).

Habitat: On bark.

Distribution: Chile.

CHARACTERS OF THE COMPSOCIDAE

Belonging to the Troctomorpha. Antennae 13- or 14-segmented. Frontal sutures present. Lacinia tip with lateral cusp curved outward and bearing a few indistinct, rounded denticles. Row of denticles present on anterior carina of first femur. Tarsi 3-segmented. Claws each with two preapical teeth. Pterostigma closed basally. Fore wing with 2A joining IA. In hind wing basal section of Rs present or absent. M unbranched. Gonapophyses with external valve deeply bilobed. Subgenital plate with T-shaped sclerite. Phallosome with arched or median linear aedeagus and distally broadened parameres.

GENERA INCLUDED IN THE COMPSOCIDAE

Compsocus Banks, 1930
Electrentomopsis Mockford, 1967

Compsocus Banks (1 species)

Compsocus Banks, 1930. Psyche 37: 184.
Type species: C. elegans Banks.

Antennae 14-segmented. Claw with two preapical teeth. Hind wing (fig. 4.233) with basal section of Rs present. Scale-like structures present on fore wing surface. Lacinia (fig. 4.234) with median cusp lightly divided; lateral cusp with apex simple, bearing two low, rounded denticles rising at same level near apex. Anterior femur with 15-16 denticles in ♂, more than 30 in ♀, some bifid. Hypandrium (fig. 4.235) with apical margin curved, slightly emarginate in middle. Phallosome (fig. 4.236) in form of a Y but closed posteriorly, each arm dividing about half way to produce a more membranous lateral branch and a more sclerotized median branch; the latter terminates in a sac surrounding the median branch and becoming closely associated medially with complex sclerites of phallosome. Trichobothria present.

Subgenital plate (fig. 4.237) tapering toward apex, apex with two long setae. T-shaped sclerite present. Gonopophyses (fig. 4.238). Complex spermatheca.

Habitat: On bark.

Distribution: Panama, Mexico.

Electrentomopsis Mockford (1 species)

Electrentomopsis Mockford, 1967. Psyche 74: 149.
Type species: E. variegatus Mockford.

Antennae 13-segmented. Micro-vestiture of fore wing in form of small points. Antennae arising from pit. Frons and vertex sculptured. Eyes pubescent. Lacinia (fig. 4.239). Anterior femur with thirteen spines. Claw with two preapical teeth. Hypandrium with rounded hind margin, bearing numerous setae, two close to centre longer than others. Phallosome (fig. 4.240) in form of a Y; around posterior end of each arm a membranous sac, slightly sclerotized posteriorly, these sacs apparently continuous medially with the endophallus (a bilobed sac containing on its inner walls several longitudinal rows of denticles, fused to form saw-like structures). Trichobothria present. Subgenital plate (fig. 4.241) tapering towards apex, apex truncate and bearing a few setae longer than others. T-shaped sclerite present but evanescent. Gonapophyses (fig. 4.242). Fore wing (fig. 4.243). Hind wing (fig. 4.244).

Habitat: On bark.

Distribution: Mexico.

CHARACTERS OF THE GROUP NANOPSOCETAE

Head short. Antennae usually 15-, sometimes 17-segmented, (exceptionally 9-segmented) with secondary annulations. No maxillary palp sensillum. Labial palp unsegmented. Wings usually reduced or absent; no nodulus. Scales never present. Tarsi 3-segmented. Meso- and metanotum often fused. Claws with one tooth. Winged forms usually carry wings horizontally over abdomen. Paraprocts without spur; no trichobothria. Gonapophyses complete but small, glabrous. Eggs smooth, layed singly, encrusted with debris.

CHARACTERS OF THE LIPOSCELIDAE

Body strongly depressed dorsoventrally; hind legs not extending beyond apex of body. Antennae relatively short. Epicranial suture absent or indicated by a break in sculpturing. Compound eyes reduced, a little larger in winged forms. Ocelli fairly close together but not grouped on a tubercle. Antennae secondarily annulated. Labial palpi of characteristic shape with three external subapical sensilla. Pronotum divided into three lobes, median lobe with median longitudinal line. Meso- and metanota separate in winged forms, fused in apterous forms. Thoracic sterna broad. Hind femora dilated. Tarsi 3-segmented. Wings elongate, rounded apically. Veins reduced to indistinct thickenings of membrane. Fore wings with M and R unbranched, not reaching wing margin. Sc only barely visible. Hind wing with R long, but not reaching margin. Sc and M barely visible. Female with abdominal terga 8 and 9 fused medially, 9 and 10 fused completely. Male with terga 9 and 10 fused. Female subgenital plate with T-shaped sclerite. Gonapophyses complete; external valve broad, without setae and divided into lobes. Phallosome with apically inwardly curving parameres flanking a complex aedeagus; anteriorly the phallosome is extended in a narrow process, the halves of which may be separated giving an anteriorly open phallosome.

GENERA INCLUDED IN THE LIPOSCELIDAE

Liposcelis Motschulsky, 1853
Embidopsocus Hagen, 1866
Belapha Enderlein, 1917
Belaphotroctes Roesler, 1943
Belaphopsocus Badonnel, 1955
Troctulus Badonnel, 1935

Subfamily EMBIDOPSOCINAE

Belapha Enderlein (2 species)

Belapha Enderlein, 1917. Zool. Anz. 49: 254.

Type species: B. schoutedeni Enderlein

Very similar to Embidopsocus. It differs only in the almost circular fourth maxillary palp segment. Claw with one preapical tooth. Females apterous strongly reduced eyes, no ocelli. Fifteenth segment of antenna reduced. Tarsi 3-segmented.

Habitat: On tree trunks, in herbarium, under bark.

Distribution: Congo, Angola, British Guinea.

Belaphopsocus Badonnel (1 species)

Belaphopsocus Badonnel, 1955. Pub. cult. Cia. Diamant Angola 26: 96.

Type species: B. vilhenai Badonnel.

Maxillary palps (fig. 4.245) as in Belapha, i.e. with globular fourth segment. Eyes reduced to two ommatidia. Sternal plastron relatively narrow, setose (fig. 4.246). Femora of third pair of legs enlarged. Some setae apically truncate. Antennae reduced to nine segments, not secondarily annulated. Tarsi 2-segmented. Claws (fig. 4.247) without preapical tooth; pulvillus broad. No apical tibial spines. Apterous (females only known). No epicranial sutures. Lacinia as in Liposcelis. Second segment of maxillary palp also dilated. Labial palp unsegmented. Prothorax not divided into lobes. Subgenital plate simple, rounded behind, setose, some setae truncate. No T-shaped sclerite. Gonapophyses (fig. 4.248) narrow, with reduced ventral valve, dorsal valve elongate, external valve divided into two lobes. No trichobothria.

Habitat: Leaf litter.

Distribution: Angola.

Note: The relatively narrow thorax, the globular abdomen and the genitalia are reminiscent of the Pachytroctidae but most of the characters are distinctly Liposcelid-like.

Belaphotroctes Roesler (7 species)

Belaphotroctes Roesler, 1943. Stettin. ent. Ztg. 104: 13.
Type species: Eutroctes traegardhi Ribaga.

Both sexes apterous, or male apterous with polymorphic alate and apterous females. Alates have long wings (fig. 4.249, 4.250), three ocelli, compound eyes with numerous ommatidia and thoracic structure (fig. 4.251) of Embidopsocus type. Apterous forms are without ocelli; eyes reduced to a few ommatidia. Lacinia (fig. 4.252). Fourth segment of maxillary palp somewhat swollen, sometimes with a dense group of short setae on ventral surface in females. All flagellar segments secondarily annulated. Phallosome (fig. 4.253, 4.254) with parameres fused basally. Subgenital plate rounded behind. Gonapophyses (fig. 4.255) weakly sclerotized. Head sculptured.

Habitat: Leaf litter, shrubs.

Distribution: Angola, Congo, South Africa, Madagascar, North America.

Embidopsocus Hagen (25 species)

Embidopsocus Hagen, 1866. Ent. mon. Mag. 2: 170.

Type species: E. luteus Hagen.

Body strongly depressed. Males apterous, females alate or apterous. Cuticle sculptured with fine ridges. Epicranial sutures absent in all forms. Three ocelli in winged forms, none in apterous. Eyes hairless, with many ommatidia in alates, two in apterous forms (fig. 4.256). Median lobe of pronotum (fig. 4.257, 4.258) either elongate and bordered laterally with a strongly sclerotized ridge of cuticle or transversely oval. Margin of lateral lobes of pronotum rounded with coxal attachment lateral and partly visible from above. In apterous forms relative size of anterior areas on meso-metanotum characteristic; the transverse furrows typically situated almost midway between anterior and posterior margins of fused meso-metanotum. In winged forms, mesothoracic region greatly enlarged and tergal areas similar to those of other winged psocids. Middle coxae typically situated almost halfway between anterior and posterior margins of meso-metanotum, coxal attachment lateral and partly visible from above. A sclerotized intersegmental plate between pro- and meso-metathoracic sterna (fig. 4.259). Hind femora without a dorsal protuberance at its greatest breadth. A single stout spur on distal end of hind tibia on inner side. Hind tibiae with very long setae, as long as, or longer than, first tarsal segment. Bristles on the last three abdominal segments pointed. No T-shaped sclerite on subgenital plate. Gonapophyses (fig. 4.260). Phallosome (figs. 4.261, 4.262). Fore wings (fig. 4.264). Hind wings (fig. 4.265).

Habitat: On bark, in leaf litter, under bark on fallen trees and dead branches.

Distribution: Ivory Coast, Congo, Angola, Mozambique, Cameroons, Madagascar, India, Ceylon, Philippines, North America, Cuba, Porto Rica, Argentina, Paraguay, Europe.

Troctulus Badonnel (1 species)

Troctulus Badonnel, 1955. Pub. cult. Cia. Diamant Angola 26: 94.
Type species: T. machadoi Badonnel.

With the characters of the Liposcelidae similar to Liposcelis and Belaphotroctes from which it may be distinguished by the following:- Tarsi 2-segmented. Antennae 10-segmented. Fourth segment of maxillary palp ovoid but with acuminate apex. Posterior tibia without spines and metathoracic femur without proximal external prominence. Gonapophyses narrow, as in Belaphopsocus. Additional characters:- No epicranial sutures. No ocelli. Eyes reduced to two ommatidia. Antennae without annulations except for first three or four flagellar segments. Lacinia trifid (fig. 4.266). Third segment of maxillary palp short; fourth with sensilla as in Belaphotroctes. Dorsal thoracic sclerites as in Belaphotroctes. Sternites as in Liposcelis. Claw without preapical tooth, very strongly curved. Subgenital plate without T-shaped sclerite. Gonapophyses (fig. 4.267). Apterous. Males unknown.

Habitat: Under bark.

Distribution: Angola.

Subfamily LIPOSCELINAE

* Liposcelis Motschulsky (64 species)

Liposcelis Motschulsky, 1852. Etudes entomologiques 1: 19.
Type species: L. brunneus Motschulsky.

Body moderately depressed. Apterous in both sexes.

Cuticle on dorsal surface of body sculptured with arched ridges or minute tubercles or both. Epicranial sutures absent or represented only by break in sculpturation. No ocelli. Two to eight ommatidia to each eye. Lacinia (fig. 4.268). Median lobe of pronotum transversely oval. Margin of lateral lobes of pronotum acute with coxal attachments ventral and not visible from above. Relative size of anterior areas on mesonotum characteristic; the transverse furrow situated anteriorly and almost reaching the antero-lateral angle of the fused meso-metanotum (fig. 4.269). Middle coxae situated near anterior margin of meso-metathorax, coxal attachment ventral and not visible from above. No sclerotized intersegmental plate between pro- and meso-metathoracic sterna (fig. 4.272). Hind femora with a dorsal obtuse protuberance at its greatest breadth. No stout spur on distal end of hind tibia. Hind tibia with hairs of uniform length, these much shorter than first tarsal segment. Bristles on last three abdominal segments truncate. Subgenital plate with T-shaped sclerite. Gonapophyses (figs. 4.270, 4.271). Phallosome (figs. 4.273, 4.274).

Habitat: On bark, under bark, in leaf litter, in stored products, in human habitation, insect and herbarium collections etc.

Distribution: Cosmopolitan.

Note: This genus includes species usually referred to as "the book louse". The close association between man and several species in this genus has resulted in their becoming worldwide in distribution.

CHARACTERS OF THE PACHYTROCTIDAE

Belonging to the Troctomorpha. Body not depressed, hind legs usually extending beyond apex of abdomen. Frontal sutures absent or indistinct. Lacinia with few apical teeth. Ocelli spaced. Compound eyes relatively large even in apterous forms. First 4 or 5 flagellar segments not secondarily annulated. Thoracic sterna narrow. No subdivision of pronotum. Meso- and metanota separate in winged and apterous forms. Hind femora not dilated. Wings elongate, apically rounded. Veins distinct. Pterostigma not thickened. Fore wing with M 2-branched. Areola postica long and flat, that is, Cu_{1a} relatively long. Cu_2 and IA ending separately at the wing margin (i.e. no nodulus). Abdominal terga membranous or only basal and apical terga sclerotized. Subgenital plate sometimes without T-shaped sclerite. Female gonapophyses complete; dorsal valve somewhat broadened, external valve large, not divided into lobes, somewhat rectangular and without setae. Phallosome anteriorly closed; parameres apically inwardly curving, flanking complex aedeagal structures.

GENERA INCLUDED IN THE PACHYTROCTIDAE

Psylloneura Enderlein, 1903
Tapinella Enderlein, 1908
Antilopsocus Gurney, 1965
Pachytroctes Enderlein, 1905

Subfamily TAPINELLINAE

* *Psylloneura* Enderlein (4 species)

Psylloneura Enderlein, 1903. *Ann. hist. -nat. Mus. hung.* 1: 317.
Type species: *P. simbangana* Enderlein.

Maxillary palp with small first segment. Fourth segment basally broad, narrowing distally. Three ocelli present. Tarsi

3-segmented. In fore wing basal Sc short. Distal section of Sc long. Pterostigma triangular. Rs arises from the point of separation of Sc and R_1. Rs and M joined by a crossvein, media 2-branched. Areola postica long. IA present. In hind wing R_1 ends free in membrane. Basal section of Rs absent. Wing broadest in basal half due to posterior extension of wing in region where Cu_1 meets wing margin. Wings glabrous.

Habitat: Not recorded.

Distribution: Burma (in amber). Cuba, New Guinea, Guam, Uganda.

Note: This genus has been poorly characterized. Badonnel (1955: 99, footnote) has suggested that it should be synonymized with *Pachytroctes*.

Tapinella Enderlein (12 species)

Tapinella Enderlein, 1908. *Zool. Anz.* 33: 772.
Type species: *T. formosana* Enderlein.

With the characters of the family and as follows: Apterous and winged forms known. Compound eyes large, even in apterous forms. Subgenital plate (fig. 4.275) with a T-shaped sclerite. Dorsal valves of gonapophyses (fig. 4.276) delicate, much less developed than the external valves. Areola postica long and low. Fore wings (figs. 4.278, 4.279) with variable venation. Basal Sc small when present, ending in costa. Distal Sc and R_1 well developed. Rs and M joined by a crossvein. M 2-branched. Hind wing (figs. 4.280, 4.281) without Sc and without basal section of Rs. M simple. Ocelli present in winged forms, evanescent in apterous forms. Lacinia (fig. 4.277). Phallosome (figs. 4.282, 4.283). Ninth abdominal tergite usually with two small protuberances, one on either side of the midline, in the male.

Habitat: On palm leaves, in nest of rat, on dead leaves, in birds' nests, in houses, in leaf litter.

Distribution: Congo, Ivory Coast, Nigeria, Angola, Madagascar, India, Formosa, Japan, New Hebrides, Hawaii, England.

Subfamily PACHYTROCTINAE

Antilopsocus Gurney (1 species)

Antilopsocus Gurney, 1965. Ent. News 76:1.
Type species: A. nadleri Gurney

General body form much as in Pachytroctes but with "horns" on vertex (fig. 4.284). Head with rough sculpture. Median epicranial suture present, anterior arms evanescent. Ocelli absent. Eyes large, glabrous. Antennae 15-segmented. Lacinia (fig. 4.285) with two apical teeth and a smaller inner one. Pronotum distinct; meso- and metanotum fused but with a separating suture. Gonapophyses inconspicuous. Subgenital plate broad, with T-shaped sclerite (fig. 4.286). Apterous. Claw (fig. 4.287) long, with small preapical tooth.

Habitat: Leaf litter, vegetation.

Distribution: Brazil, Trinidad.

Pachytroctes Enderlein (23 species)

Pachytroctes Enderlein, 1905. Res. Swed. Exp. Egypt. 18: 46.
Type species: P. aegyptius Enderlein.

Characters of the family and as follows: Apterous and winged forms known. Compound eyes relatively small. Subgenital plate without T-shaped sclerite. Dorsal valves of gonapophyses (figs. 4.288, 4.289) with rigid sclerified armature, as long as external valves. Areola postica relatively tall. Fore wings (fig. 4.290) with variable venation. Basal Sc present as a small vein ending in R. Distal Sc and R_1 well developed. Rs and M meeting in a point or joined by a crossvein. M 2-branched. Areola postica relatively tall. Hind wing (fig. 4.291) with R_1; basal section of Rs absent. Apterous forms without ocelli; alate forms with ocelli. Lacinia (fig. 4.292). Ninth abdominal tergite simple. Epicranial plates sometimes expanded into prominences. Phallosome (figs. 4.293, 4.294).

Habitat: On bark, in birds' nests, in leaf litter, dead leaves.

Distribution: Egypt, Angola, Ivory Coast, Congo, South Africa, India, Formosa, Brazil, France.

CHARACTERS OF THE SPHAEROPSOCIDAE

Belonging to the Troctomorpha. Body not depressed, hind legs usually extending beyond apex of abdomen. Anterior arms of median epicranial sutures evanescent or absent. Lacinia apex divided. Compound eyes in both alate and apterous forms composed of a few ocelloids. Thoracic sterna narrow without cilia. Pronotum simple, not divided into lobes. Meso- and metanota fused in apterous forms. Hind femora not dilated. In alate forms only fore wings present, convex, elytriform, with incomplete venation. Abdominal terga 8 and 9 fused. Subgenital plate with T-shaped sclerite. Gonapophyses complete with dorsal valve somewhat broadened; external valve large, not divided into lobes, somewhat rectangular, and without setae. Phallosome anteriorly closed; parameres apically inwardly curving, flanking the aedeagal structure.

GENERA INCLUDED IN THE SPHAEROPSOCIDAE

Sphaeropsocus Hagen, 1882
Badonnelia Pearman, 1953
Sphaeropsocopsis Badonnel, 1963

* *Sphaeropsocus* Hagen (1 species)

Sphaeropsocus Hagen, 1882. *Stettin. ent. Ztg*. 43: 225.
Type species: *S. kunowi* Hagen.

With the characters of the family and the following: Fore wings (fig. 4.295) not bent ventrally along lateral margin. Five main veins. Membrane of wing with granulations grouped into polygonal areas. Number of ommatidia variable. Sculpturation of body granular. Fourth segment of maxillary palp fusiform. R_1 and Rs simple. M and Cu_1 branched.

Habitat: Unknown.

Distribution: East Prussia (in amber).

Badonnelia Pearman (3 species)

Females alate, fore wings only (fig. 4.296); males apterous. Eyes with seven ocelloid elements. Antennae 15-segmented, annulations on f_1 and f_2. Fourth segment of maxillary palp long. Pronotum flat, synthoracic nota flat, some clear subdivision in female, male with antedorsum barely demarcated. Sterna narrow, undefined. Abdomen with terga 2-4 fused, 5-7 free, 8-9 fused (clunium). In female 2-6 unsclerotized, 7 lightly sclerotized in middle. In male all terga weakly sclerotized, 1-4 completely fused. Subgenital plate with T-shaped sclerite (fig. 4.297). Gonapophyses (fig. 4.298). Phallosome (figs. 4.299, 4.300, 4.301).

Fore wings bent ventrally laterally. Two veins only. Membrane with a reticulated pattern. Seven ommatidia. Fourth segment of maxillary palp subcylindrical, very long. Mesothoracic lobes distinct.

Habitat: In building, in leaf litter, in fork of tree, in moss, in caves.

Distribution: England, France, Chile, Switzerland.

Sphaeropsocopsis Badonnel (5 species)

Sphaeropsocopsis Badonnel, 1963. Biol. l'Amer. austr. 2: 322.
Type species: S. chilensis Badonnel.

With the characters of the family, and as follows: Fore wings elytriform, not bent laterally. Four or five veins, simple, (Cu_2 absent) confluent apically or not (figs. 4.302, 4.303). Three to ten ommatidia. Wing membrane with granulations grouped into polygenal areas. Fourth segment of maxillary palp fusiform. Thoracic tergites not divided into lobes. No ocelli. Males unknown.

Habitat: Under stones, in moss, in leaf litter.

Distribution: Tasmania, Argentina, Chile.

CHARACTERS OF THE SUBORDER PSOCOMORPHA

Labial palps 1-segmented. Antennae with 13 or fewer segments. Adults with 2- or 3-segmented tarsi. Antennae never secondarily annulated. Winged forms with ctenidiobothria. Scales never present. Pterostigma thickened. Pearman's organ usually present, well developed and strongly chitinized. Subgenital plate without T-shaped sclerite. Gonapophyses various, but with external valve setose. Maxillary palp without sensillum. Hypopharynx with chitinous filaments separated in posterior part. Coupling apparatus of nodulus and stigmapophysis not in form of separate hooks.

CHARACTERS OF THE GROUP EPIPSOCETAE

Head long, vertical. Genae long. Labial palp short and appressed, somewhat semicircular, 1-segmented. Apical third of lacinia broadening toward apex; usually many-toothed. Gonapophyses reduced; external valve present and setose. Labrum on inner side with two strongly sclerotized ridges, often converging towards and fused with fore margin and showing through to outer surface. Outer edge of mandible bluntly angled. Claws straight, with preapical tooth. Tarsi 2- or 3-segmented. Ocelli grouped. Areola postica usually free, low and elongate. Eggs smooth, layed singly, encrusted.

CHARACTERS OF THE EPIPSOCIDAE

Belonging to the Psocomorpha. Two strongly sclerotized anteriorly converging rods transversing the labrum. Genae long, that is, head long. Ocelli grouped on a tubercle. Mandibles with outer margin bluntly, not sharply, angled. Lacinia with apex broadened and divided into about 8 to 10 teeth or extended into a projection on one side. Labial palps small and appressed. Fore wing with Rs and M joined by a cross-vein. Stem of Rs relatively straight before bifurcation. Setae on veins and margin in a single row. Cu_2 glabrous. Pterostigma and areola postica usually long and narrow. Hind wing with Rs and M fused for a length. Veins in distal part of hind wing sometimes with one row of setae. Margin setose. Tarsi 2-segmented. Claws relatively straight with preapical tooth and fine pulvillus. Female subgenital plate simple. Gonapophyses sometimes reduced; ventral valve sometimes absent; dorsal valve, when present, long and finely pointed, fused to external valve which is setose. Hypandrium simple or lobed. Phallosome open anteriorly; aedeagus forming a pointed arch posteriorly, external parameres broad, tapering to a blunt, posterior apex.

Eggs laid singly, covered with an encrustation and without silk.

GENERA INCLUDED IN THE EPIPSOCIDAE

Epipsocus Hagen, 1866.

Epipsocopsis Badonnel, 1955

Neurostigma Enderlein, 1900

Goja Navas, 1927.

Subfamily EPIPSOCINAE

* Epipsocus Hagen (35 species)

Epipsocus Hagen, 1866. Verh. zool. -bot. Ges. Wien 16: 203.
Type species: Psocus ciliatus Hagen.

Characters of the family and as follows: Winged in both sexes or with winged males and brachypterous or apterous females. Veins in proximal part of hind wing glabrous. Postclypeus and labrum very large. Antennae long and fine. Subgenital plate simple. Gonapophyses (figs. 4.304, 4.309, 4.310) with ventral valves long and pointed with dilatation in the distal third. Dorsal and external valves fused, the former long and pointed the latter becoming a setose lobe attached to the former; sometimes ventral valve absent. Lacinia (fig. 4.305). Fore wing (figs. 4.306, 4.307). Hind wing (fig. 4.308). Lacinia (figs. 4.311, 4.312). Phallosome with parameres open anteriorly with or without complex aedeagal sclerifications (figs. 4.313, 4.314).

Habitat: Under stones, in caves, on dead branches in humid forests, in leaf litter (damp), on bark. (This group appears to be found in particularly damp situations, nowhere very common).

Distribution: Angola, Reunion, India, Malaya, Borneo, Sarawak, Philippines, Java, Formosa, Japan, North America, Santa Domingo, Jamaica, Colombia, Brazil, Bolivia, Peru, Guatamala, Argentina, Europe, East Prussia (in amber).

Epipsocopsis Badonnel (5 species)

Epipsocopsis Badonnel, 1955. Pub. cult. Cia. Diamant Angola 26: 118.
Type species: E. machadoi Badonnel.

Characters as in Epipsocus but differing as follows: Lacinia (fig. 4.315) hardly broadened apically, with a narrow internal tooth and an external tooth rounded, then extended apically into a blunt or pointed process. Gonapophyses (fig. 4.316) reduced to the external valve which is elongate, setose, extended into a long posterior pointed process (dorsal valve remnant?) Other characters: both sexes winged. Fore wing (fig. 4.317) rounded. Rs more flexuous than in Epipsocus. Veins (except glabrous Cu_2) with a single row of setae. Hind wing (fig. 4.318) with veins setose in distal half of wing. Rs fused with M for a length. Coxal organ well developed. Hypandrium divided into symmetrical lobes, setose. Phallosome (figs. 4.319, 4.320) open anteriorly, parameres fused apically. Subgenital plate simple. Gonapophyses (fig. 4.316). Epiproct simple. Paraproct with large field of trichobothria, including one seta without "rosette" base.

Habitat: On vegetation.

Distribution: Angola, Madagascar.

Subfamily GOJINAE

Goja Navas (1 species)

Goja Navas, 1927. Rev. Acad. Cienc. Zaragoza 11: 58.

Type species: G. ditata Navas.

Fore wing with Rs 4-branched and M 7-branched. Hind with Rs 4-branched and M 5-branched. 2A absent. Tarsi 2-segmented.

Habitat: Unknown.

Distribution: Costa Rica.

Note: This genus is known only from one incomplete specimen (without head). Roesler, (1940b) has re-examined the type and considers it to belong to the Epipsocidae.

Subfamily NEUROSTIGMINAE

Neurostigma Enderlein (2 species)

Neurostigma Enderlein, 1900. Zool. Jb. Abt. Syst. 14: 157.
Type species: N. chaetocephalum Enderlein.

Head a little shorter than usual in the family, with shaggy pubescence. Antennae very thin, long-haired. Coxal organ present. Claw with strong preapical tooth. Fore wing (fig. 4.321) with strong series of transverse thickenings crossing pterostigma, which is broad. Rs and M joined by a crossvein. Branches of veins sinuous. Veins and margin with more than one row of setae. Cu_2 with one row. Areola postica tall, Cu_{1a} sinuous. Cu_{1a} arises separately from Cu, i.e. areola postica stands free; Cu_{1a} sometimes fused with M_1 thus giving the impression that the areola postica is lacking. Hind wing (fig. 4.322) with Rs and M fused for a length. Costal margin near base strongly setose, glabrous as far as R_1, then long setose. Rs 2-branched. M simple. Branches of veins and whole of Cu_2 and IA with more than one row of setae. Labrum with strong transverse chitinous rods. Lacinia broad at apex with many small teeth. Subgenital plate simple, with thickened hind margin, setose. Gonapophyses (fig. 4.323) reduced to one valve which probably represents fused external and dorsal valves or setose external valve alone (as in Epipsocopsis). Hypandrium simple, truncate. Phallosome (fig. 4.324) with parameres open proximally, fused distally, with median aedeagal sclerifications (similar to Epipsocopsis). Paraprocts with trichobothrial field, large in male.

<u>Habitat</u>: On bark.

<u>Distribution</u>: Brazil, Peru.

CHARACTERS OF THE PTILONEURIDAE

Belonging to the Psocomopha. Two strongly sclerotized ridges transversing the labrum. Genae long. Ocelli grouped. Lacinia with broad apex divided into several teeth. Labial palps appressed. Fore wing with Rs and M joined by a cross-vein. Rs usually relatively straight before forking. Distal branches sinuous. Pterostigma elongate and flat. Media frequently more than 3-branched. Areola postica elongate but with Cu_{1a} sinuous giving a fairly tall cell. Veins with more than one row of setae. Cu_2 setose. Two anal veins present. Hind wing with Rs and M fused for a length. Veins in distal part of wing with more than one row of setae. M branched or unbranched, sometimes more than 2-branched. Tarsi 3-segmented. Claws with preapical tooth. Subgenital plate simple. Female gonapophyses with ventral valve pointed with preapical dilatation. Dorsal valve narrow elongate, pointed; external valve broad setose, fused with dorsal valve near base. Hypandrium strongly sclerotized with various projections, spines, apophyses and other irregularities, symmetrically arranged. Phallosome closed anteriorly, parameres sometimes complex. Aedeagus and bulb of phallosome with various complex sclerifications. Paraprocts with trichobothrial field; spinous and sometimes with a rugose area and other ornamentation.

GENERA INCLUDED IN THE PTILONEURIDAE

Ptiloneura Enderlein, 1900

Euplocania Enderlein, 1910

Cladiopsocus Roesler, 1940

Ptiloneuropsis Roesler, 1940

Triplocania Roesler, 1940

Ptiloneura Enderlein (6 species)

Ptiloneura Enderlein, 1900. Zool. Jb. Abt. Syst. 14: 147.
Type species: P. bidorsalis Enderlein.

Head and body long pilose. Antennae with shorter setae. Fore wing (fig. 4.325) with Rs long, branches sinuous. Pterostigma fairly low. Areola postica tall. Rs 2-branched. M multi-branched. Margin setose. 2A present. Veins with a double row of setae; except Cu_2, which has a single row. In hind wing (fig. 4.326) costal margin glabrous as far as R_1 then setose. Veins in distal part of wing with double row of setae, basally glabrous. Cu_2 glabrous. M in hind wing 2-branched or more. Coxal organ present. Claws straight with strong preapical tooth. Subgenital plate simple. Gonapophyses (fig. 4.327) with pointed ventral valve with preapical expansion. Glabrous dorsal valve and setose external valve fused near base. Spermatheoal opening with complex sclerification.

Habitat: On bark.

Distribution: Peru, Bolivia, Brazil, Costa Rica, Guatamala.

Triplocania Roesler (7 species)

Triplocania Roesler, 1940. Zool. Anz. 129: 239.
Type species: T. maginifica Roesler.

Head and body strongly pubescent. Antennae thickly setose. Lacinia (fig. 4.328) broad at apex, divided into several teeth. Fore wing (figs. 4.329, 4.330) with pterostigma long and flat. Margin strongly setose. Veins in apical part of wing with more than one row of setae, except Cu_2 which has one. Areola postica tall, Cu_{1a} sinuous, or areola postica relatively flat with Cu_{1a} curved; in either event, areola postica long. M 3-branched, branches sinuous. Hind wing (fig. 4.331) with basal Sc strong, ending free. Margin setose beyond R_1; veins in distal part of wing with two rows of setae. Cu_2 and IA glabrous. Subgenital plate (fig. 4.332) relatively simple, setose. Gonapophyses (fig. 4.333) as in Ptiloneura. Spermathecal opening with complex sclerification (fig. 4.334). Hypandrium either simple or with various spines, protuberances and apophyses (figs. 4.335, 4.336). Phallosome (figs. 4.337, 4.339) complex. Paraproct (fig. 4.340) with large rugose areas in male and well developed trichobothrial field.

Habitat: Not recorded - more frequently taken at light than is usual with Psocoptera.

Distribution: Angola, Brazil, Costa Rica, Guatemala.

Cladiopsocus Roesler (1 species)

Cladiopsocus Roesler, 1940. Zool. Anz. 129: 238.
Type species: Dendroneura ramulosa Enderlein.

Characters similar to Ptiloneura but fore wing with a reticulation formed by anastomosing crossveins in the distal half of the wing. In hind wing a similar network occurs on a smaller scale. Variation in detail of the arrangement of these adventitious veins is considerable. Fore wing margin and veins strongly pubescent. M unbranched in hind wing. In hind wing Cu_2 and IA glabrous.

Habitat: Not recorded.

Distribution: Peru.

Euplocania Enderlein (2 species)

Euplocania Enderlein, 1910. S.B. Ges. naturf. Fr. Berl. 1910: 69.

Type species: E. amabilis Enderlein.

Characters as in Ptiloneura but in fore wing (fig. 4.341) M is 4-branched (not 6-8-branched). Branches of M strongly sinuous. Areola postica long, but tall due to Cu_{1a} being strongly sinuous. Hind wing (fig. 4.342) with M simple and unbranched. Fore wing veins with a single row of setae. Hind wing veins in distal part of wing with single row of setae, basal parts glabrous.

Habitat: Not recorded.

Distribution: Bolivia, Paraguay.

Ptiloneuropsis Roesler (1 species)

Ptiloneuropsis Roesler, 1910. Arb. morph. taxon. Ent. Berl. 7: 236.

Type species: P. immaculata Roesler.

Characters as in Ptiloneura but in fore wing pterostigma is long and narrow. Media 7-8-branched. Areola postica tall, triangular, with pointed apex, joined to M by a crossvein. 2A present. In hind M 4-branched.

Habitat: Not recorded.

Distribution: Brazil.

CHARACTERS OF THE CALLISTOPTERIDAE

Belonging to the Psocomorpha. Labrum large, with straight anterior margin rounded laterally. Pterostigma short and broad. R_{2+3} fused with R_1 for a length, dividing cell R_1 into an open distal cell and a closed proximal one. R_{4+5} branched. Rs short and straight before branching; branches sinuous. Rs and M connected by a cross-vein. Media 3-branched, the branches all arising near the wing margin, that is, M long before branching. Cu_1 long before branching, angle acute, with Cu_{1a} curving towards wing margin giving a long, low areola postica; Cu_{1a} relatively long, continuing to meet margin at an acute angle. One anal vein. Membrane setose except in cubital and anal cells. Veins and margin with more than one row of setae. Hind wing broad. M 2-branched; Cu_1 strongly sinuous. Cu_2 and IA exceptionally long. Cu_2 glabrous, other veins with more than one row of setae. Membrane setose in distal parts of wing. Tarsi 2-segmented.

(Note: This family has not been described in the literature since the original description of *Callistoptera* Enderlein).

GENERA INCLUDED IN THE CALLISTOPTERIDAE

Callistoptera Enderlein, 1903

Callistoptera Enderlein (1 species)

Callistoptera Enderlein, 1903. *Ann. hist. -nat. Mus. hung.* 1: 240.
Type species: *C. anna* Enderlein.

Characters as for family.

Habitat: Not recorded.

Distribution: New Guinea.

CHARACTERS OF THE GROUP CAECILIETAE

Labial palps broadly triangular, laterally diverging. Lacinia narrowing apically usually without distinct teeth. Head short, transverse. Gonapophyses reduced, external valve reduced to at most a seta-bearing remnant or absent altogether. Claws without preapical tooth. Tarsi 2-segmented. Ocelli grouped. Areola postica free and tall or connected to M. Wing margin and veins more or less setose. Phallosome normal. Eggs smooth, in groups, covered with silken strands.

CHARACTERS OF THE CAECILIIDAE

Belonging to the Psocomorpha. Tarsi 2-segmented. Claws without a preapical tooth. Pulvillus broad, well developed. Labium with palps protruding, triangular. Pterostigma free, Rs and M usually fused for a length; M usually 3-branched; areola postica usually free, sometimes joined to M (some Dypsocinae). Branches of veins in fore wing with one row of setae; margin always with more than one row but setae not crossing each other as they do in Pseudocaeciliidae. Cu_2 glabrous or setose. Hypandrium simple. Phallosome closed anteriorly with some degree of, usually, rugose sclerification of the penial bulb. Subgenital plate simple. Gonapophyses reduced to dorsal and ventral valves usually slender and pointed, with external valve reduced to a small sclerified area bearing a strong seta. Eggs laid in groups, not covered with an encrustation but covered with silken strands.

This is a large family of many species but the genera, despite variation in venation exhibit little variation in genitalic characters.

GENERA INCLUDED IN THE CAECILIIDAE

Dypsocinae:

Drypsocus Hagen, 1866
Coryphosmila Enderlein, 1925
Isophanes Banks, 1937

Caeciliinae:

Asiopsocus Gunther, 1968
Caecilius Curtis, 1837
Fulleborniella Enderlein, 1902
Dasydemella Enderlein, 1909
Ptenolasia Enderlein, 1911

Tagalopsocus Banks, 1916

Ptenopsila Enderlein, 1923

Mepleres Enderlein, 1926

Teliapsocus Chapman, 1930

Paracaecilius Badonnel, 1931

Ypsiloneura Pearman, 1932

Enderleinella Badonnel, 1932

Lacroixiella Badonnel, 1943

Eocaecilius Badonnel, 1959

Schizopechinae:

Schizopechus Pearman, 1934

Subfamily DYPSOCINAE

Dypsocus Hagen (9 species)

Dypsocus Hagen, 1866. Verh. zool. -bot. Ges. Wien 16: 207.
Type species: Psocus coleoptratus Hagen.

Head vertically flattened; postclypeus, therefore, hardly protruding. Vertex sharp. Antennae may have some flagellar segments thickened. Lacinia narrowing towards apex, bidentate. Labial palps broadly triangular, somewhat protruding laterally. Claws without preapical tooth; pulvillus broad. Apical part of fore wing (fig. 4.344) reduced resulting in characteristic distortion of venational pattern in that area. Pterostigma free. Rs and M meeting in a point or joined by a cross-vein. Rs taking a sharp turn towards anterior of wing before forking; M curving back and then forwards before branching with M_1 turning back again at an angle to longitudinal axis of wing; R_{4+5} and M_1 then diverge in apical part of wing leaving a broad cell R_5. M 3-branched. Areola postica usually reduced, semicircular or distorted. Veins and margin setose, setae on branches of main veins being in a single row. Cu_2 glabrous. Branches of main veins usually reduced in length.

Hind wing (fig. 4.345) with Rs and M fused for a length. Male epiproct (fig. 4.346) with rugose area. Paraproct (fig. 4.346) with rugose area but without marginal tubercle. Hypandrium simple (fig. 4.347). Phallosome (fig. 4.348) with well developed parameres, arched aedeagus and rough penial bulb sclerifications. Subgenital plate simple. Gonapophyses reduced in fashion characteristic of the family (see e.g. *Caecilius*).

Habitat: On leaves of shrubs.

Distribution: Angola, India, Philippines, Ceylon, Java, Sumatra, New Guinea, Formosa, Japan, Peru, Brazil, Argentina.

Note: The genera, *Protodypsocus* Enderlein and *Coryphaca* Enderlein were distinguished from *Dypsocus* on antennal and minor venational differences. Roesler (1944) regarded these as subgenera of *Dypsocus* but Badonnel (1955) regarded them as not being based on adequate grounds. The venational features (Rs and M relationships and areola postica - M relationships) and antennal features (thickening of some flagellar segments) do not occur in constant correlation in the species allocated to the subgenera. The species, therefore, should all be considered as belonging to one group with generic status.

Coryphosmila Enderlein (3 species)

Coryphosmila Enderlein, 1925. *Konowia* 4: 106.
Type species: *Dyspsocus* *dolobrata* Hagen

Characters as for *Dypsocus* but venation as in *Caecilius*, not distorted.

Habitat: On leaves and twigs of shrubs.

Distribution: Singapore, Java, Ceylon, Formosa.

Note: The genera Mepachycera Enderlein and Coryphocopsis Enderlein were erected on antennal and venational characters. Roesler (1944) considered these as subgenera of Coryphosmila but it is doubtful if even this separation is warranted.

Isophanes Banks (4 species)

Isophanes Banks, 1937. Philipp. J. Sci. 62: 256.
Type species: I. decipiens Banks

Head vertically flattened, postclypeus, therefore, hardly protruding. Vertex sharp. Antennae without thickened flagellar segments. Lacinia (fig. 4.349) narrowing towards the apex, apical division reduced but discernible. Labium with triangular, laterally protruding palps. Claws without preapical tooth; pulvillus broad. Fore wings (fig. 4.350) tend to be apically reduced with shortening of branches of main veins. Rs and M fused for a length. R_{2+3} and R_{4+5} strongly diverging; pterostigma with strongly angulated hind margin; M 2-branched; Cu_{1a} fused with M. Cu_2 without or with a few setae. IA somewhat sinuous. Hind wing (fig. 4.351) with Rs and M fused for a length; marginal setae from R_{2+3} around wing apex to wing base. Veins glabrous. Male epiproct with papillate area (fig. 4.352). Paraproct (fig. 4.352) with papillate area but without marginal tubercle. Hypandrium simple. Phallosome (fig. 4.353) with strongly developed parameres, strongly narrowed but well developed aedeagus and finely rugose sclerifications of penial bulb. Epiproct and paraproct (fig. 4.352) with papillate areas; paraproct with a pair of tiny hyaline cones. Subgenital plate simple, with transverse hind margin. Gonapophyses (fig. 4.354) reduced in fashion characteristic of the family.

Habitat: On twigs, in leaf litter.

Distribution: Angola, Natal, Ceylon, Formosa.

Subfamily CAECILIINAE

Asiopsocus Gunther (1 species)

Asiopsocus Gunther, 1968. Mitt. zool. Mus. Berl. 44: 128.
Type species: A. mongolicus Gunther.

Males winged, females apterous. Fore wing (fig. 4.355) without marginal setae, veins with small, sparse setae. Rs and M fused for a length. Postclypeus strongly developed. Ocelli present in males, absent in females. Eyes large in both sexes, longer in males. Lacinia (fig. 4.356) broad, with apex truncate, without teeth. Coxal organ present in males. Hypandrium simple. Phallosome (fig. 4.357). Male paraproct (fig. 4.358) with field of trichobothria. Male epiproct (fig. 4.358) triangular. Subgenital plate (fig. 4.359) weakly incurved along posterior margin. Gonapophyses (fig. 4.360) reduced. Ventral valve absent. External valve apparently absent or its rudiment fused to base of broad, dorsal valve. Claws (fig. 4.361) without teeth. Female epiproct with rounded hind margin. Female paraproct (fig. 4.362) with reduced trichobothria. Labial palpi not particularly divergent. Tarsi 2-segmented.

Habitat: From shrubs.

Distribution: Mongolia.

* Caecilius Curtis (235 species)

Caecilius Curtis, 1837. British Entomology 14: 648.
Type species: Psocus fuscopterus Latreille.

Head with rounded vertex. Postclypeus variable, from fairly flat to strongly bulbous. Antennae variable. Lacinia with variable apex but usually showing at least some signs of bifurcation into separate teeth or with narrow transverse apex (figs. 4.363 - 4.365). Labial palps triangular, protruding. Claws without preapical tooth, pulvillus broad. Fore wings (figs. 4.366-4.368) with margin and veins setose, the hairs of the veins in one or two rows. Areola postica free and pterostigma not connected to Rs; no spur vein from pterostigma. Rs sinuous. Rs and M fused for a length; Cu_2 with or without setae. Hind wing with Rs and M fused for a length; no setae on veins but with whole margin setose. Epiproct of male (fig. 4.369) with rugose field, paraprocts (figs. 4.370, 4.371) with or without tubercles. Hypandrium simple. Female subgenital plate simple. Gonapophyses reduced (figs. 4.372-4.375) characteristic of the family. Phallosome (figs. 4.376-4.380) with well developed parameres; aedeagus arched; penial bulb rugosely sclerified to varying degree.

Habitat: Found in almost all habitats.

Distribution: World wide, also found in East Prussian amber.

Dasydemella Enderlein (3 species)

Dasydemella Enderlein, 1909. Bol. Lab. zool. Portici 3: 329.
Type species: D. silvestrii Enderlein.

Characters as in Caecilius except as follows: In fore wing (fig. 4.381) R, M and stem of radial fork with two rows of setae; branches of veins and Cu_2 with one row. In hind wing (fig. 4.382) marginal setae only between R_{2+3} and R_{4+5}. Cu_2 setose; IA with two rows of setae. Veins of hind wings glabrous. Areola postica tall. Phallosome (fig. 4.383) similar to Caecilius.

Habitat: Not recorded.

Distribution: Mexico, Brazil.

Enderleinella Badonnel (1 species)

Enderleinella Badonnel, 1932. Bull. Soc. ent. Fr. 37: 77.
Type species: Caecilius perlatus Kolbe.

Characters as in Caecilius but differing as follows: Head small but with exceptionally prominent postclypeus; lacinia (fig. 4.385) terminating in a long point; pterostigma (fig. 4.384) long and narrow, with subparallel sides and without strongly prominent hind angle. Rs almost straight before forking. Epiproct and paraproct of male without rugose areas. Female gonapophyses (fig. 4.386) with dorsal valve in the form of a broad, pointed, membranous flap; ventral valve membranous.

Habitat: On leaves.

Distribution: Europe, New Zealand.

Eocaecilius Badonnel (1 species)

Eocaecilius Badonnel, 1959. Explor. Parc. nat. Albert, Mission G.F. de Witte (1933-1935): 95: 13.
Type species: E. wittei Badonnel.

Characters as in Caecilius but differing in the following: M + Cu abnormally thickened (fig. 4.387); distal branches of veins very fine. Pterostigma without distinct hind angle. Wing apex somewhat pointed. Female gonapophyses (fig. 4.388) reduced but very different from Caecilius. Ventral valves curved, sclerotized, connected to the eighth tergite by a long peduncle; dorsal valves ovoid, dilated, sclerotized in the external half with a membranous apex armed with fine spicules. External valve absent. Spermatheca with short duct, without glands.

Habitat: Riverside vegetation.

Distribution: Belgian Congo (Albert National Park).

Fulleborniella Enderlein (18 species)

Fulleborniella Enderlein, 1902. Mitt. zool. Mus. Berl. 2: 10.
Type species: F. nyassica Enderlein.

Characters as in Caecilius but having a longer or shorter spur-vein from the hind margin of the pterostigma (fig. 4.389). Cu_2 setose. Gonapophyses (fig. 4.390) of female without setal remnant of the external valve. Sometimes one large seta amongst normal setae in trichobothrial field. Phallosome (fig. 4.391) similar to Caecilius.

Habitat: Under stones, in leaf litter, in dried leaves, on twigs and undersides of leaves.

Distribution: Angola, Congo, French Guinea, East Africa, Ivory Coast, Cameroons, South Africa, Seychelles, Singapore, Java, India, Australia.

Lacroixiella Badonnel (1 species)

Lacroixiella Badonnel, 1943. Faune de France 42: 126.
Type species: Caecilius martini Lacroix.

Characters of the wing (fig. 4.392, 4.393) similar to that of Caecilius but with somewhat pointed apex. Pterostigma narrow, pointed apically without posterior angle. Few short setae on wings. Rs long and slightly sinuous before bifurcation. Areola postica large, semicircular. Rs and M fused for a long length in both fore and hind wings.

Habitat: Uncertain - specimens found indoors.

Distribution: France (introduced?)

Note: Very little is known of this genus; only two specimens are known from a hospital in France. They were probably introduced from elsewhere as the species has not been found since.

Mepleres Enderlein (9 species)

Mepleres Enderlein, 1926. Zool. Meded. 9: 61.
Type species: M. maeandricus Enderlein.

Characters as in Caecilius but with M in fore wing 2-branched.

Habitat: On plants.

Distribution: Ceylon, Formosa, Java, Queensland, Sarawak, Guam, Hawaii, Samoa, Japan, Thailand.

Paracaecilius Badonnel (4 species)

Paracaecilius Badonnel, 1931. Ann. Sci. nat. Zool. (10) 14: 235.
Type species: P. berlandi Badonnel.

Characters as in Caecilius, but with following characters: Fore wing (fig. 4.394) with pterostigma with subparallel sides; fore wing with longer setae, in two rows on R and IA; Cu_2 setose. Female gonapophyses (fig. 4.395) reduced but differing in form from Caecilius in that the ventral valve is in the form of a chitinized strip, broadened basally, and surrounded by a membranous flange; dorsal valve in form of a broad, feebly chitinized lobe, triangular, with little sclerification and with a few apical spinules; external valve represented by a seta arising from the base of the dorsal valve. Spermatheca with numerous glands in its distal narrow area and the external glandular area reduced (fig. 4.396). Phallosome (fig. 4.397).

Habitat: Under stones in sandy desert area.

Distribution: Mozambique, Madagascar, Angola, Ivory Coast.

* Ptenolasia Enderlein (1 species)

Ptenolasia Enderlein, 1911. Palaeontographica 58: 321.
Type species: Caecilius pilosus Hagen.

Head with rounded vertex, strongly setose. Lacinia gently narrowing towards apex, fairly truncate. Claws without preapical tooth. Pulvillus broad. Fore wing with pterostigma having a fairly strongly angled hind margin. Rs and M fused for a short length. M 3-branched. Branches of veins, except Cu_2, with a single row of setae. Wing margin hairs crossing each other between M_2 and Cu_1. Wing membrane sparsely setose in distal half of wing. Hind wing with margin setose along whole length. Veins glabrous. Tarsi 2-segmented. Epiproct and paraproct not known. Subgenital plate with a rounded posterior lobe. Genitalia unknown.

Habitat: Unknown.

Distribution: East Prussia (in amber).

Tagalopsocus Banks (2 species)

Tagalopsocus Banks, 1916. Philipp. J. Sci. 11: 201.
Type species: T. luzonensis Banks.

Characters as in Caecilius but differing as follows: In the fore wing the pterostigma long and narrow, without prominent hind angle. Rs and M meeting in a point. In hind wing the radial fork is narrow, i.e. R_{2+3} and R_{4+5} diverge at a small angle, with R_{2+3} reaching the margin much nearer the wing apex than is usual.

Habitat: Unknown.

Distribution: Philippine Islands.

Note: The published descriptions of the two species in this genus are very sketchy and no mention is made of genitalia, tarsi or mouthparts. Like Ptenopsila, this genus must remain in the Caeciliidae with some reservation until further material is available.

Ptenopsila Enderlein (1 species)

Ptenopsila Enderlein, 1923. Zool. Anz. 55: 246.
Type species: Psocus delicatellus Blanchard.

Characters of the Caeciliidae. Claws without teeth. Media 3-branched. Rs forked. Rs and M fused for a long length in both fore and hind wings. Margin and veins glabrous. Pterostigma long and narrow, apex rounded. Tarsi 2-segmented.

Habitat: Not known.

Distribution: Chile, Cape Horn.

Note: Little information is available on this genus and there are very few known specimens. The venation is that of Caecilius but the large size of the wing, lack of setae and shape of pterostigma are unusual for the Caeciliidae. These features are more like those of the Psocidae as are the long antennae. It seems likely that Ptenopsila would be more appropriately placed near the Psocidae but without studies of the genitalia and mouthparts the problem cannot be resolved. This genus is left, therefore, in the Caeciliidae with reservation.

Teliapsocus Chapman (1 species)

Teliapsocus Chapman, 1930. J.N.Y. ent. Soc. 38: 334.
Type species: Psocus conterminus Walsh.

Lacinia broad, apex without teeth, truncate. Fore wings with venation of Caecilius; pterostigma with fairly prominent rounded hind margin; Rs and M fused for a length; stem of Rs sinuous; areola postica free; M 3-branched. Margin setose; setae in a single row on branches of veins; membrane setose strongly so in basal half of wings. Hind wings as in Caecilius, but with sparse marginal setae only between R_{2+3} and R_{4+5}. Veins glabrous. Claws without preapical tooth; points strongly curved; pulvillus broad. Paraprocts with large field of trichobothria and a large cone flanked by two very large setae on the hind margin in both sexes. No rugose areas on epiproct or paraproct. Subgenital plate with transverse hind margin rounded laterally, strongly setose, well sclerotized. Gonapophyses reduced to two valves. Ventral valve pointed with a membranous ventral flange; dorsal valve similar but with a strong, flat postero-dorsally directed process arising from near the base without a seta. Hypandrium simple, setose, with rounded hind margin. Phallosome with broad parameres and narrow aedeagal arch; penial bulb with sclerifications; frame of phallosome with small anterior break.

Habitat: On vegetation.

Distribution: North America.

Note: Teliapsocus has many Caeciliid features but also some Amphipsocid features and in the latter is clearly similar to Dasypsocus Enderlein. The presence of hairs on the wing membrane, the lack of a seta representing the remnants of the external valve of the female gonapophyses; the presence of a cone flanked by large setae and the lack of rugose areas on the epiproct and paraprocts are Dasypsocus-like rather than Caecilius-like features. Also, the strong basal extension to the dorsal valve of the gonapophyses is an exaggeration of a condition found in some Dasypsocus species. In Dasypsocus, however, the setae on the branches of the veins are in two rows, not one as in Teliapsocus and other Caeciliidae, and the marginal setae are stronger and more numerous in Dasypsocus than in Teliapsocus. In the hind wing Teliapsocus bears setae only on the margin between R_{2+3} and R_{4+5} and then only very sparse and short setae occur whereas in Dasypsocus the marginal setae occur all along the margin and are dense and strong.

Ypsiloneura Pearman (2 species)

Ypsiloneura Pearman, 1932. Stylops 1: 91.

Type species: Y. kirkpatricki Pearman.

Characters as in Caecilius but with M in fore wing 2-branched; Rs branched or not (fig. 4.398). Pterostigma with a small spur-vein. Legs long. Gonapophyses (fig. 4.399) of female reduced as in Caecilius but with valves a little broadened; no vestige of external valve, not even the usual remnant represented by a strong seta. One large seta among normally sized trichobothrial setae. No cone on paraproct. Phallosome (fig. 4.400).

Habitat: On undersides of green leaves.

Distribution: Angola, Kenya, Tanganyika.

Note: Ypsiloneura is very similar to Fulleborniella but has reduced branching of M and sometimes Rs. Features in common are the lack of any vestige of an external valve to the gonapophyses and one conspicuously stronger seta amongst those of the trichobothria; both genera have a pterostigmal spur vein.

Subfamily SCHIZOPECHINAE

Schizopechus Pearman (1 species)

Schizopechus Pearman, 1934. Stylops 3: 131.
Type species: S. marshalli Pearman.

Vertex hairy and normally curved. Ocelli absent. Lacinia as in Caecilius. Claws without prepaical tooth; pulvillus broad. Fore wings (fig. 4.401) broad. Pterostigma with rounded hind margin without spur vein, Rs and M meeting in a point; M 3-branched, the branches short and ending near wing apex; areola postica large, free, Cu_1 many-branched. Margin and veins long-setose; branches of veins with more than one row of setae; Cu_2 with a single row; pterostigma setose; some cilia on wing membrane apically between vein endings and near pterostigma. Hind wing with margin setose from R_1 to Cu. Paraproct with a double cone and adjacent seta on hind margin. Subgenital plate simple, setose; gonapophyses reduced to two valves, ventral and dorsal, but without setal remnant of external valve. Male not known.

Habitat: Unknown.

Distribution: Uganda, French Guinea, Congo.

Note: A perusal of the characters of this genus indicates clearly that it is closely related to Dasypsocus rather than Caecilius and would fall in the family Amphipsocidae. The setal characters of the wings on membrane and veins, and the lack of any vestige of an external valve of the gonapophyses are features found in Dasypsocus. Hairiness of vertex and the multiple branching of veins (in this case Cu_{1a}) are features commonly found in Amphipsocids. Schizopechus should, therefore be included in the Amphipsocidae and not in the Caeciliidae. The lack of a pterostigmal spur vein would place it in the subfamily Kolbeinae.

CHARACTERS OF THE STENOPSOCIDAE

Belonging to the Psocomorpha. Tarsi 2-segmented. Claws without preapical tooth; pulvillus broad. Labium with palps protruding triangular. Pterostigma with vein arising from posterior margin usually to Rs, Rs and M fused for a length, M 3-branched; areola postica joined to M by a cross-vein. Fore wings with veins (except Cu_2) setose, with one row of setae, marginal setae not crossing each other. Hypandrium simple. Phallosome closed anteriorly, with rugose sclerification of penial bulb. Subgenital plate simple. Gonapophyses reduced to slender, pointed ventral and dorsal valves with external valve reduced to a small sclerified area bearing a seta. Eggs laid in groups, not encrusted but covered with silken strands.

Note: This definition excludes some genera e.g. Taeniostigma, Matsumuraiella.

GENERA INCLUDED IN THE STENOPSOCIDAE

Stenopsocus Hagen, 1866
Graphopsocus Kolbe, 1880
Kodamaius Okamoto, 1907
Matsumuraiella Enderlein, 1906
Taeniostigma Enderlein, 1901
Epikodamaius Kuwayama, 1961

Stenopsocus Hagen (20 species)

Stenopsocus Hagen, 1866. Verh. zool. -bot. Ges. Wien 16: 203.
Type species: Psocus immaculatus Stephens.

Fore wing (fig. 4.402) with pterostigma elongate, not strongly angled behind. Crossvein from Cu_{1a} to M long.

Little colour pattern. Veins and margin clearly pubescent. Hind wing with setae on margin only between R_{2+3} and R_{4+5}. Gonapophyses (figs. 4.403, 4.404) with ventral valves with well developed membranous areas. External valve reduced to a small sclerite at base of dorsal valves.

Habitat: On leaves.

Distribution: India, Malaya, Ceylon, Java, Tonkin, Philippines, China, Formosa, Japan, Europe, South Australia.

Graphopsocus Kolbe (5 species)

Graphopsocus Kolbe, 1880. Jber. westf. ProvVer. Wiss. Kunst 8: 124.

Type species: Hemerobius cruciatus Linnaeus.

Brachyptery known in females of some species. Fore wings (fig. 4.405) strongly patterned. Pterostigma strongly angled behind. Areola postica very high, the crossvein between Cu_{1a} and M very short. Veins with feeble pilosity. Margin entirely glabrous behind with only a few fine hairs otherwise on margin.Gonapophyses strongly atrophied (fig. 4.406).

Habitat: On foliage.

Distribution: Angola, Morocco, Canary Islands, Europe, Ceylon, Java, Philippines, China, Singapore, Japan, Mexico, Brazil, North America, Europe.

Matsumuraiella Enderlein (2 species)

Matsumuraiella Enderlein, 1906. Zool. Jb. Abt. Syst. 23: 248.

Type species: M. radiopicta Enderlein.

Head and antennae long and densely pubescent. Lacinia with simple apex. Tarsi 2-segmented. Claws without preapical tooth. Fore wing (fig. 4.407) with pterostigma well rounded behind. Rs and M fused for a length. Rs strongly sinuous before branching. M strongly sinuous after separating from Rs and before branching. M 3-branched. Areola postica very tall, sometimes Cu_{1a} fused with M, sometimes areola postica free. Veins and margin strongly setose, setae in single row on branches of veins. Cu_2 setose. Hind margin between base of wing and nodulus glabrous. Scattered setae on membrane in basal half of wing. Hind wing (fig. 4.408) with basal Sc thickened. Glabrous except for margin between R_{2+3} and R_{4+5}. Hypandrium simple. Phallosome of Caecilius type (fig. 4.409). Subgenital plate simple. Gonapophyses (fig. 4.410) reduced but three valves present. Ventral valve elongate with rounded apex. Dorsal valve elongate, somewhat membranous with rounded apex. External valve long, irregularly elongate, glabrous. Eggs laid in groups, bare, with silken covering.

Habitat: On bamboo leaves.

Distribution: Japan, Formosa.

(Note: The position of this genus needs investigating).

Taeniostigma Enderlein (6 species)

Taeniostigma Enderlein, 1901. Zool. Jb. Abt. Syst. 14: 546.
Type species: Psocus elongatus Hagen.

Fore wing (fig. 4.411) long, with rounded apex. Pterostigma very long, flat and with smoothly curving hind margin. Rs and M fused for a length. Rs with long stem before forking. M 3-branched. Areola postica tall, Cu_{1a} fused with M for a length. Margin and veins setose, in some species strongly so, with more than one row of setae on distal veins. Cu_2 with one row. Margin glabrous between base and nodulus. Hind wing with short basal Sc. Margin setose from R_1. Veins in distal part of wing with few setae. Gonapophyses (fig. 4.412) very lightly sclerotized, reduced to a pointed ventral valve and a pointed dorsal valve.

Habitat: On leaves.

Distribution: Ceylon, Malaya, Sula, Java, Bismarck Archipelago, Philippines, Tonkin, China, Formosa, Japan, Australia.

Note: The position of this genus needs investigation.

Kodamaius Okamoto (5 species)

Kodamaius Okamoto, 1907. Trans. Sapporo nat. Hist. Soc. 2: 138.
Type species: K. brevicornis Okamoto.

Fore wing (fig. 4.413) with Rs and M joined by a crossvein. Cu_{1a} joined to M by a crossvein. Spurvein from apex of pterostigma. Veins with more than one row of setae except in apical quarter of wing. Cu_2 setose, with one row of setae. A few setae on membrane in cell Cu_2. Hind wing (fig. 4.414) glabrous except for the margin beyond R_1 and a few setae on R_1. Claws (fig. 4.415) without preapical tooth. Pulvillus broad. Phallosome (fig. 4.416) as in Caecilius with sclerification of penial bulb. Gonapophyses (fig. 4.417) as in Caecilius, with setal remnant of external valve. Lacinia (fig. 4.418) as in Caecilius.

Habitat: Not recorded.

Distribution: Angola, Congo, French Guinea, Japan, Formosa.

Epikodamaius Kuwayama (1 species)

Epikodamaius Kuwayama, 1961. Nature and Life in S.E. Asia 1: 203.

Type species: E. ikomai Kuwayama.

Characters of Kodamaius but with M_1 divided near wing margin (fig. 4.419).

Habitat: Not recorded.

Distribution: Thailand.

(Note: This is probably a venational aberration).

CHARACTERS OF THE AMPHIPSOCIDAE

Belonging to the Psocomorpha. Tarsi 2-segmented. Claws without a preapical tooth. Pulvillus broad. Labium with palps protruding, triangular. Wings broad, costal margin thickened and densely hairy between base of pterostigma and wing apex. Pterostigma frequently with posterior spur-vein. Rs and M fused for a length; branches of Rs and M sometimes increased beyond the usual two and three respectively. Veins with more than one row of setae. Cu_2 setose. Areola postica large. Hind wing sometimes with setae on membrane in distal part of wing, veins setose, with more than one row of hairs; Cu_2 setose. Hypandrium simple. Phallosome with variously rugose sclerifications of penial bulb. Subgenital plate simple with slight posterior emargination. Gonapophyses reduced to slender pointed dorsal and ventral valves; external valve remnant seen only as a slight basal extension of the sclerotization of the dorsal valve, seta absent. Eggs laid in groups, not covered with an encrustation but with silken strands.

GENERA INCLUDED IN THE AMPHIPSOCIDAE

Amphipsocinae:

Amphipsocus McLachlan, 1872
Xenopsocus Kolbe, 1885
Harpezoneura Enderlein, 1909
Pentathyrsus Enderlein, 1912
Amphipsocopsis Smithers, 1964.

Kolbeinae:

Kolbea Bertkau, 1883
Dasypsocus Enderlein, 1906

Subfamily AMPHIPSOCINAE

Amphipsocus McLachlan (42 species)

Amphipsocus McLachlan, 1872. Ent. mon. Mag. 9: 77.
Type species: A. pilosus McLachlan

Head and wings strongly pubescent. Lacinia (fig. 4.420) narrowing towards apex, with barely indication of apical division. Fore wing (fig. 4.421) with pterostigma with strong posterior angle and with a spur vein arising from it. Costa thickened in region of pterostigma and anterior margin. Rs and M fused for a short length or meeting in a point. Rs branches long. M 3-branched. Areola postica tall, Cu_{1a} curved. Veins and margin strongly pubescent. Veins with more than one row of setae, except Cu_2 with one row. Hind wing (fig. 4.422) with margin setose. Rs and M fused for a length. Veins in distal half of wing with more than one row of setae. Gonapophyses (fig. 4.423) reduced to ventral and dorsal valves, without any remnant of external valve. Phallosome (fig. 4.424) in general similar to that of Caeciliidae.

Habitat: On green leaves.

Distribution: Congo, Cameroons, East Africa, Angola, Madagascar, India, Java, China, Japan, Formosa, Philippines.

Xenopsocus Kolbe (1 species)

Xenopsocus Kolbe, 1885. Berl. ent. Z. 29: 187.
Type species: X. hageni Kolbe.

Characters as for Amphipsocus but in hind wing Rs is more than 2-branched and in the fore wing (fig. 4.425) R_{2+3} is divided and M is 4-branched.

Habitat: Not recorded.

Distribution: Madagascar

Harpezoneura Enderlein (12 species)

Characters as for Amphipsocus but setae tending to form dense tufts on some of the main veins. Hind wing with Rs more than 2-branched. In fore wing R_{2+3} divides more than once, M more than 4-branched (fig. 4.426). Membrane sometimes with setae in basal part of wing. Head normal, pterostigma spur-vein only exceptionally reaching Rs. Phallosome (fig. 4.427).

Habitat: On leaves.

Distribution: Congo, Angola, Madagascar, French Guinea, East Africa, Sierra Leone.

Pentathyrsus Enderlein (1 species)

Pentathyrsus Enderlein, 1912. Zool. Anz. 39: 300.
Type species: P. vespertilio Enderlein.

Characters of Amphipsocus but with tendency to form tufts of setae on main veins. Fore wing (fig. 4.428) with R_{2+3} dividing more than once. M more than 4-branched. Vertex (fig. 4.429) with dorsal dilations bearing extremely long, fine setae. Thoracic lobes also bearing similar setae. Pterostigma spurvein reaching Rs. Hind wing (fig. 4.430) with Rs more than 2-branched. Gonapophyses (fig. 4.431) as in Amphipsocus but with dorsal valve stouter and shorter.

Habitat: Not recorded.

Distribution: Madagascar

Amphipsocopsis Smithers (1 species)

Amphipsocopsis Smithers, 1964. Rev. Zool. Bot. afr. 70: 225.
Type species: A. surculosus Smithers.

Characters of Amphipsocus but in fore wing (fig. 4.432) M more than 3-branched. Lacinia (fig. 4.433) with a long, pointed, apical tooth.

Habitat: Not recorded.

Distribution: Madagascar.

Subfamily KOLBEINAE

* Kolbea Bertkau (11 species)

Kolbia Bertkau 1883. Verh. Ver. Rhein. 39: 129.
Type species: Kolbia quisquiliarum Bertkau.

Kolbea Enderlein 1901. Zool. Jb. Abt. Syst. 14: 538.
Type species: Kolbia quisquiliarum Bertkau (name emended).

With the characters of the family but without a pterostigma spur vein. Males winged, females sometimes apterous. Fore wing (fig. 4.435). Costal margin of wing thickened in distal region. Veins and margin strongly setose. Veins with more than one row of setae, except for Cu_2, which has one row. Rs before forking long and almost straight. No setae on membrane. Lacinia (fig. 4.434) narrowing, with little evidence of division at apex. Phallosome (fig. 4.436) similar to that of Caeciliidae. Gonapophyses similar to Dasypsocus.

Habitat: In leaf litter, under lichens.

Distribution: Philippines, India, Formosa, China, Japan, Madagascar, Sarawak, Brazil, Europe, East Prussia (in amber).

Dasypsocus Enderlein (7 species)

Dasypsocus Enderlein, 1906. Zool. Jb. Abt. Syst. 23: 250.
Type species: Kolbea solox Enderlein.

Characters of Kolbea but with pilosity more dense on body and wings. Fore wings (fig. 4.437) with some setae on membrane. Hind wing (fig. 4.438) with more than one row of setae on veins in distal part of wing and a single row on Cu_2. Lacinia (fig. 4.439). Gonapophyses as in Amphipsocus (fig. 4.440). Phallosome (fig. 4.441).

Habitat: In an ant's nest, leaf litter, in vegetation.

Distribution: Angola, Congo, Japan, Singapore.

CHARACTERS OF THE POLYPSOCIDAE

Belonging to the Psocomorpha. Tarsi 2-segmented. Claws without a preapical tooth. Pulvillus broad. Labium with palps protruding, triangular. Pterostigma without spur vein, long. Rs and M joined by a cross-vein. M 2-branched or not branched. Stem of Rs very short before bifurcation, the branches sinuous and long; M long before bifurcation. Areola postica long and low; Cu_{1b} very short, Cu_{1a} long. Veins with more than one row of setae; Cu_2 setose. Setae on the membrane in a band along the edge of the wing. Hind wing with Rs and M fused for a length. M not branched. Veins setose, with more than one row of setae. Setae on membrane in a band along edge of wing. Hypandrium simple. Phallosome with some rugose sclerification of penial bulb. Subgenital plate simple. Gonapophyses with dorsal and ventral valves reduced to slender pointed valves; external valve reduced to a small sclerotized area at base of dorsal valve, without seta.

Eggs not known.

GENERA INCLUDED IN THE POLYPSOCIDAE

Polypsocus Hagen, 1866

Monocladellus Enderlein, 1909

Polypsocus Hagen (17 species)

Polypsocus Hagen, 1866. Verh. zool. -bot. Ges. Wien 16: 203.

Type species: Psocus corruptus Hagen.

Males fully winged, females often with short, elytriform wings in which venation is indistinct. Head and body thickly clothed with short setae. Veins and margin of fore wing (fig. 4.442) setose. The margin bears several rows of setae. Veins, with the exception of Cu_2, with more than one row of setae. Rs and M joined by a crossvein. Rs stem very short, dividing near separation from M. M sinuous and long basad of division. M 2-branched. Areola postica very long, low. Membrane setose in a marginal zone. Hind wing (fig. 4.443) marginally setose from R_1. Veins in distal part of wing with more than one row, except glabrous IA. In some cases, main veins also setose. Membrane setose in distal parts of wing. Rs and M fused for a short length. M simple. Subgenital plate simple. Gonapophyses (fig. 4.444) reduced to ventral and dorsal valves, poorly chitinized.

Habitat: Not recorded.

Distribution: Chile, Brazil, Peru, Bolivia, Ecuador, Argentina, Cuba, Porto Rica, North America.

Monocladellus Enderlein (1 species)

Monocladellus Enderlein, 1909. Stettin. ent. Ztg. 70: 266.
Type species: M. chausianus Enderlein.

Characters as in Polypsocus but M in fore wing simple (fig. 4.445).

Habitat: Not recorded.

Distribution: Ecuador

CHARACTERS OF THE GROUP HOMILOPSOCIDEA

(Note: This group was erected by Pearman (1936) provisionally to hold those families which could not easily be associated with families in his other family groups. The result is a heterogeneous assemblage of families within the Psocomorpha).

The ocelli are grouped on a tubercle. The wing venation is similar to *Caecilius* or can be derived easily by simple modification from it. Tarsi 2- or 3-segmented. Egg laying habits vary considerably.

Owing to the varied nature of the insects included in this group of families and as it is an artificial assemblage of forms for which a place could not be found in Pearman's system, definition at a level above family is impossible.

CHARACTERS OF THE LACHESILLIDAE

Belonging to the Psocomorpha. Tarsi 2-segmented. Claws with a preapical tooth; pulvillus narrow. Venation of the *Caecilius* type. Fore and hind wings glabrous. Male genitalia of characteristic form. Female subgenital plate simple. Gonapophyses reduced to setose external valves in most species. Eighth sternite of male often with complex sclerifications. Eggs ridged, without encrustation, deposited singly, without silken threads.

GENERA INCLUDED IN THE LACHESILLIDAE

Lachesilla Westwood, 1840

Eolachesilla Badonnel, 1967

Lachesilla Westwood (62 species)

Lachesilla Westwood, 1840. *Syn. gen. Brit. Ins.* p. 47.
Type species: *Termes fatidicum* Linnaeus.

Lacinia (fig. 4.446) with almost parallel sides, with divided apex. Claws with preapical tooth; pulvillus narrow. Fore and hind wings glabrous. Fore wing (fig. 4.447) with Rs and M fused for a length. M 3-branched. Epiproct and ninth tergite of male with or without processes of various shapes and sizes (figs. 4.448, 4.449). Paraprocts of male with or without processes of various shapes and sizes. Hypandrium (fig. 4.450) frequently with strong processes. Phallosome usually in the form of a Y-shaped sclerite. Subgenital plate (fig. 4.451) simple or emarginate. Gonapophyses (fig. 4.452) reduced to the external valve; eighth sternite (fig. 4.453) with or without sclerification around entrance to spermatheca. Eggs laid singly, without encrustation and without silk. Polymorphism known in some species.

Habitat: Dried leaves, leaf litter, bark, in stored products, in buildings.

Distribution: Widespread.

Eolachesilla Badonnel (1 species)

Eolachesilla Badonnel, 1967. *Biol. l'Amer. austr.* 3: 583.
Type species: *E. chilensis* Badonnel.

Pilosity of head fairly long, not very dense, similar on thorax but less dense. Lacinia (fig. 4.454). Fore wings (fig. 4.455) with margin and veins setose. Veins with a single row of setae except for glabrous Cu_2. Hind wing (fig. 4.456) glabrous. Tarsi 3-segmented. Claws (fig. 4.457) with a small preapical tooth. Pulvillus fairly broad, expanded apically. Gonapophyses complete (fig. 4.458). Ventral valve broad, pointed, membranous. Dorsal valve conical, membranous with only a transverse basal sclerite. External valve narrow, elongate rounded at end, setose. Spermatheca with sclerification at opening. Males unknown.

Habitat: Leaf litter.

Distribution: Chile

Note: This genus was described and placed in the Lachesillidae long after the family Lachesillidae was defined and it does not fall within the family so defined.

CHARACTERS OF THE PERIPSOCIDAE

Belonging to the Psocomorpha. Fore wing without areola postica. Tarsi 2-segmented. Gonapophyses complete or reduced. Hypandrium simple. Phallosome with complex sclerifications of penial bulb. Eggs (a) rough, encrusted with debris, apex clearly pointed, laid singly, or, (b) eggs smooth, not encrusted with debris, ovoid, laid in groups, covered with silken threads.

GENERA INCLUDED IN PERIPSOCIDAE

Peripsocus Hagen, 1866
Ectopsocus McLachlan, 1899
Notiopsocus Banks, 1913
Kaestneriella Roesler, 1943
Interpsocus Edwards, 1950
Ectopsocopsis Badonnel, 1951
Anomopsocus Roesler, 1940

Subfamily PERIPSOCINAE

Peripsocus Hagen (61 species)

Peripsocus Hagen, 1866. *Verh. zool. -bot. Ges. Wien* 16: 203
Type species: *Psocus phaeopterus* Stephens.

Lacinia narrowing towards apex with end divided. Claws with preapical tooth, filamentous pulvillus. Fore wing (fig. 4.460) with R_1 curved to give normal pterostigma shape. Rs and M fused for a length. M 3-branched. Veins and wing margin glabrous. Hind wing with Rs and M fused for a length. Veins and wing margin glabrous. Ninth abdominal tergite (fig. 4.461) of male usually with a caudal "comb" or other structure on its posterior border. Epiproct simple. Phallosome (figs. 4.462, 4.463) with external parameres fused anteriorly into a more or less broad plate and reunited posteriorly in a point.

Penial bulb with complex sclerifications in form of strongly chitinized, variously shaped rods and irregular structures, usually arranged symmetrically. Internal parameres separated posteriorly. Subgenital plate (fig. 4.465) with strong median posterior lobe. Gonapophyses (fig. 4.464) complete; ventral valves rather thick, bluntly pointed at apex. Dorsal valves dilated basally and unusual in bearing a tuft of terminal setae. External valves somewhat reduced, setose. Eggs laid singly, rough, apex somewhat pointed, covered with an encrustation of debris.

Habitat: Usually found on bark of trunks, branches and twigs of trees and shrubs.

Distribution: Worldwide.

Kaestneriella Roesler (1 species)

Kaestneriella Roesler, 1943. Stettin. ent. Ztg. 104: 10.
Type species: K. pilosa Roesler.

Lacinia undescribed. Claws with preapical tooth; condition of pulvillus not described. Fore wing (fig. 4.466) with pterostigma of normal shape. Rs and M fused for a length. M 3-branched. Veins with more than one row of setae on branches, except for Cu_2 which has one row. Margin only setose in basal half of wing. A few setae on pterostigma and a few scattered on wing membrane. Hind wing with Rs and M fused for a length. Hind wing glabrous. Ninth abdominal tergite of male not described. Epiproct not described. Phallosome (fig. 4.467) with external parameres fused anteriorly into a very broad plate and reunited posteriorly in a point. Penial bulb with sclerotizations in form of strongly chitinized rods, symmetrically arranged. Internal parameres separate posteriorly. Female unknown.

Habitat: Not known.

Distribution: Costa Rica.

Notiopsocus Banks (3 species)

Notiopsocus Banks, 1913. Psyche Camb., Mass 20: 84.
Type species: N. simplex Banks

Lacinia (fig. 4.468) hollowed apically into a cup and with a strong preapical asymmetrical dilatation. Claws without preapical tooth; pulvillus very fine. Fore wing (fig. 4.469) with pterostigma of usual form. Rs and M fused for a length. M 2-branched, M being exceptionally long before branching. Margin and veins, except Cu_2 setose. Hind wing with Rs and M fused for a length. Veins glabrous, margin setose between R_{2+3} and R_{4+5}. Male unknown. Epiproct undescribed. Subgenital plate simple, without apophyses. Gonapophyses (fig. 4.470) partly reduced; ventral valves short, poorly sclerotized lobes; dorsal valves poorly sclerotized lobes with a strengthening chitinized band along dorsal edge; external valves reduced to a sclerotized lobe bearing a single terminal seta.

Habitat: Under lichen, with silk.

Distribution: Angola, Brazil.

Subfamily ECTOPSOCINAE

Interpsocus Edwards (1 species)

Interpsocus Edwards, 1950. Pap. roy. Soc. Tasm. 1949: 126.
Type species: I. brunneus Edwards.

Lacinia (fig. 4.471) narrowing towards apex with end divided. Claws without preapical tooth; pulvillus dilated. Fore wing (fig. 4.472) with pterostigma more or less rectangular. Rs and M meeting in a point. M 3-branched. Veins (except Cu_2) and margin setose. Hind wing with Rs and M fused for a length. Hind wing with setae on margin between R_{2+3} and R_{4+5}. Ninth tergite of male simple. Epiproct triangular, without "comb". Phallosome (fig. 4.473) with external parameres free posteriorly; united anteriorly into a rounded plate. Penial bulb with heavy, irregular sclerotizations. Subgenital plate (fig. 4.474) bilobed. Gonapophyses (fig. 4.475) complete; ventral valves broad at base tapering to apex; dorsal valves dilated, without setae; external valves dilated, setose. Eggs laid in groups, covered with an encrustation of debris, with silken threads.

Habitat: Dry leaves.

Distribution: Tasmania.

Ectopsocus McLachlan (45 species)

Ectopsocus McLachlan, 1899. Ent. mon. Mag. 35: 277.
Type species: E. briggsi McLachlan.

Lacinia (fig. 4.476) narrowing towards apex with end divided. Claws without preapical tooth, pulvillus dilated. Fore wing (fig. 4.477) with rectangular pterostigma. Rs and M meeting in a point or fused for a very short length. M 3-branched. Veins and margin setose, although setae sometimes very small. Hind wing with Rs and M connected by a cross vein. Hind wing with marginal setae between R_{2+3} and R_{4+5}, sometimes setae small and sparse. Ninth tergite (fig. 4.478) of male with strong transverse "comb" of spurs. Epiproct often with row of spurs similar to those of ninth tergite across its hind margin. Phallosome (fig. 4.479) with parameres chitinized only in posterior parts; internal parameres fused posteriorly; external parameres free posteriorly. Penial bulb with complex irregular sclerotizations, often asymmetrical in arrangement. Subgenital plate (fig. 4.480) bilobed with strong setae at the apex of each lobe. Gonapophyses (fig. 4.481) complete; ventral valves pointed; dorsal valves often triangular, poorly chitinized, broad, without setae; external valves well chitinized, elongated with subparallel sides and apically setose. Eggs laid in groups, without an encrustation of debris, covered with silken threads.

Habitat: Usually in dry leaves, leaf litter and similar situations.

Distribution: Worldwide.

Ectopsocopsis Badonnel (9 species)

Ectopsocopsis Badonnel, 1955. Pub. cult. Cia. Diamant Angola 26: 185.

Type species: Ectopsocus balli Badonnel.

Lacinia narrowing towards apex with end divided. Claws without preapical tooth; pulvillus dilated. Fore wing with rectangular pterostigma. Rs and M meeting in a point or fused for a very short length. M 3-branched. Veins, except Cu_1 and margin setose, although setae sometimes very small. Hind wing with Rs and M connected by a cross vein. Hind wing with marginal setae between R_{2+3} and R_{4+5}, sometimes setae very small and sparse. Ninth tergite of male (fig. 4.482) with more or less complex chitinized structures consisting of a variety of forms of apophyses and tubercles and which may include a "comb". Epiproct without comb. Phallosome (fig. 4.483) with external and internal parameres sclerotized only in posterior parts; internal parameres fused; external parameres free posteriorly. Penial bulb with complex, irregular sclerifications, often asymmetrical in arrangement. Subgenital plate (fig. 4.484) with reduced posterior lobes or with a median posterior lobe. Gonapophyses (fig. 4.485) reduced to rudiments of external valve which is setose. Spermathecal opening (fig. 4.485) with sclerification. Eggs laid in groups, without encrustation of debris, covered with silken threads.

Habitat: Usually dried leaves, leaf litter and similar situations.

Distribution. Africa (except for one widespread species not so far found in Africa).

Anomopsocus Roesler (1 species)

Anomopsocus Roesler, 1940. Arb. morph. taxon. Ent. 7: 239.
Type species: Psocus amabilis Walsh.

Fore wing with basal Sc absent. Venation as in Caecilius but with an areola postica fused to M. Veins in basal third of wing with setae, otherwise glabrous. Margin glabrous. Pterostigma with prominent hind angle, rounded. M 3-branched. Hypandrium short, shield like, a pair of inconspicuous short teeth on distal margin. Phallosome closed anteriorly by a plate, parameres fused into a short beak posteriorly as in Kaestneriella. Penial bulb with sclerification in form of a broad Y. Subgenital plate simple. Gonapophyses reduced to elongate, setose, external valves.

Habitat: In dry leaves.

Distribution: North America.

CHARACTERS OF THE HEMIPSOCIDAE

Belonging to the Psocomorpha. Lacinia (fig. 4.486) with unevenly divided apex. Tarsi 2-segmented. Claws with preapical tooth; pulvillus broad. Fore wing (fig. 4.487) with M 2-branched; areola postica connected to M by a cross-vein. Pterostigma somewhat flattened; Rs and M meeting in a point. Veins (except Cu_2) with one row of setae; margin setose. Hind wing glabrous.

Epiproct (fig. 4.488) of male with various rugose areas and processes and marginal setae. Paraproct (fig. 4.489) of male with strong processes. Hypandrium simple. Phallosome (figs. 4.490, 4.491) pointed anteriorly with internal parameres reduced; external parameres thin, frame of phallosome thin; penial bulb with rugose sclerifications.

Subgenital plate (fig. 4.492) emarginate. Gonapophyses complete; ventral valve broad, pointed; dorsal valve broad, pointed; external valve large, triangular with very few setae. Eggs smooth, encrusted.

GENERA INCLUDED IN THE HEMIPSOCIDAE

Hemipsocus Selys-Longchamps, 1872
Anopistoscena Enderlein, 1912

Hemipsocus Selys-Longchamps (9 species)

Hemipsocus Selys-Longchamps, 1872. *Ent. mon. Mag.* 9: 146.
Type species: *Psocus chloroticus* Hagen.

Characters as for the family.

Habitat: Dry leaves, leaf litter.

Distribution: East Africa, Congo, Angola, Seychelles, Madagascar, India, Ceylon, Thailand, Japan, Formosa, Philippines

Singapore, New Guinea, Sumatra, Java, Sarawak, Queensland, Samoa, Guam, Hawaii, Florida, West Indies, Central America.

Anopistoscena Enderlein (1 species)

Anopistoscena Enderlein, 1912. Zool. Anz. 39: 298.
Type species: A. specularifrons Enderlein.

Claws with preapical tooth. Fore wing (fig. 4.493) as in Hemipsocus but with the distal section of Cu_{1a} missing so that the areola postica is fused with cell M_3. Fore wing with Rs and M fused for a length. M 2-branched. Veins (except Cu_2) with a single row of setae. Hind wing with Rs and M fused for a length. Veins and margin glabrous.

Habitat: Not recorded.

Distribution: Seychelles.

CHARACTERS OF THE CALOPSOCIDAE

Belonging to the Psocomorpha. Lacinia with apex divided, one division being broader than the other. Claws with small preapical tooth; pulvillus broad. Head with very sharp vertex, with strong median emargination. Fore wings broad. Costal margin thickened in area of pterostigma. Rs and M joined by a cross-vein. Areola postica joined to media by a cross-vein. Cu_{1a} and Cu_{1b} separating well basad of junction of Cu_{1b} and wing margin to give an elongate areola postica. Branches of R connected by a network of accessory veins. Veins and wing margin with more than one row of setae except Cu_2 which has a single row. Setae on margin crossing each other between wing apex and last branch of M. Wing membrane setose. Hind wing broad. M 2-branched. Veins in distal half with more than one row of setae. Marginal setae between R_{4+5} and Cu_2 crossing each other. Membrane setose in distal half. Ninth tergite of male with rugose areas and transverse comb; epiproct with few marginal setae. Hypandrium simple. Phallosome with anterior border interrupted; penial bulb with strong sclerifications. Subgenital plate simple. Gonapophyses complete; ventral valve pointed with spicules and strong preapical lobe; dorsal valve long and triangular with rounded apex and strong preapical process with spicules; external valve very large, almost circular, setose, with strong marginal setae some of which are curved.

GENERA INCLUDED IN THE CALOPSOCIDAE

Calopsocus Hagen, 1866

Neurosema McLachlan, 1866

Dirla Navas, 1924

Similar to Calopsocus but with wings elongate and venational reticulation (fig. 4.503) restricted to area immediately behind pterostigma. Cu_1 dividing well away from wing margin to give a narrow fork. Hind wing (fig. 4.504) similar to Calopsocus.

Habitat: Not recorded.

Distribution: Java.

CHARACTERS OF THE PSEUDOCAECILIIDAE

Belonging to the Psocomorpha. Claws with or without preapical tooth, pulvillus broad. Venation usually of the Caecilius type. Fore wing with pterostigma long and somewhat flattened; areola postica somewhat flattened; branches of veins with more than one row of setae; Cu_2 glabrous; marginal setae strong, crossing each other in region posterior to wing apex. Hind wing with at least some setae on branches of Rs and on M; margin setose, setae crossing. Tarsi 2-segmented. Hypandrium well sclerotized with apophyses, papillae and other structures of varying complexity. Phallosome well sclerotized with or without sclerification of penial bulb. Subgenital plate simple or with bilobed apex, lobes carrying a few apical setae. Gonapophyses complete, ventral valve pointed, lobed; dorsal valve pointed, apically spiculate with strong preapical lobe; external valve variable with strong setae. Eggs smooth, with encrustation of debris.

GENERA INCLUDED IN THE PSEUDOCAECILIIDAE

Pseudocaecilius Enderlein, 1903.
Cladioneura Enderlein, 1906.
Ophiodopelma Enderlein, 1908.
Mesocaecilius Okamoto, 1910.
Scottiella Enderlein, 1931.
Scytopsocus Roesler, 1940.
Pseudoscottiella Badonnel, 1946.
Allocaecilius Lee and Thornton, 1967.
Heterocaecilius Lee and Thornton, 1967.
Lobocaecilius Lee and Thornton, 1967.
Phallocaecilius Lee and Thornton, 1967.
Scytopsocopsis Lee and Thornton, 1967.
Trichocaecilius Badonnel, 1967.
Electropsocus Roesler, 1940.

Subfamily PSEUDOCAECILIINAE

Pseudocaecilius Enderlein (36 species)

Pseudocaecilius Enderlein, 1903. Ann. hist. -nat. Mus. hung. 1: 260.

Type species: Pseudocaecilius elutus Enderlein.

Venation as in Caecilius (fig. 4.505). Stem of Rs long. Rs and M relationship variable. Areola postica elongate, low. Veins with setae in more than one row. Hind wing setose all along margin. Gonapophyses (fig. 4.506) complete. Ventral and dorsal valves with fringe of barbules, without lobes. External valve narrowing apically. Subgenital plate (fig. 4.507) bilobed, each lobe with a single apical seta. Phallosome (fig. 4.508) with penial bulb without sclerification. Hypandrium (fig. 4.509) with an apical pair of sclerites. Ninth tergite of male with median sclerification. Claw without preapical tooth. Eggs smooth, encrusted with debris.

Habitat: Green foliage.

Distribution: Angola, Congo, Mozambique, South Africa, Madagascar, India, Malaya, Hong Kong, Java, Palau Is., Mariane Islands, Hawaii, North America, Porto Rica, Tahiti, Ceylon, New Guinea, Australia, New Zealand, Philippines, Formosa, East Africa, Japan, Guam, Tahiti, Fiji.

Cladioneura Enderlein (1 species)

Cladioneura Enderlein, 1906. Zool. Jb. Abt. Syst. 23: 404.

Type species: C. pulchripennis Enderlein.

Lacinia (fig. 4.510) with divided apex. One claw of each pair with and one without preapical tooth, pulvillus broad. Fore wing with pterostigma fairly flattened (fig. 4.511). Costa thickened from base of pterostigma to wing apex. Rs and M fused for a length. M 3-branched. Fore wing veins (except Cu_2) with more than one row of setae; margin setose, hairs crossing each other posterior to wing apex. No setae on wing membrane. Hind wing (fig. 4.512) with setae on branches of Rs and on M; margin setose; setae crossing each other posterior to apex. Ninth tergite with rugose hind margin. Paraproct (fig. 4.513) with rugose raised area. Epiproct without particular features. Hypandrium (fig. 4.514) with strongly chitinized protuberances behind. Phallosome (fig. 4.515) with anterior border interrupted; external parameres broad and elongated; internal parameres forming a long arch; penial bulb with strong sclerifications. Subgenital plate (fig. 4.516) with bilobed plate on posterior margin bearing four setae. Gonapophyses (fig. 4.517) complete; ventral valve broad basally, pointed apically, lobed, with spicules near apex; dorsal valve pointed with spicules and a strong preapical lobe; external valve rounded, setose.

Habitat: On branches.

Distribution: Australia.

Ophiodopelma Enderlein (6 species)

Ophiodopelma Enderlein, 1908. Zool. Anz. 33: 767.
Type species: O. ornatipenne Enderlein.

Fore wings (fig. 4.518) with Caecilius venation. Areola postica tall. Rs and M fused for a length, Rs sinuous. In hind wing R_{2+3} meets wing margin and Rs and R_{4+5} at right angles. Gonopophyses (fig. 4.519) with dorsal and ventral valves lobate. External valve fusiform. Subgenital plate (fig. 4.520) bilobed, each lobe with a seta near base and one at base of mesial region. Phallosome (fig. 4.521) angular anteriorly, with rod-like sclerotizations of penial bulb. Hypandrium (fig. 4.522) without accessory sclerites or projections. Ninth tergite of male with papillate area. Claws without preapical tooth. Ocelli sometimes absent.

Habitat: Foliage, thatch.

Distribution: Ceylon, Philippines, Formosa, New Guinea.

Mesocaecilius Okamoto (1 species)

Mesocaecilius Okamoto, 1910. Ann. hist. -nat. Mus. hung. 8: 197.
Type species: M. quadrimaculata Okamoto.

Lacinia undescribed. Claw with small preapical tooth; pulvillus undescribed. Eyes hairy. Fore wing (fig. 4.523) with pterostigma fairly flat but with areola postica tall. Rs and M fused for a length. M 3-branched. Veins (except Cu_2) with more than one row of setae; margin setose, hairs crossing each other posterior to apex of wing. No setae on wing membrane. Hind wing (fig. 4.524) with setae on branches of Rs and M; with marginal setae. Ninth tergite, epiproct and paraproct undescribed. Hypandrium and phallosome undescribed. Subgenital plate (fig. 4.525) bilobed on posterior margin, each lobe with a strong seta. Gonapophyses (fig. 4.526) complete. Ventral valve pointed with spicules near apex, lobate. Dorsal valve pointed, with spicules and a very broad lobe. External valve ovoid, setose.

Habitat: Not recorded.

Distribution: Formosa.

Scottiella Enderlein (3 species)

Scottiella Enderlein, 1931. Trans. Linn. Soc. Lond. (2) Zool. 19: 216.

Type species: S. micans Enderlein.

Lacinia undescribed. Claws without preapical tooth. Fore wing (fig. 4.527) with pterostigma somewhat flattened with sharp apical angle; areola postica flattened but not particularly elongated. Rs and M fused for a length. M 2-branched. Veins (except Cu_2) with more than one row of setae; margin setose, hairs crossing each other posterior to wing apex. No setae on wing membrane. Hind wing (fig. 4.528) with veins glabrous; margin setose, hairs crossing each other posterior to apex. Genitalia undescribed. Eggs undescribed.

Habitat: Not mentioned.

Distribution: Seychelles.

Scytopsocus Roesler (2 species)

Scytopsocus Roesler, 1940. Zool. Anz. 130: 11.

Type species: S. coriaceus Roesler.

Fore wing (fig. 4.529) of male with venation as in Pseudocaecilius but with R very thick and Rs and M joined by a crossvein. Rs very short before bifurcation, setae inserted alongside veins and scattered setae on membrane. Female somewhat brachypterous, wing rather elytriform, venation weak. Male with sense-papillae in anal cell of fore wing. Hind wing (fig. 4.530) with R_{2+3} oblique. Veins in distal part of wing setose. Gonapophyses (fig. 4.531) with dorsal and ventral valves lobed. Subgenital plate (fig. 4.534) bilobed each lobe with an apical seta and a more basal seta near mesial margin. Phallosome (fig. 4.532) with rod-shaped sclerites but with some sclerification of penial bulb. Hypandrium (fig. 4.533) with a pair of posterior processes and lateral sclerotized bars with spine-like processes.

Habitat: Foliage.

Distribution: Brazil.

Pseudoscottiella Badonnel (5 species)

Pseudoscottiella Badonnel, 1946. Rev. Zool. Bot. afr. 39: 170.
Type species: P. megops Badonnel.

Lacinia (fig. 4.535) with divided apex, one half longer than the other. Claws undescribed. Fore wing (fig. 4.536) with pterostigma and areola postica flattened. Costa thickened from base to wing apex. Rs and M fused for a length. M 2-branched. Fore wing veins (except Cu_2) with more than one row of setae; margin setose, hairs crossing each other posterior to apex. No setae on wing membrane. Hind wing with some hairs on branches of Rs and on M; setae of margin crossing posterior to apex. Ninth tergite of male (fig. 4.537) with rugose protuberances on either side of midline. Epiproct of male strongly chitinized, sometimes bearing rugose areas of various forms. Hypandrium (fig. 4.538) with strongly chitinized, protuberances or spurs which may bear spines or spicules. Phallosome (fig. 4.539) without internal parameres and without sclerifications of the penial bulb. Subgenital plate rounded behind or coming to a very blunt median point with some internal sclerites to which the ventral valves of the gonapophyses appear to be attached. Gonapophyses (fig. 4.540) complete; ventral valve broad-based, pointed, with spicules and with a preapical lobe; dorsal valves pointed, with spicules and lobed; external valve ovoid, setose.

Habitat: Leaf dwellers.

Distribution: Angola, Congo.

Allocaecilius Lee and Thornton (5 species)

Allocaecilius Lee and Thornton, 1967. Pacific Ins. Monogr. 16: 12.

Type species: A. heterothorax Lee and Thornton.

Venation as in Caecilius. Fore wing (fig. 4.541) with Rs and M fused for a length. Rs stem long and strongly curved basally. Areola postica high, more or less triangular. Basal veins with setae in more than one row, distal veins with setae in single row of two lengths. Gonapophyses (fig. 4.542) with ventral and dorsal valves lobed. Phallosome (fig. 4.543) with only rod-shaped sclerites. Hypandrium (fig. 4.544) with lateral sclerotized bars bearing spines. Epiproct tuberculate. Claw without preapical tooth. Subgenital plate (fig. 4.545).

Habitat: Foliage.

Distribution: Hong Kong, India, Malaya.

Heterocaecilius Lee and Thornton (20 species)

Heterocaecilius Lee and Thornton, 1967. Pacific Ins. Monogr. 16: 13.

Type species: None designated (Rule 42c. International Code).

Venation as in Caecilius. Fore wing with stem of Rs at least as long as R_{4+5}. Male fore wing usually lack sense papillae. Gonapophyses with dorsal and ventral valves with lobes. Subgenital plate bilobed each lobe triangular bearing a single seta at or near apex and usually another near mesial base of lobe. Hypandrium with at least one pair of posterior, sclerotized projections. Phallosome usually with rod-shaped sclerites.

Habitat: Dead vegetation and foliage.

Distribution: Caroline Is., Hong Kong, Gilbert Is., New Guinea, Fiji, Mariana Is., Philippines, India, Malaya.

Note: This is a heterogeneous assemblage of species, none of which could be placed by Lee and Thornton (1967) in other genera of the family. It was proposed as a "collective group" and no type species was designated. A detailed revision of the family at specific level on a worldwide basis would be needed before the species included here could be placed in existing genera or distributed in new genera.

Lobocaecilius (6 species)

Lobocaecilius Lee and Thornton, 1967. Pacific Ins. Monogr. 16: 12.

Type species: L. cynara Lee and Thornton.

Venation as in Pseudocaecilius. Fore wing (fig. 4.546) with stem of Rs short. Male fore wing sometimes with papillae associated with R. Gonapophyses (fig. 4.547) with dorsal and ventral valves lobed. External valve widens apically, lateral border indented. Subgenital plate (fig. 4.548) bilobed each lobe rounded, a single seta at apex and one at mesial base of each, the latter often on a distinct smaller lobe. Phallosome (fig. 4.549) with penial bulb sclerifications consisting of small spines only. Parameres divergent. Hypandrium complex (fig. 4.550) usually with two, three or four pairs of fingernail-like sclerites posteriorly. Epiproct of male tuberculate. Claw without preapical tooth.

Habitat: Foliage, dead and live fern fronds, dead leaves.

Distribution: Tahiti, Society Is., Caroline Is., Malaya, Hawaii, Fiji, Marianas, Guam.

Phallocaecilius Lee and Thornton (1 species)

Phallocaecilius Lee and Thornton, 1967. Pacific Ins. Monogr. 16: 12.

Type species: Pseudocaecilius hirsutus Thornton.

Venation as in Pseudocaecilius. Fore wing of male with sense papillae in anal area. Rs and M joined by a cross-vein. Hind wing veins glabrous. Gonapophyses (fig. 4.551) with dorsal and ventral valves fleshy, not lobed, without barbules. External valve very small. Phallosome (fig. 4.552) without inner parameres; a median ribbon and three large thorn-like sclerites present. Hypandrium simple, unsclerotized, setose. Subgenital plate (fig. 4.553) bilobed, apically setose.

Habitat: On Sterculia.

Distribution: Hong Kong.

Scytopsocopsis Lee and Thornton (1 species)

Scytopsocopsis Lee and Thornton, 1967. Pacific Ins. Monogr. 16: 11.

Type species: S. hirtipenna Lee and Thornton.

Similar to Scytopsocus but with Rs stem long, setae on veins. Male fore wing (fig. 4.554) lacks anal sense papilla field. Phallosome (fig. 4.555) with rods as well as minute spines. Hypandrium (fig. 4.556) with a short spine and a curved hook posteriorly at each side. Females unknown.

Habitat: On shrubs.

Distribution: India.

Trichocaecilius Badonnel (1 species)

Trichocaecilius Badonnel, 1967. Faune de Madagascar 23: 140.
Type species: T. delicatus Badonnel.

Head and thorax with long hairs. Lacinia (fig. 4.557) with two unequal apical teeth. Fore wing (fig. 4.558) with costal margin thickened. Pterostigma oblong. Rs and M fused for a length. M 3-branched. Areola postica free, with broad base. Two rows of setae on R, R_1 and IA. A single row on other veins. Setae crossing each other on wing margin behind wing apex. Membrane setose. Some sense papillae in anal cell of male. Hind wing as in Pseudocaecilius, with crossing setae, membrane with some setae. Claws asymmetrical, one with a small preapical tooth, the other without. Hypandrium (fig. 4.559) with hooks. Phallosome (fig. 4.560) narrow, no sclerites to penial bulb. Subgenital plate (fig. 4.561) with two lobes, setose. Gonapophyses (fig. 4.562) with ventral valve membranous, dilated, ending in a curved, spiculate point. Dorsal valve lobed, with spiculate point. External valve elliptical, setose.

Habitat: Not recorded.

Distribution: Madagascar.

Subfamily ELECTROPSOCINAE

* Electropsocus Roesler (1 species)

Electropsocus Roesler, 1940. Arb. morph. taxon. Ent. Berl. 7: 244.

Type species: E. unguidens Roesler.

Lacinia undescribed. Claw with strong preapical tooth. Fore wing with concave pterostigma, areola postica tall; Rs and M fused for a short length or meeting in a point. M 3-branched. Fore wing veins and margin glabrous. Hind wing undescribed.

"Die genital-anhange bei ♂ und ♀ ahnlich Mesopsocus Klbe". Subgenital plate with posterior lobe. "Dorsal- und Ventralvalven erkenbaar, die ahnlich denen von Amphigerontia". Dorsal valve broad with long point.

Habitat: Unknown.

Distribution: East Prussia (in amber).

CHARACTERS OF THE TRICHOPSOCIDAE

Belonging to the Psocomorpha. Claws without preapical tooth; pulvillus broad. Tarsi 2-segmented. Venation of the Caecilius type. Pterostigma without prominent hind angle. Fore wing with margin and veins setose, setae in a single row on branches of veins; apical marginal setae not crossing one another. Hind wing with veins glabrous; apical marginal setae not crossing one another, those of hind margin alternately longer and shorter. Hypandrium simple. Phallosome with sclerifications of penial bulb. Subgenital plate simple. Gonapophyses complete. Eggs covered with encrustation of debris, without silk.

GENERA INCLUDED IN THE TRICHOPSOCIDAE

Trichopsocus Kolbe, 1888.

Palaeopsocus Kolbe, 1883

Trichopsocus Kolbe (5 species)

Trichopsocus Kolbe, 1888. Jber. Ver. Naturk. Zwickau 1887: 177.
Type species: Caecilius hirtellus McLachlan.

Lacinia with apex divided into two diverging teeth, these with indications of subdivision. Claws without preapical tooth; pulvillus broad. Fore wing (fig. 4.563) with veins (except Cu_2) with setae; branches of veins with single row of setae; margin setose. Hind wing (fig. 4.564) with veins glabrous, margin setose, setae of hind margin alternately longer and shorter. Epiproct of female (fig. 4.565) with four strong dorsal setae near hind margin, with a smaller median seta; median seta flanked by two more on posterior margin. Hypandrium simple. Phallosome (fig. 4.566) with sclerifications of penial bulb. Subgenital plate simple. Gonapophyses complete (fig. 4.567); ventral valve pointed; dorsal valve conical with very strong subapical process; external valve broad, almost circular, with long setae, some of which are curved. Eggs covered with encrustation of debris.

Habitat: On leaves.

Distribution: Europe, Morocco, Madeira, Canary Islands, Tasmania, Algeria, Latvia, Caucasus.

* Palaeopsocus Kolbe (1 species)

Palaeopsocus Kolbe, 1883. Stettin. ent. Ztg. 44: 190.
Type species: Psocus tener Hagen.

Lacinia apically divided into two diverging teeth. Claw without preapical tooth. Tarsi 2-segmented. Venation of Caecilius type but with Cu_{1a} not reaching wing margin and Rs not branched. Veins (including Cu_2) and margin setose. Hind wing with basal section of Rs absent. Veins and margin glabrous. Subgenital plate simple.

Habitat: Unknown.

Distribution: East Prussia (in amber).

CHARACTERS OF THE ARCHIPSOCIDAE

Belonging to the Psocomorpha. Fore and hind wings with reduced, evanescent venation; membranes, veins and wing margin setose in fore wing; hind wing veins glabrous; membrane and margin setose. Tarsi 2-segmented. Gonapophyses reduced or absent (in viviparous species). Subgenital plate simple. Hypandrium simple. Phallosome without complex penial bulb sclerifications; external parameres absent, the phallosome being fairly simply ring-like or elongate. Eggs ovoid, encrusted with debris, without silk.

GENERA INCLUDED IN THE ARCHIPSOCIDAE

Archipsocus Hagen, 1882

Archipsocopsis Badonnel, 1966

* *Archipsocus* Hagen (12 species)

Archipsocus Hagen, 1882. *Stettin. ent. Ztg.* 43: 225.

Type species: *A. puber* Hagen.

Females oviparous. Gonapophyses (fig. 4.568) reduced to a small styliform dorsal valve and a broad, sub-triangular, setose external lobe bearing a row of setae on its distal edge. Flagellar segments six and ten with a placoid sensillum bearing a long filament. Lacinia (fig. 4.569) narrowing towards divided apex. Claw without pre-apical tooth. Pulvillus broad. Alary polymorphism frequent. Males brachypterous or apterous; females macropterous or brachypterous. Fore wing (fig. 4.570) with reduced, evanescent venation. Margin, membrane and veins setose. Hind wings (fig. 4.571) with reduced but more distinct venation. Veins glabrous. Margin and membrane in distal region setose. Setae on margin crossing each other posterior to wing apex. Tarsi 2-segmented. Epiproct simple, rounded behind, setose.

Paraprocts (fig. 4.573) simple, setose, with one or two trichobothria in winged forms. Hypandrium simple. Phallosome (fig. 4.572) with external parameres absent; no penial bulb sclerifications. Phallosome broad, oval. Subgenital plate simple. Eggs ovoid, somewhat narrower towards one end; encrusted with debris but without silken threads.

Habitat: On tree trunks under large communal webs.

Distribution: East Prussia (in amber), Brazil, Porto Rica, Paraguay, Queensland, North America, Angola, Congo, Madagascar, Ivory Coast, Gold Coast, Singapore, Ceylon, Java, Formosa, Hong Kong, East Africa, French Guinea.

Archipsocopsis Badonnel (13 species)

Archipsocopsis Badonnel, 1966. Bull. Mus. Hist. nat. Paris (2) 38: 413.

Type species: Archipsocus mendax Badonnel.

Characters as in Archipsocus but females viviparous, lacking gonapophyses or with only a tiny rudiment of an external valve. Placoid sensilla of sixth and tenth flagellar segments with a small central cone. Phallosome (fig. 4.574) narrow, elongate-ovoid.

Habitat: On tree trunks under large communal webs.

Distribution: Congo, Angola, Madagascar, Nigeria, Ceylon, Florida, Queensland.

CHARACTERS OF THE ELIPSOCIDAE

Antennae long, 13-segmented (may be fewer in Nepiomorpha). Fore wing with pterostigma clearly convex, not connected to Rs by a cross-vein; Rs and M usually fused for a length but may be merely connected by a cross-vein (Palmicola, Propsocus, sometimes Pseudopsocus); areola postica free (except in Propsocus, Pentacladus, Palistreptus; absent in Nepiomorpha, Palmicola); media usually three-branched (2-branched in Nepiomorpha, 5-branched in Pentacladus); margin and veins setose, setae sometimes sparse and small (Nepiomorpha, Spilopsocus, Propsocus, Pentacladus, absent in Palmicola). Hind wings with Rs and M fused for a length (except in Reuterella); setae on margin only between R_{2+3} and R_{4+5}. Tarsi 3-segmented, exceptionally 2-segmented (Nepiomorpha, Paedomorpha, Palmicola, Reuterella); coxal stridulatory organs present, sometimes absent (Palmicola, Reuterella and some neotenic forms); claws with pulvillus of various forms, a stiff basal seta and a preapical tooth. Hypandrium of male simple or lobed, without ornamentation. Subgenital plate of female usually bilobed or with indication of lobing (sometimes with a median lobe - subfamily Nepiomorphinae and genus Palmicola) with preapical, transverse band of strong setae and a small group of strong setae at the extremity of each lobe. Gonapophyses of female complete; ventral valve pointed; dorsal valve usually divided at apex; external valve large, setose, with strong marginal setae. Polymorphism common; brachypterous or apterous forms occur, in which other neotenic features are found such as reduction of trichobothrial field, ocelli, antennae and tarsal segments and retention of duplex setae on paraprocts of adults. Eggs laid in groups, covered with an encrustation.

GENERA INCLUDED IN THE ELIPSOCIDAE

Elipsocus Hagen, 1866.

Propsocus McLachlan, 1866.

Pseudopsocus Kolbe, 1882.

Hemineura Tetens, 1891.

Reuterella Enderlein, 1903.

Pentacladus Enderlein, 1906.

Kilauella Enderlein, 1913.

Palistreptus Enderlein, 1920.

Lesneia Badonnel, 1931.

Nepiomorpha Pearman, 1936.

Cuneopalpus Badonnel, 1943.

Antarctopsocus Badonnel, 1947.

Palmicola Mockford, 1955.

Lenkoella Machado - Allison and Papavero, 1962.

Spilopsocus Smithers, 1963.

Drymopsocus Smithers, 1963.

Paedomorpha Smithers, 1963.

Roesleria Badonnel, 1963.

? Graphocaecilius Enderlein, 1900.

? Hemicaecilius Enderlein, 1903.

Nothopsocus Badonnel, 1967.

Nepiomorpha Pearman (3 species)

Nepiomorpha Pearman, 1936. Spolia zeylan. 20: 4.

Type species: N. crucifera Pearman.

Antennae may have fewer than 13 segments; short in apterous forms. Ocelli absent in apterous females and males, present in winged females. Fourth segment of maxillary palp elongate, rounded apically. Fore wing (fig. 4.575) without strong patterning; areola postica absent; media 3-branched (sometimes 2-branched); setae fine and sparse; no setae on

Cu_2. Tarsi 2-segmented. Coxal stridulatory organ absent in apterous forms. Pulvillus fine, hardly expanded apically. Trichobothria absent in apterous males and females, present in winged females. Duplex setae strongly developed in apterous forms, reduced in winged females. Hypandrium simple. Phallosome (fig. 4.576) broad and short; parameres very broad and free; sclerotisations of penial bulb absent. Subgenital plate (fig. 4.577) with strong median lobe; hind margin of lobe setose; a band of preapical setae present. Dorsal valve of gonapophyses (fig. 4.578) with outer division bearing small spinules and inner division having the form of a broad lobe; external valve hatchet-shaped with marginal setae. Setae plumose in some regions of body. Males apterous, females brachypterous, apterous or macropterous.

Habitat: Under bark, in leaf litter, on shrubs, on bark.

Distribution: Angola, Ceylon, Florida.

Paedomorpha Smithers (1 species)

Paedomorpha Smithers, 1963. Proc. R. ent. Soc. Lond. (B) 32: 32.

Type species: P. gayi Smithers.

Antennae shorter in apterous females than in winged females. Ocelli absent in apterous females, present in macropterous females. Fourth segment of maxillary palp elongate, rounded apically. Fore wing (fig. 4.579) not strongly patterned; setae present on Cu_2. Hind wing setae on margin between R_{2+3} and R_{4+5} strong. Tarsi 2-segmented (apterous females) or 3-segmented (macropterous females). Coxal stridulatory organ present in macropterous forms, absent in apterous. Pulvillus fine and slightly expanded apically.

Paraproct (fig. 4.580) with strong dorsal sclerotised band. Trichobothria absent in apterous females, present in macropterous females. Duplex setae absent. Subgenital plate (fig. 4.581) with a strong median lobe, the lobe carrying a row of setae on its hind border; a row of preapical setae present. Gonapophyses (fig. 4.582) with ventral valve much reduced to a small membranous flap; dorsal valve with outer part pointed and carrying recurrent spinules, inner part in the form of a lightly sclerotised lobe; external valve roughly triangular with marginal setae; these being closer together at dorsoposterior and ventroposterior angles than along posterior margin. Setae knobbed, that is, with expanded tips. Females of two forms, apterous and macropterous (males unknown).

Habitat: On bark and paling fences.

Distribution: Australia.

Palmicola Mockford (3 species)

Palmicola Mockford, 1955. Proc. Ent. Soc. Wash. 57: 102.
Type species: P. aphrodite Mockford.

Antennae short in both sexes but longer in male than in female. Ocelli absent in female, present in male. Fourth segment of maxillary palp elongate and rounded apically. Fore wing (fig. 4.583) without pattern; Rs and M joined by a cross-vein; areola postica absent; media 3-branched (sometimes 2-branched or simple, a variable character); no setae on wings. Hind wing with Rs and M joined by a cross vein; without setae. Tarsi 2-segmented. Coxal stridulatory organ absent. Pulvillus fine, expanded a little apically. Paraprocts (fig. 4.584) without dorsal chitinised band. Trichobothria present in male, absent in female. Duplex setae larger in male than in female. Phallosome (fig. 4.585) with broad parameres. Subgenital plate (fig. 4.586) with median lobe; with setae on lobe; preapical row of setae present. Gonapophyses (fig. 4.587) with dorsal valve somewhat similar to Reuterella, external valve rounded with marginal setae, long, closer to each other near posterodorsal angle than along rest of margin. Males macropterous, females apterous.

Habitat: On tree trunks.

Distribution: Florida, Jamaica.

Reuterella Enderlein (1 species)

Reuterella Enderlein, 1903. Zool. Anz. 27: 132.
Type species: Leptella helvimacula Enderlein.

Antennae short in females, longer in males. Ocelli absent in females, present in males. Fourth segment of maxillary palp elongate and rounded apically. Fore wing (fig. 4.588) without strong pattern; Rs and M fused for a length or joined by a cross-vein, Cu_2 without setae. Hind wing (fig. 4.589) with Rs and M joined by a cross vein. Tarsi 2-segmented. Coxal stridulatory organs absent. Pulvillus long, fine, slightly expanded apically. Paraproct without a dorsal sclerotised band. Trichobothria absent in females, present in males. Duplex setae absent. Hypandrium simple. Phallosome fairly broad; parameres broad; sclerotisations of penial bulb present but not strong. Subgenital plate (fig. 4.590) with indication of posteriorly bilobed condition, a small group of setae at apex of each lobe; preapical band of setae present. Gonapophyses (fig. 4.591) with dorsal valve with outer lobe pointed, inner lobe rounded and less sclerotised; external valve rounded with marginal setae, latter more or less evenly spaced. Females apterous, males macropterous. Eggs laid singly or in groups, encrusted.

Habitat: On bark.

Distribution: Europe and N. America.

Pseudopsocus Kolbe (4 species)

Pseudopsocus Kolbe, 1882. Ent. Nachr. 8: 208.
Type species: P. rostocki Kolbe.

Antennae shorter in females, longer in males. Ocelli absent in females, present in males. Maxillary palp with fourth segment elongate with rounded apex. Fore wing (fig. 4.592) without strong pattern. Rs and M fused (sometimes joined by a cross-vein); Cu_2 without setae. Hind wing (fig. 4.593) with Rs and M relationship variable (from fusion to being joined by a cross vein). Coxal stridulatory organ absent in female, present in male. Pulvillus fine, with slight apical expansion. Paraproct without chitinised dorsal band. Trichobothria present in male, absent in female. Duplex setae present on paraproct of female. Hypandrium simple. Phallosome similar to that of Reuterella. Subgenital plate (fig. 4.594) with indication of posteriorly bilobed condition, a few setae on each lobe; a preapical band of setae present. Gonapophyses (fig. 4.595) with dorsal valve apically divided, inner part in the form of a lobe, outer pointed; external valve rounded with evenly spaced marginal setae. Females apterous, males macropterous. Eggs laid in masses, encrusted.

Habitat: On bark.

Distribution: Europe.

Spilopsocus Smithers (3 species)

Spilopsocus Smithers, 1963. Pacific Ins. 5: 894.
Type species: S. ruidis Smithers.

Antennae fairly long. Ocelli present. Fourth segment of maxillary palp elongate, rounded apically. Fore wing patterned (fig. 4.596); setae present, but small and sparse, on wing margin and veins; Cu_2 setose. Hind wing (fig. 4.597) with Rs and M fused for a length; setae on margin between R_{2+3} and R_{4+5} fine and few. Pulvillus fine and long. Paraproct of female in some species with sclerotized ridge along dorsal margin; in male of some species, paraproct with a rugose dome posteriorly. Trichobothria present. Duplex setae absent in macropterous forms, present in brachypterous. Hypandrium (fig. 4.598) with lateral lobes. Phallosome (fig. 4.599) broad anteriorly, tapering posteriorly; penial bulb with sclerotisations. Subgenital plate (fig. 4.600) with suggestion of being bilobed; preapical setae arranged as a median group; a few setae on each lobe. Gonapophyses (fig. 4.601) with dorsal valve with inner part in the form of a lobe and outer part pointed; external valve hatchet-shaped, setose, with a row of evenly-spaced marginal setae. Macropterous and brachypterous forms known in both sexes in some species, in other males macropterous and female brachypterous.

Habitat: On vegetation.

Distribution: Australia, New Zealand and Campbell Island.

Antarctopsocus Badonnel (1 species)

Antarctopsocus Badonnel, 1947. Mem. Mus. Hist. nat. (N.S.) 20: 26.
Type species: A. jeanneli Badonnel.

Antennae fairly long. Ocelli absent in both sexes. Fourth maxillary segment elongate and rounded apically. Fore wings (fig. 4.602) reduced in length in both sexes, with hardly a trace of veins; a few scattered setae present. Hind wings (fig. 4.603) reduced to small lobes. Coxal stridulatory organs absent. Pulvillus broad, apically expanded. Claws without preapical tooth, a small bulge occurring in position usually occupied by tooth. Pulvillus broad. Paraprocts without dorsal sclerotised band. Trichobothria absent. Duplex setae present in both sexes. Hypandrium simple. Phallosome (fig. 4.604) broad, with broad parameres. Subgenital plate (fig. 4.605) bilobed; several setae at apex of each lobe; preapical setae reduced to two. Gonapophyses (fig. 4.606) with two parts of about equal size; external valve hatchet-shaped, with more or less evenly spaced marginal setae. Both sexes brachypterous.

Habitat: Under stones.

Distribution: Marion Island.

Pentacladus Enderlein (1 species)

Pentacladus Enderlein, 1906. Zool. Jb. Abt. Syst. 23: 408.
Type species: P. eucalypti Enderlein.

Antennae fairly long. Ocelli present. Fourth segment of maxillary palp elongate with rounded apex. Fore wing (fig. 4.607) with strong pattern, areola postica joined to media (usually in a point); media with more than 3 branches; setae of margin and veins very small, sparse, sometimes difficult to see; Cu_2 with very fine short setae. Hind wing with a few fine, short setae on margin between R_{2+3} and R_{4+5}. Pulvillus very broad. Paraproct without dorsal sclerotised band, posteriorly a little rugose. Trichobothria present. Duplex setae absent. Hypandrium (figs. 4.608, 4.609) with strong lateral lobes. Phallosome (fig. 4.610) broad. Subgenital plate (fig. 4.611) bilobed; 2 setae at apex of each lobe; preapical band of setae reduced to 2 pairs, each pair arising from a lightly sclerotised area. Gonapophyses (fig. 4.612) with dorsal valve similar to Spilopsocus; external valve hatchet-shaped with marginal setae a little closer together near the posterodorsal angle than elsewhere. Both sexes winged.

Habitat: On dead leaves, on bark.

Distribution: Australia.

* Propsocus McLachlan (3 species)

Propsocus McLachlan, 1866. Trans. Ent. Soc. Lond. 3: 352.
Type species: Psocus pallipes McLachlan.

Antennae fairly long. Ocelli present. Fourth segment of maxillary palp elongate and rounded apically. Fore wings (fig. 4.612) strongly patterned; Rs and M meeting in a point or joined by a cross vein (variable character); areola postica connected to media (usually in a point); setae of margin and veins very short, sparse and fine; Cu_2 with fine, short setae. Hind wing without setae. Pulvillus very broad.

Claws with or without preapical tooth. Paraproct without a dorsal sclerotised band. Trichobothria present. Duplex setae absent. Hypandrium (fig. 4.614) with lobes. Phallosome (fig. 4.615) elongate; sclerifications of penial bulb strong. Subgenital plate (fig. 4.616) bilobed; a few setae on lobes; preapical setae in a single row. Gonapophyses (fig. 4.617) with dorsal valve somewhat as in Spilopsocus; external valve hatchet shaped, marginal setae being more or less evenly distributed along the posterior margin. Brachypterous and macropterous forms may occur in both sexes. Eggs laid in groups, encrusted.

Habitat: Leaf litter, dry grass, under stones.

Distribution: Australia, Hawaii, Rhodesia, South Africa, East Prussia (in amber), Chile.

Cuneopalpus Badonnel (1 species)

Cuneopalpus Badonnel, 1943. Faune de France 42: 76.
Type species: Elipsocus cyanops Rostock.

Antennae fairly long. Ocelli present. Fourth segment of maxillary palp short, broad, truncate (fig. 4.620). Fore wing without conspicuous pattern; Cu_2 with setae present in some specimens (original description suggests that Cu_2 is always without setae). Pulvillus narrow, with expanded tip. Paraproct lightly sclerotised, without dorsal sclerotised ridge. Trichobothria present. Duplex setae present in males. Hypandrium simple. Phallosome elongate, with sclerifications of penial bulb. Subgenital plate (fig. 4.618) bilobed, lightly sclerotised, similar to that in Elipsocus; a few setae on each lobe; preapical setae arranged in a band. Gonapophyses (fig. 4.619) with dorsal valve lightly sclerotised, apically divided into a large fleshy lobe internally and a smaller pointed external apophysis; external valve somewhat rectangular, lightly sclerotised, bearing a small setose lobe; marginal setae more or less evenly spaced. Both sexes macropterous.

Distribution: Europe.

* Elipsocus Hagen (26 species)

Elipsocus Hagen, 1866. Verh. zool. -bot. Ges. Wien 16: 203.
Type species: E. westwoodi McLachlan.

Antennae fairly long. Ocelli present. Fourth segment of maxillary palp elongate, rounded apically. Fore wing usually without striking pattern, sometimes diffuse markings present, usually stronger in females than in males (fig. 4.621); sometimes setae well developed, sometimes sparse and small; Cu_2 setose. Pulvillus narrow, fine, not apically expanded. Paraprocts with dorsal sclerotised band in male, absent in female. Trichobothria present. Duplex setae normally absent (present in males of some species). Hypandrium simple. Phallosome (fig. 4.622) variable, with sclerotisations of penial bulb. Subgenital plate (fig. 4.623) bilobed; a few setae on each lobe; preapical setae in irregular transverse row. Gonopophyses (fig. 4.624) with dorsal valve more or less triangular with a small ventral apophysis; external valve of various forms, setose, setae not arranged in a row along margin. Both sexes macropterous. Eggs laid singly, covered with an encrustation.

Habitat: Twigs and stems of woody shrubs and trees, on bark.

Distribution: Europe, Russia, Peru, India, Hong Kong, British Columbia, Costa Rica, Haiti, Tanganyika, Argentina, Ceylon, Canary Islands, South Africa, Canada, U.S.A., Northern and Southern Rhodesia, East Prussia (in amber), Azores, Chile.

Hemineura Tetens (2 species)

Hemineura Tetens, 1891. Ent. Nachr. 17: 372.
Type species: H. dispar Tetens.

Antennae fairly long. Ocelli present in male, almost invisible in female. Fourth segment of maxillary palp elongate, with rounded apex. Fore wing without strong pattern; setae on veins and wing margin few, sparse and small; Cu_2 without setae. Pulvillus fine. Paraproct of female without sclerotised band (male ?). Trichobothria present in both sexes. Phallosome with sclerifications of penial bulb. Subgenital plate (fig. 4.625) bilobed, as in Elipsocus; a few setae at apex of each lobe; preapical band of setae on lightly sclerotised area. Gonapophyses (fig. 4.626) with dorsal valve broad, with a small apophysis; external valve setose, without distinct row of marginal setae. Females brachypterous or apterous, males macropterous.

Habitat: ?

Distribution: Europe.

Kilauella Enderlein (8 species)

Kilauella Enderlein, 1913. Zool. Anz. 41: 357.
Type species: Elipsocus erythrostictus Perkins.

Antennae fairly long. Ocelli present. Fourth segment of maxillary palp elongate, with rounded apex. Fore wings (fig. 4.627) without strong pattern; Cu_2 setose. Coxal stridulatory organ reduced. Pulvillus fairly broad, expanded apically. Claws without preapical tooth. Paraproct of male with strong posterior rugose lobe; female normal, without sclerotised band. Trichobothria present. Duplex setae absent. Hypandrium simple. Phallosome with parameres expanded internally into strong, rugose lobes, aedeagus well developed; sclerotisations of penial bulb strong. Subgenital plate bilobed, lightly sclerotised; 2 apical setae on each lobe; preapical setae band reduced to a row of 4 strong setae. Gonapophyses with ventral valve pointed, with a membranous basal lobe; dorsal valve elongated, pointed, with small subapical apophysis; external valve broad, triangular, setose, with marginal setae more or less evenly spaced. Both sexes macropterous.

Habitat: High altitudes, in forests.

Distribution: Hawaii.

Drymopsocus Smithers (1 species)

Drymopsocus Smithers, 1963. Proc. R. ent. Soc. Lond. (B) 32: 36.
Type species: D. brunneus Smithers.

Antennae a little shorter in female than in male. Ocelli present in both sexes. Fourth segment of maxillary palp elongate, rounded apically. Fore wing without pattern; Rs and M fused for a length (male) (wings reduced in female); setae of veins and margin fine, sparse and short; Cu_2 without setae. Hind wings with a few marginal setae between R_{2+3} and R_{4+5} fine, sparse and short. Coxal stridulatory organ present in both sexes. Pulvillus fairly broad, expanded apically. Claws with slight suggestion of preapical tooth. Paraprocts without dorsal sclerotised band in both sexes. Trichobothria present. Duplex setae absent. Hypandrium simple. Phallosome posteriorly narrowed, parameres narrow, sclerotisations of penial bulb present. Subgenital plate (fig. 4.628) with suggestion of being bilobed, lightly sclerotised between lobes; lobes with a few apical setae; preapical setae arranged in a band. Gonapophyses (fig. 4.629) with ventral valve pointed but somewhat shortened; dorsal valve broad, apex slightly emarginate, suggesting incipient division; external valve roughly hatchet-shaped; setose; marginal setae reduced to a small group at posterodorsal angle of valve. Males macropterous, females brachypterous.

Habitat: On bark.

Distribution: Australia.

Palistreptus Enderlein (2 species)

Palistreptus Enderlein, 1920. Zool. Jb. Abt. Syst. 43: 457.
Type species: Elipsocus inconstans Perkins.

Antennae long. Ocelli present. Fourth segment of maxillary palp elongate, rounded apically. Fore wing (fig. 4.630) strongly patterned; areola postica free or meeting M; Cu_2 setose. Pulvillus fairly broad and long, truncate. Paraproct without sclerotised band but with posterior lobe in male. Trichobothria present, large. Duplex setae absent. Hypandrium with inwardly curved hind margin, lateral parts more strongly sclerotised than median. Phallosome with parameres slightly expanded apically, aedeagus fine; penial bulb with sclerotisations. Subgenital plate bilobed (of the Pseudopsocus type); a few apical setae on each lobe; preapical setae concentrated in a median transverse group. Gonapophyses with ventral valve long and pointed, a basal lobe present; dorsal valve broad, rectangular, with strong subapical apophysis (the whole valve being reminiscent of the Mesopsocid type of valve); external valve with a few marginal setae. Both sexes macropterous.

Habitat: ?

Distribution: Hawaii.

Lesneia Badonnel (2 species)

Lesneia Badonnel, 1931. Ann. Sci. nat. (Zool.) 14: 247.
Type species: L. capensis Badonnel.

Tarsi 3-segmented; lacinia (fig. 4.631) truncate with 2 equal lateral teeth; 4 spines at apex of tibiae of meso- and metathoracic legs; claws with pulvillus apically expanded and preapical tooth. Fore wings of male with pubescent membrane. Penial bulb (fig. 4.632) with sclerifications; hypandrium simple. Female without coxal stridulatory organs; apterous; gonapophyses lacking; subgenital plate simple without any indication of lobing; paraprocts with duplex setae; abdomen with coalescent tergites. Males macropterous, females apterous.

Habitat: ?

Distribution: South Africa.

Lenkoella Machado-Allison and Papavero (1 species)

Lenkoella Machado-Allison and Papavero, 1962. Pap. Dep. Zool. Sec. Agric. Sao Paulo 15: 312.
Type species: L. neotropica Machado-Allison and Papavero.

Lacinia not described. Antenna with 13th segment conical. Claws without preapical tooth; pulvillus undescribed. Tarsi 2-segmented. Fore wing (fig. 4.632) with pterostigma relatively long. Rs and M fused for a long length. M 2-branched, branching near wing margin. Veins (including Cu_2) and margin with setae. Hind wing (fig. 4.633) with Rs and M fused for a fairly long length. Veins glabrous; margin setose; Cu_2 apparently absent. Epiproct trapezoidal with two large subapical setae. Females macropterous, males apterous.

Habitat: In dry branch.

Distribution: Brazil.

Roesleria Badonnel (1 species)

Roesleria Badonnel, 1963. Biol. l'Amer. austr. 2: 331.
Type species: R. chilensis Badonnel.

Females apterous (males not known). Coxal organs and ocelli absent. Lacinia (fig. 4.635) with two equal apical teeth. Tarsi 3-segmented. Four spines at apex of tibia. Claw (fig. 4.636) with preapical tooth. Pulvillus setiform. Subgenital plate (fig. 4.637) without lateral lobes or median lobe but with two groups of symmetrical macrochaetae and a transverse row of long setae. Gonapophyses (fig. 4.638) with ventral valve reduced to a small, triangular, membranous flap, dorsal valve short, reduced to a lobe bearing a short spiculate process. External valve sclerotized, setose. Edge of paraproct (fig. 4.639) with a large seta and two small hyaline cones.

Habitat: On lichen on rocks.

Distribution: Chile.

Nothopsocus Badonnel (1 species)

Nothopsocus Badonnel, 1967. Biol. l'Amer. austr. 3: 577.
Type species: N. oxyurus Badonnel.

Females micropterous. Tarsi 3-segmented, ocelli present. Subgenital plate (fig. 4.640) with apical median lobe bearing two groups of long setae. Gonopophyses (fig. 4.641) with long pointed, ventral valve without lobe. Dorsal valve in form of a triangular lobe with a strong, pointed, sclerotized process. External valve hatchet-shaped, setose. Paraprocts with two macrochaetae, with two small separate hyaline cones. Claws with preapical tooth. Pulvillus fine. Spermathecal opening with circular sclerotized area.

Distribution: Chile.

Graphocaecilius Enderlein (6 species)

Graphocaecilius Enderlein, 1900. Zool. Jb. Abt. Syst. 14: 155.
Type species: G. trypetoides Enderlein.

Lacinia narrow, weakly curved, apically with two unequal teeth. Tarsi 2-segmented. Claws long, curved, with strong preapical tooth. Fore wing (fig. 4.642) with Caecilius type venation. Veins in distal part of wing with a single row of setae; Cu_2 glabrous. Margin setose. Hind wing (fig. 4.643) with Rs and M fused for a length. Glabrous except for margin between R_{2+3} and R_{4+5}. Hypandrium weakly sclerotized, with straight posterior margin, with a small lateral hook on each side. Phallosome (fig. 4.644) with sclerification of penial bulb. Subgenital plate simple, with transverse hind margin in the middle. Gonapophyses (fig. 4.645) represented only by the external, setose valve and a small pointed remnant which may represent the dorsal valve.

Distribution: Peru, Bolivia, Brazil, Santo Domingo.

Hemicaecilius Enderlein (1 species)

Hemicaecilius Enderlein, 1903. Zool. Jb. Abt. Syst. 18: 357.
Type species: H. bogotanus Enderlein.

Characters as for Graphocaecilius. M 2-branched. Tarsi 2-segmented.

Distribution: Colombia.

(Note: There is little known of this genus other than its venation and number of tarsal segments).

CHARACTERS OF THE PSOCULIDAE

Belonging to the Psocomorpha. Tarsi 2-segmented. Claws with preapical tooth and fine pulvillus. Apterous. Eyes small, ocelli absent. Gonapophyses complete. Males unknown, probably parthenogenetic. Eggs smooth, with encrustation and covered with silken threads.

GENERA INCLUDED IN THE PSOCULIDAE

Psoculus Roesler

Psoculus Roesler (1 species)

Psoculus Roesler, 1954. Beitr. zur Ent. 4: 570.
Type species: Reuterella neglecta Roesler.

Lacinia with 3-4 teeth at apex. Claws with preapical tooth and fine pulvillus. Ocelli absent, eyes small. Tarsi 2-segmented. Apterous. Paraproct without trichobothria. Males unknown. Subgenital plate (fig. 4.646) with triangular posterior lobe, apex of lobe with group of setae. Gonapophyses complete (fig. 4.647); ventral valve broad, truncate, with small median apical extension; dorsal valve broad, almost rectangular, with apical process; external valve long, ovoid, setose. Eggs laid singly or in loose groups, smooth, covered with encrustation and silken threads.

Habitat: On bark.

Distribution: Germany.

CHARACTERS OF THE PHILOTARSIDAE

Belonging to the Psocomorpha. Venation of the *Caecilius* type. Margin and veins of fore wings and margin of hind wings strongly setose. Branches of veins usually with more than one row of setae; some veins of hind wing setose. At apex of wings marginal setae cross each other in characteristic fashion. Tarsi 3-segmented. Claws with preapical tooth; pulvillus narrow. Subgenital plate with posterior lobe. Gonapophyses complete. Phallosome usually with sclerifications of penial bulb. Nymphs with glandular setae.

GENERA INCLUDED IN THE PHILOTARSIDAE

Philotarsus Kolbe, 1880.
Zelandopsocus Tillyard, 1923.
Aaroniella Mockford, 1951.
Haplophallus Thornton, 1959.
Austropsocus Smithers, 1962.

* *Philotarsus* Kolbe (15 species)

Philotarsus Kolbe, 1880. *J.B. Zool. Sect. westf. Ver.* 8: 116.
Type species: *Hemerobius picicornis* Fabricius.

Lacinia with apex transverse, divided into small teeth (fig. 4.648). Claws with preapical tooth; pulvillus narrow. Fore wing (fig. 4.649) without setae on Cu_2; apical marginal setae crossing. Hind wing (fig. 4.650) with R_1, R_{4+5}, M and Cu_1 setose; apical marginal setae crossing; other setae not alternately longer and shorter. Epiproct of male narrow-based, spatuliform, long-oblong. Paraproct (fig. 4.651) of male tapering, the trichobothria field distorted. Hypandrium broad-based, with small median emargination. Phallosome (fig.

4.654) apically complex, basally expanded to form a cordiform sclerite; no sclerifications of penial bulb. Subgenital plate lobe elongate (fig. 4.652), twice as long as broad, setae at apex. Gonapophyses (fig. 4.653) complete; ventral valve long and pointed; dorsal valve pointed apically, with small process; external valve oval - rectangular, setose. Eggs laid singly, encrusted with debris, each with a set of silken threads. Nymphs with glandular hairs. Brachyptery unknown.

Habitat: On bark.

Distribution: East Prussia (in amber), Argentina, Bolivia, Australia, Costa Rica, New Zealand, North America, Europe, Samoa, Falkland Islands, Malvinas Island.

Zelandopsocus (2 species)

Zelandopsocus Tillyard, 1923. Trans. N.Z. Inst. 54: 183.
Type species: Z. formosellus Tillyard.

Lacinia (fig. 4.656) with apex divided into two unequal teeth. Claw without preapical tooth; pulvillus broad. Fore wing (fig. 4.655) without setae on Cu_2; vein branches with single row of setae; apical marginal setae not crossing. Hind wing with veins glabrous; marginal apical setae not crossing but those between R_{2+3} and R_{4+5} longer than remaining marginal setae. Epiproct of male simple, broad-based, rounded behind. Paraproct of male simple; trichobothrial field normal. Hypandrium trilobed, (more strongly so than in Austropsocus). Phallosome apically simple, basal curvature normal; strong sclerifications of penial bulb. Subgenital plate (fig. 4.657) with short, median lobe with apical setae. Gonapophyses (fig. 4.658) complete; ventral valve pointed with a preapical lobe; dorsal valve triangular with strong process; external valve triangular large, strongly setose. Eggs and nymphs unknown. Brachyptery unknown.

Habitat: Leaf litter, in branch axils.

Distribution: New Zealand, South Australia.

Aaroniella Mockford (8 species)

Aaroniella Mockford, 1951. Psyche 58: 102.
Type species: Elipsocus maculosus Aaron.

Lacinia (fig. 4.659) with apex bearing a small tooth, remainder of apex divided into small teeth. Claw with preapical tooth; pulvillus undescribed. Fore wing (fig. 4.660) without setae on Cu_2; apical marginal setae crossing. Hind wing (fig. 4.661) with R_1, Rs, R_{2+3}, R_{4+5} setose, Cu_1 glabrous; apical marginal setae crossing; other setae not alternately longer and shorter. Epiproct of male more or less triangular. Paraproct of male normal, trichobothrial field not distorted. Hypandrium narrowing at base, emarginate. Phallosome (fig. 4.662) apically simple; basal curvature normal; some penial bulb sclerifications. Subgenital plate lobe broad, shorter than basal width, tapering with a separated sclerite at the apex. Gonapophyses (fig. 4.663) complete; ventral valve pointed; dorsal valve broad, subrectangular, with process reduced to a small, rugose, raised area; external valve triangular, setose. Eggs undescribed. Nymphs with glandular hairs. Brachyptery unknown.

Habitat: Foliage and lichen covered twigs.

Distribution: Eastern Europe, North America, Hong

Kong, Madagascar, Samoa.

Haplophallus Thornton (5 species)

Haplophallus Thornton, 1959. Trans. R. ent. Soc. Lond. 111: 336.

Type species: H. orientalis Thornton.

Lacinia with apex truncate with small teeth. Claw with preapical tooth; pulvillus narrow, slightly expanded apically. Fore wing (fig. 4.664) with or without setae on Cu_2; apical marginal setae crossing. Hind wing (fig. 4.665) with setae on R_1, R_{4+5}, M and Cu_1; apical marginal setae crossing; other setae not alternately longer and shorter. Epiproct of male broad-based, oblong. Paraproct (fig. 4.666) of male normal, trichobothrial field normal. Hypandrium (fig. 4.667) broad-based, emarginate. Phallosome (fig. 4.668) apically simple, basal curvature normal; penial bulb without sclerifications. Subgenital plate lobe strip-like (fig. 4.669) more than twice as long as broad, with apical setae. Gonapophyses (fig. 4.670) complete; ventral valve long and pointed; dorsal valve rectangular with small apical process; external valves oval, setose. Eggs undescribed. Nymphs with glandular hairs. Brachyptery unknown.

Habitat: On bark of trees and shrubs.

Distribution: Tanganyika, Seychelles, New Zealand, Tasmania, Hong Kong.

Austropsocus Smithers (1 species)

Austropsocus Smithers, 1962. Pacific Ins. 4: 930.

Type species: A. insularis Smithers.

Lacinia (fig. 4.671) with apex bearing a small tooth, remainder of apex divided into small teeth. Claw (fig. 4.672) without preapical tooth; pulvillus broad. Fore wings (fig. 4.673) reduced to small, ovoid, well chitinized rudiments, strongly setose. Venation not discernible. Hind wings absent. Epiproct of male simple. Paraproct of male simple, rounded behind without distinct trichobothrial field. Hypandrium simple with small indentations of the posterior margin giving a lobed appearance. Phallosome (figs. 4.674, 4.675) apically simple, basal curvature normal, penial bulb with slight sclerotizations. Subgenital plate with posterior median lobe, lobe rectangular, with two posterior setae. Gonapophyses (fig. 4.676) complete; ventral valve long and pointed, with preapical lobe; dorsal valve triangular with strong process; external valve large, rectangular and strongly setose. Eggs unknown. Nymphs without glandular hairs.

<u>Habitat</u>: In dead leaves and leaf litter.

<u>Distribution</u>: Campbell Island, Macquarie Island, New Zealand.

CHARACTERS OF THE MESOPSOCIDAE

Belonging to the Psocomorpha. Venation of the Caecilius type, but with Rs - M relationship variable. Tarsi 3-segmented. Veins and wing margins completely glabrous; aptery common. Gonapophyses complete; dorsal valve with apical or preapical process; subgenital plate with a strong median lobe. Hypandrium simple. Phallosome without complex sclerotizations of penial bulb. External parameres dilated before apex. Eggs laid in groups, smooth, encrusted with debris, covered with silk.

GENERA INCLUDED IN THE MESOPSOCIDAE

Mesopsocus Kolbe, 1880.
Hexacyrtoma Enderlein, 1908.
Labocoria Enderlein, 1910.

Mesopsocus Kolbe (20 species)

Mesopsocus Kolbe, 1880. J.B. Zool. Sect. westf. Ver. 1880: 112.

Type species: Psocus unipunctatus Muller.

Lacinia with apex truncate, divided. Pulvillus fine. Claws with preapical tooth. Fore wing (fig. 4.677) with Rs and M fused, meeting in a point or joined by a vein. Veins and wing margin glabrous. Epiproct with rounded hind margin. Paraproct with well-developed trichobothrial field in winged forms, reduced in apterous forms. Hypandrium simple. Phallosome (fig. 4.678) curved anteriorly; internal parameres fused into simple arch; external parameres dilated before apex; penial bulb with simple rugose sclerifications. Subgenital plate (fig. 4.679) with median lobe. Gonapophyses (fig. 4.680) complete; ventral valve pointed, dilated before apex; external valve broad, almost rectangular with apical or subapical process; external valve variously shaped, usually ovoid, setose. Eggs laid in groups, smooth, covered with an encrustation, and with silken threads. Nymphs without glandular hairs.

Polymorphism: Both sexes winged, or males winged and females apterous.

Habitat: Bark dwellers.

Distribution: Bolivia, Europe, East Africa, Morocco, Tunis, South Africa, Hong Kong, S. Rhodesia, North America, Iceland.

Labocoria Enderlein (1 species)

Labocoria Enderlein, 1910. S.B. Ges. naturf. Freunde 1910: 71.
Type species: Mesopsocus diopsis Enderlein.

Characters as in Mesopsocus but eyes on lateral extensions of the head. Both sexes winged.

Distribution: East Africa.

Hexacyrtoma Enderlein (1 species)

Hexacyrtoma Enderlein, 1908. Jena Denkschr. Med. Ges. 13: 349.
Type species: H. capensis Enderlein.

Lacinia undescribed. Claws with preapical tooth, pulvillus fine. Ocelli absent. Apterous (female only known). Abdomen with protuberances on segments 1 to 6. Epiproct undescribed. Paraproct without trichobothria. Gonapophyses (fig. 4.681) complete; ventral valve pointed, not dilated before apex; dorsal valve broad, rounded at tip, with strong preapical process; external valve ovoid. Eggs not known. Nymph without glandular hairs. Males unknown; females apterous.

Distribution: Southwest Africa.

CHARACTERS OF THE GROUP PSOCETAE

Labial palps short and appressed, somewhat semicircular. Lacinia equally broad or slightly narrowing in distal third usually with few large teeth. Gonapophyses of female usually complete, but of various forms; external valve setose. Labrum on inner side with at most a small tubercle on either side. Mandible with outer margin smoothly curved. Head short, transverse. Genae short. Claws curved, with preapical tooth. Cu_{1a} fused with M for a length. Ocelli grouped. Eggs smooth, grouped, encrusted.

CHARACTERS OF THE PSOCIDAE

Belonging to the Psocomorpha. Lacinia with a few apical teeth. Antennae of variable length, 13-segmented. Fore wings glabrous. Basal Sc usually present. Areola postica joined to M in a point or for a length, occasionally by a short cross vein. Rs and M with variable relationship. In hind wing Rs and M fused for a length. Glabrous except for a few short hairs on margin between R_{2+3} and R_{4+5}. Claws with or without preapical tooth. Paraproct of males with strong, curved, pointed processes. Hypandrium asymmetrical or not, usually and variously ornamented with teeth, apophyses, hooks, spines, grooves, ridges or tubercles. Phallosome closed anteriorly without apically free parameres or reduced to separate, anteriorly and posteriorly detailed sclerites. Subgenital plate usually with a median posterior lobe which bears marginal setae. Gonapophyses complete. Ventral valve pointed; dorsal valve broader, fleshy, apically pointed or not; external valve large, strongly setose, frequently strongly transverse. Spermathecal opening with sclerifications. Eggs laid singly or in groups, covered with an encrustation, exceptionally also with silk.

Habitat: On bark and rocks.

GENERA INCLUDED IN THE PSOCIDAE

Amphigerontiinae:

Amphigerontia Kolbe, 1880.
Blaste Kolbe, 1883
Neopsocopsis Badonnel, 1936.
Elaphopsocus Roesler, 1940
Blastopsocidus Badonnel, 1955
Neoblaste Thornton, 1960.

Antipsocinae:

Antipsocus Roesler, 1940.

Cerastipsocinae:

Cerastipsocini:

Eremopsocus McLachlan, 1866

Cerastipsocus Kolbe, 1884

Psococerastis Pearman, 1932

Scaphopsocus Smithers, 1960

Metylophorini:

Diplacanthoda Enderlein, 1909

Brachinodiscus Enderlein, 1925

Metylophorus Pearman, 1932

Pilipsocus Badonnel, 1935

Cycetini:

Cycetes Enderlein, 1907

Psocinae:

Psocus Latreille, 1794

Neopsocus Kolbe, 1882

Copostigma Enderlein, 1903

Ptycta Enderlein, 1925

Trichadenotecnum Enderlein, 1909

Steleops Enderlein, 1910

Psocidus Pearman, 1934

Oreopsocus Roesler, 1939

Pearmania Badonnel, 1946

Atlantopsocus Badonnel, 1944

Ghesquierella Badonnel, 1949

Hyalopsocus Roesler, 1954

Camelopsocus Mockford, 1965

Subfamily AMPHIGERONTIINAE

Amphigerontia Kolbe (29 species)

Amphigerontia Kolbe, 1880. J.B. Sect. westf. Ver. 8: 104.
Type species: Psocus bifasciatus Latreille.

Fore wing (fig. 4.682) with Rs and M joined by a well developed crossvein. Discoidal cell narrow, sides nearly parallel but a little convergent towards distal end. Apex of areola postica longer than the first free section of Cu_{1a}. Hind wing with a few marginal setae between R_{2+3} and R_{4+5}. Eighth sternite of male strongly sclerotized forming a close association with hypandrium. Hypandrium (fig. 4.683) symmetrical with apex trilobed, the lobes not armed with spines or tubercles. Parameres (fig. 4.684) separate, enlarged posteriorly into a bifurcated plate. Parameres alone remain of the phallosome. Subgenital plate (fig. 4.685) with a short median posterior lobe, pigmented in the form of a rough T. Gonapophyses (fig. 4.686) with ventral valve with a preapical dilatation and terminated by a strong point. Dorsal valves fleshy, lobe-like, with a terminal point. External valves bilobed, transverse, curving around in a short lobe applied to the dorsal valve. Sclerifications present at the entrance to the spermatheca (fig. 4.687). Eggs laid in masses, covered with an encrustation.

Distribution: Peru, Argentina, Bolivia, Paraguay, Colombia, China, Burma, Chile, Costa Rica, East Africa, Europe, North America, Canary Islands, Fiji, Queensland, Japan, Formosa, Java, Tonkin.

(Note: Some of the species at present included in this genus are probably misplaced. It seems likely that Amphigerontia is a genus with Holarctic distribution).

Blaste Kolbe (35 species)

Blaste Kolbe, 1883. Stettin. ent. Ztg. 44: 79.
Type species: Blaste juvenilis Kolbe.

Fore wing (fig. 4.688) with distal section of Cu_{1a} more or less at right angles to M and to wing margin. Cu_{1b} and the first and second sections of Cu_{1a} subequal, with a distinct angle between the sections of Cu_{1a}. Relations between Rs and M variable. Hypandrium and eighth sternite strongly sclerotized. Hypandrium (figs. 4.689, 4.690) terminated by bilobed structure, the lobes of which may be variously complex. Parameres (figs. 4.691, 4.692) proximally with a membranous connection, free posteriorly, terminated by one or two pointed hooks. Subgenital plate (figs. 4.693, 4.694) with an apical median lobe, with pigmentation generally in the form of a V. Gonapophyses (fig. 4.695) with dorsal valves terminating in a long point with barbules. Ventral valve long and pointed. External valve with well developed posterior lobe. Entrance to spermatheca with sclerification. Eggs laid in groups, covered with an encrustation.

Distribution: Angola, Madagascar, Morocco, Java, India, Europe, Malaya, North America, Australia, Colombia, Ceylon, Japan, Cameroons, Congo, Southern Rhodesia, South Africa.

Neopsocopsis Badonnel (2 species)

Neopsocopsis Badonnel, 1936. Bull. Soc. zool. Fr. 60: 419.
Type species: N. pyrenaicus Badonnel.

Sexually dimorphic; males macropterous, females micropterous. Cephalic glandular setae persisting in adults. Fore wing (fig. 4.696) of male with pterostigma broadly rounded behind, without a clearly angular region. Discoidal cell broad. Areola postica relatively well developed with distal section of Cu_{1a} meeting hind margin at an angle. Hypandrium and eighth sternite well sclerotized. Hypandrium (fig. 4.697) symmetrical with a trilobed apex, the median lobe flanked by a pair of apophyses. Lateral lobes armed with tubercles. Parameres (fig. 4.698) connected anteriorly by membrane, free posteriorly. Gonapophyses (fig. 4.699) with ventral valves with preapical dilatation and pointed apically. Dorsal valves broad terminated by a short process. External valves prolonged by a lobe. Female fore wing (fig. 4.700). Subgenital plate (fig. 4.701) with small median posterior lobe.

Distribution: Europe.

Elaphopsocus Roesler (1 species)

Elaphopsocus Roesler, 1940. Arb. morph. taxon. Ent. 7: 236.
Type species: E. glaphyrostigma Roesler.

Eighth sternite sclerotized and forming one structure with hypandrium. Fore wing (fig. 4.702) with pterostigma with strongly formed rounded apex. Rs and M joined by a short crossvein. Areola postica connected to M by a crossvein. First section of Cu_{1a} slightly curved. Hypandrium simple, without any processes, apophyses or tubercles. Parameres (fig. 4.703). Females unknown.

Distribution: Brazil.

Blastopsocidus Badonnel (9 species)

Blastopsocidus Badonnel, 1967. Faune de Madagascar 23: 212.
Type species: Blaste maculatus Badonnel.

Similar to Blaste but with hypandrium (figs. 4.704, 4.705) with lateral apophyses prolonged by two internal toothed claspers crossing each other medially. Parameres (figs. 4.706, 4.707) united proximally at a chitinous point or by a membrane, narrow, terminating distally in a feeble tooth. Subgenital plate (fig. 4.708) usually with a short lobe with a Y-shaped pigmented area, the arms being wide and open. Sclerification of spermathecal opening usually with a posterior point. First and second sections of Cu_{1a} usually more or less in a straight line (variable feature) (figs. 4.709, 4.710). Gonapophyses (figs. 4.711, 4.712) with ventral valve long, sometimes a small preapical lobe present. Dorsal valve long, broad, usually with a longitudinal sclerotized supporting rod; end bluntly rounded, spinulate. External valve with strong lobe.

Distribution: Madagascar, Angola.

Neoblaste Thornton (2 species)

Neoblaste Thornton, 1960. Trans. R. ent. Soc. Lond. 112: 239.
Type species: N. papillosus Thornton.

Male hypandrium (fig. 4.713) symmetrical, with bluntly rounded lateral lobes, two pairs of accessory sclerites, one median accessory sclerite. Eighth sternite sclerotized. Parameres (fig. 4.714) strong, symmetrical, free, with apical hooks. Venation of fore wing (fig. 4.715) as in Blaste with Rs and M fused for a length and areola postica with second section of Cu_{1a} as long as or longer than first section and at an angle to it. Subgenital plate (fig. 4.716) with median lobe and pigmentation in form of a wide V. Gonapophyses (fig. 4.717) with ventral valve narrowing sharply to an elongate pointed end. Dorsal valve broad, with spinulate apophysis. External valve with strong lobe. Entrance to spermatheca with sclerification (fig. 4.718).

Distribution: Hong Kong.

Subfamily ANTIPSOCINAE

Antipsocus Roesler (1 species)

Antipsocus Roesler, 1940. Arb. morph. taxon. Ent. 7: 241.
Type species: A. radiolosus Roesler.

Antennae shorter than fore wings, strongly setose. Claws strongly curved, without preapical tooth. Fore wing short and broad. Pterostigma very short and broad, basad of the apex strongly convex. Apex rounded, R_1 meeting margin in a right angle. Rs and M fused for a length. Rs and M separating at an angle of 175^{o}. Rs strongly sinuous. Apex of pterostigma approaching R_{2+3} and M_1 approaching R_{4+5}. Areola postica tall with very broad apex. First and second sections of Cu_{1a} almost straight in line. Third section of Cu_{1a} at a sharp angle to M. Margin and veins (except Cu_2) with a single row of fine hairs. Hind wing with Rs and M fused for a length. R_{2+3} at right angles to wing margin. Margin with sparse setae only between R_{2+3} and R_{4+5}.

Distribution: Costa Rica.

Subfamily CERASTIPSOCINAE

Tribe CERASTIPSOCINI

Eremopsocus McLachlan (7 species)

Eremopsocus McLachlan, 1866. Trans. Ent. Soc. (3) 5: 347.
Type species: E. infumatus McLachlan.

Antennae much longer than wings. Flagellum thickened in at least the first segment but more slender distally. Fore wings (fig. 4.719) with arms of radial fork close together but diverging distally. Discoidal cell large. Areola postica with pointed apex, joined to M by a short vein. Veins without setae, in the distal half of the wing with broad, pale interruptions. R_{2+3} and R_{4+5} separating at an angle greater than a right angle. In hind wing (fig. 4.720) Rs and M meet in a point. Fourth segment of maxillary palp short and relatively broad. Subgenital plate (fig. 4.721) of female with apical lobe, pigment T-shaped. Gonapophyses with ventral valve pointed, spiculate at apex. Dorsal valve broad, fleshy, with a terminal papilla. External valve with lobe. Hypandrium (fig. 4.723) with two small apical teeth and one at each side; a rugose median flap present. Phallosome (fig. 4.722) simple, ring-like, with a posterior median projection. Nymphs cluster in groups.

Distribution: Borneo, Philippines, Sarawak, Malaya, Mexico, Venezuela, Brazil, Costa Rica, Colombia.

Cerastipsocus Kolbe (16 species)

Cerastipsocus Kolbe, 1884. Berl. ent. Z. 28: 38.
Type species: Psocus venosus Burmeister.

Antennae much longer than fore wings. Fore wing (fig. 4.724). Venation similar to Eremopsocus but with Rs and M fused for a longer length and the apex of the areola postica fused with M. No pale interruptions of veins. R_{2+3} and R_{4+5} diverging at a right angle or a greater angle. Hypandrium (fig. 4.725) with a median bifid lobe, strongly sclerotized, flanked by two sclerified, toothed processes. Phallosome (fig. 4.726) closed, subtriangular, with membranous apex and with sclerification of the penial bulb. Gonapophyses similar to those of Psococerastis.

Distribution: Colombia, Brazil, Argentina, Cuba, New Granada, Peru, Costa Rica, North America, Malaya, India, Sumatra, Java.

Psococerastis Pearman (15 species)

Psococerastis Pearman, 1932. Ent. mon. Mag. 68: 202.
Type species: Cerastipsocus gibbosus (Sulzer).

Antennae much longer than fore wings. Fourth segment of maxillary palp short and thick. Fore wings (fig. 4.727) with pterostigma elongate the posterior angle not very pronounced. Rs and M fused for a length, sometimes meeting in a point. R_{2+3} and R_{4+5} diverging at an acute angle of about 60^{o}. Apex of areola postica shorter than the first section of Cu_{1a} but never with Cu_{1a} meeting M in a point. Discoidal cell subrectangular. Subgenital plate (fig. 4.728) with a short median lobe, pigmentation in form of a T. Gonapophyses (fig. 4.729) with pointed ventral valve. Dorsal valve long, broad, with at most a short bluntly pointed apex. External valve strongly lobed. Hypandrium (figs. 4.729, 4.730) ornamented with strong hooks and processes, asymmetrical. Phallosome (fig. 4.731) simple, somewhat triangular, or simply ring-like, closed anteriorly with a posterior median process. Spermathecal opening with sclerification (fig. 4.732). Nymphs without knobbed glandular setae. Not living in groups.

Distribution: East Africa, Congo, South Africa, Sierra Leone, Mozambique, Angola, India, Malaya, Ceylon, Philippines, Java, Sumatra, Sarawak, Burma, Borneo, Hong Kong, Formosa, Japan, Canary Islands, Europe, China, Northern Asia, Brazil.

Scaphopsocus Smithers (2 species)

Scaphopsocus Smithers, 1960. Ann. Mus. Congo 88: 373.
Type species: S. phaeotherus Smithers.

Antennae long. Fore wing (fig. 4.733). Apex of pterostigma strongly angled. Rs and M confluent for a short length. Radial fork narrow near bifurcation but the arms diverging distally. Cu_{1a} meeting M in a point or fused with M for a short length. Angle of divergence of arms of radial fork about 90^o. Veins with pale interruptions at forking of Rs, apex of areola postica and origin of Cu_{1a}. Fourth segment of maxillary palp short and broad. Subgenital plate (fig. 4.734) with a short median lobe. Gonapophyses (fig. 4.735) with long, pointed ventral valve. Dorsal valve long, broad, fleshy, with rounded apex. External valve large, long-oval, transverse, not lobed. Spermathecal opening with sclerification (fig. 4.736). Hypandrium (fig. 4.737) simple, sclerotized, curving upwards posteriorly and laterally to form a bowl in which lies the phallosome. Phallosome acuminate proximally, broad distally with narrower transverse posterior border to phallic frame.

Distribution: Tanganyika, Formosa, Japan.

Tribe METYLOPHORINI

Metylophorus Pearman (6 species)

Metylophorus Pearman, 1932. Ent. mon. Mag. 68: 202.
Type species: Psocus nebulosus Stephens.

Antennae longer than fore wings. Fourth segment of maxillary palp elongate. Fore wing (fig. 4.739) with pterostigma with distinct, rounded apex. Basal Sc ending free in membrane. Rs and M fused for a short length or meeting in a point, even occasionally joined by a short cross-vein. Apex of areola postica short. Discoidal cell sub-rectangular. Veins pale at radial forking and at distal end of discoidal cell. Hypandrium (fig. 4.740) with asymmetrical apophyses. Phallosome (fig. 4.741) symmetrical, simple, elongate with phallic frame thin. Subgenital plate (fig. 4.742) with long posterior lobe. Gonopophyses (fig. 4.743) with dorsal and ventral valves long; ventral valve pointed, dorsal valve broad, fleshy, with rounded apex. External valve long, transverse, not lobed. Spermatheoal opening with sclerification (fig. 4.744).

Distribution: Angola, Europe, Japan, China, India, North America, Brazil, Bolivia, Fiji.

Brachinodiscus Enderlein (1 species)

Brachinodiscus Enderlein, 1925. Konowia 4: 103.

Type species: Amphigerontia cinctipes Enderlein.

Enderlein (1925): "Dieses Genus unterscheidet sich von Copostigma. Der 2. Medianabschnitt an der Discoidalzelle so lang wie der 1. Aschnitt von cu_1. Fuhlergeissel des ♂ mit auffallig langer struppig abstehander Pubescenz. Die Radiomedianquerader lang, Synonym zu B. cinctipes ist Psocus lepidus Banks 1920 aus Brasilien".

Distribution: Peru, Paraguay, Brazil.

Note: It has not been possible to increase our knowledge of this genus. Roesler (1944) places it in his Metylophorini, implying that the antennae are long and that the female dorsal valve is rounded at the end. The fourth maxillary palp is presumably long. With such features it cannot be associated with Copostigma. Its position cannot be determined at present. The illustration of a fore wing available (Banks, 1920) strongly suggests that it may be synonymous with Amphigerontia in which the type species was originally placed by Enderlein (1900b).

Diplacanthoda Enderlein (1 species)

Diplacanthoda Enderlein, 1910. Bull. Mus. Paris 15: 488.
Type species: D. bouvieri Enderlein.

Antennae longer than wings, with few setae except on first flagellar segment. Claw with a strong preapical tooth. Coxal organ with an exceptionally large tympanum. Mesothorax and metathorax each with a large dorsal spine. Fore wing (fig. 4.745) with narrowly rounded apex. Pterostigma low and narrow. Rs and M joined by a crossvein. Angle between arms of radial fork small. M_1 after separating from Rs-M crossvein, runs posteriorly across wing to apex of areola postica. Fusion of M with Cu_{1a} very short. Areola postica very tall with narrow apex, Cu_{1a} after apex running straight and obliquely to wing margin. Veins with longer hairs in basal part of wing, shorter hairs in distal parts. Margin glabrous. Hypandrium (fig. 4.746) curving dorsally, strongly sclerified, the margin with small teeth and with an area of conical tubercles at the apex. Phallosome (fig. 4.747) triangular with pointed posterior end to the aedeagus. Parameres membranous. Subgenital plate (fig. 4.748) with subrectangular posterior lobe. Gonopophyses (fig. 4.749) with long dorsal and ventral valves. Ventral valve pointed. Dorsal valve broad with apical spinules. External valve trapezoidal, short. Entrance to spermatheca with simple sclerification (fig. 4.750).

Distribution: Madagascar.

Pilipsocus Badonnel (7 species)

Pilipsocus Badonnel, 1935. Rev. franc. Ent. 2: 77.
Type species: Psocus intricatus Enderlein.

Antennae very long and fine. Fore wing (fig. 4.751) similar to Metylophorus but with apex of areola postica longer and margin sometimes incurved between branches of M. R_{4+5} curving strongly at its origin. Hypandrium (fig. 4.752) asymmetrical, ornamented with chitinous tubercles and ridges. Phallosome (fig. 4.753) symmetrical, narrowing posteriorly. Subgenital plate (fig. 4.754) with small posterior lobe. Gonapophyses (fig. 4.755) with ventral valve short, pointed, apically with small spinules. Dorsal valve short, broad, rounded posteriorly, the distal part heavily clothed in spinules. External valve oval, with lobe.

Distribution: Angola, Congo, East Africa, Cameroons, French Guinea.

Tribe CYCETINI

Cycetes (1 species)

Cycetes Enderlein, 1907. Notes Leiden Mus. 29: 108.
Type species: C. thyrsophoroides Enderlein.

Antennae long. Fore wing (fig. 4.756) with basal Sc ending in costa. Pterostigma with normal apex. Rs and M meeting in a point; Rs stem curved, the branches parting at a wide angle, R_{4+5} touching M and then running toward wing margin in sinuous fashion. M_1 reaching margin at wing apex. Areola postica tall; Cu_{1a} fused with M for a length. In hind wing basal Sc ends in costa. Rs and M fused for a length. Subgenital plate (fig. 4.757) with short apical lobe and three large colourless areas which are not setose as the rest of the plate. Gonopophyses (fig. 4.758) with ventral valve long, pointed, with apical spinules. Dorsal valve broad, fleshy. External valve with a small postero-dorsal apophysis and a long setose antero-ventral prolongation.

Distribution: Java.

Subfamily PSOCINAE

Psocus Latreille (19 species)

Psocus Latreille, 1794. Bull. Soc. philom. Paris 1: 85.
Type species: Hemerobius bipunctatus Linnaeus.

Antennae only little longer than fore wings, strong in males, setose. Fourth segment of maxillary palp elongate. Fore wing (fig. 4.759) with pterostigma having a well rounded apex. Basal Sc ending in R. Rs and M fused for a length or meeting in a point. Rs straight, arms of fork of Rs diverging. Discoidal cell subrectangular. Areola postica tall, with second section of Cu_{1a} shorter than first section. Hypandrium (fig. 4.760) conical with asymmetrical apophyses. Phallosome (fig. 4.761) elongate, rounded anteriorly, the apex produced into an asymmetrical lobe. Subgenital plate (fig. 4.762) with elongate, slightly tapering posterior lobe. Gonapophyses (fig. 4.763) with ventral valve with preapical dilatation, terminating in a smooth point. Dorsal valve in the form of a fleshy lobe terminating in a short rigid point with spinules on the ventral end of the lobe and on the point. External valve somewhat variable, but tending to be oval to almost circular with a small lobe. Eggs covered with an encrustation and silk.

Distribution: Philippines, Jamaica, Santo Domingo, Europe, Argentina, Morocco, Japan, Formosa, Algeria, North America.

Note: Pearman (1932a) redefined the genus Psocus and restricted its members to species closely resembling the type species. The great number of species thus excluded he later (1934b) placed in a "holding" genus, Psocidus. It is assumed here that species described after the appearance of Pearman's paper are assigned correctly to this restricted genus, although it is likely that several of these later described species do not fall within the limits of the redefinition. The distribution given is based on the assumption of correct placement (see also note under Psocidus).

Neopsocus Kolbe (1 species)

Neopsocus Kolbe, 1882. Ent. Nachr. 8: 207.
Type species: N. rhenanus Kolbe.

Strongly sexually dimorphic, the males macropterous, females micropterous. Glandular setae persisting in adults (fig. 4.764). Antennae only a little longer than fore wings. Fourth segment of maxillary palp elongate. Fore wing (fig. 4.765) with basal Sc ending free. Pterostigma with clearly angled apex; usually with a rudiment of a spurvein. Rs and M fused for a length. Areola postica with first section of Cu_{1a} longer than second; second section fused with M or meeting it in a point or joined to M by a short crossvein. Hypandrium (fig. 4.766) symmetrical, with postero-lateral points and a median lobe. Phallosome (fig. 4.767) simple, sub-triangular, with small posterior median extension. Gonapophyses (fig. 4.768) with short, broad, posterior lobe; pigmentation in form of a stout T with arms expanded. Gonapophyses (fig. 4.769) with ventral valve pointed. Dorsal valve broad, fleshy, tapering to rounded point. External valve with large lobe. Fore wing of female (fig. 4.770).

Distribution: Europe.

Copostigma Enderlein (17 species)

Copostigma Enderlein, 1903. Ann. Mus. hist. -nat. hung. 1: 229.
Type species: C. dorsopunctatum Enderlein.
(see under Ptycta Enderlein).

Ptycta Enderlein (19 species)

Ptycta Enderlein, 1925. Konowia 4: 102.
Type species: Psocus haleakalae Perkins.

Fore wing (fig. 4.771) similar to Psocus but with a spurvein at the apex of the pterostigma and with second section of Cu_{1a} longer than the first. Subgenital plate (figs. 4.772, 4.773) with a broad posterior lobe. Gonapophyses (fig. 4.774) with preapical dilatation on ventral valve, pointed beyond. Dorsal valve broad, with short point. External valve with small lobe. Hypandrium symmetrical (fig. 4.775) with a strong median curved sclerotized band. Phallosome (fig. 4.776) simple with extended posterior end and a lateral apophysis on each side about half way along.

Distribution: Ptycta: Hawaii, Java, Japan, Hong Kong, Krakatau, Seychelles, Madagascar, Cape Verde Islands, Angola.

Copostigma: Australia, New Guinea, Samoa, Chile, Haiti, Santo Domingo, Paraguay, Argentina, Japan, Formosa, India, Ceylon, Europe, Tunis.

Note: The genera Copostigma and Ptycta appear to form a complex, together with the groups previously referred to as Clematostigma and Maheella (Badonnel 1967, p. 193). Numerous species of Ptycta from Hawaii are under study by Professor I.W.B. Thornton, the group having had an explosive evolution on the Hawaiian Islands. Until these studies are completed there is little purpose served by a detailed study of other available material and for the present the Copostigma - Ptycta - Maheella - Clematostigma complex can be dealt with as a unit.

* Trichadenotecnum Enderlein (37 species)

Trichadenotecnum Enderlein, 1909. Boll. Lab. zool. Portici 3: 329.

Type species: Hemerobius sexpunctatus Linnaeus

Antennae not much longer than fore wings. Fourth segment of maxillary palp elongate. Fore wings (fig. 4.777) usually strongly patterned. Venation as in Psocus but with first and second sections of Cu_{1a} without an angle between them, continuing in a straight line. The distal section of Cu_{1a} is somewhat recurved on separating from M so that the areola postica comes to have a characteristic, almost triangular shape. Hypandrium (fig. 4.778) asymmetrical, sometimes with complex hooks, apophyses, tubercles or similar adventitious structures. Phallosome (fig. 4.779) simple, variable, sometimes with wing like expansions near posterior end. Subgenital plate (fig. 4.780) with a short broad posterior median lobe. Gonapophyses (fig. 4.781).

Distribution: North America, Europe, East Prussia (in amber), Angola, South Africa, Madagascar, Hong Kong, Ceylon, Java, Formosa, Japan, Chile, Brazil, Australia.

Steleops Enderlein (2 species)

Steleops Enderlein, 1910. S.B. Ges. naturf. Fr. Berlin 1910: 64.

Type species: S. punctipennis Enderlein.

Antennae a little longer than fore wings. Eyes on dorso-lateral extensions of the head capsule. Fore wing (fig. 4.782) without basal Sc. R_1 regularly rounded to give a pterostigma which is smoothly rounded behind. Rs and M joined by a crossvein or fused for a short length. Arms of radial fork diverging at a very small angle, each area curving smoothly towards the margin in the same direction but slightly divergent. R_{4+5} reaching margin near wing apex but R_{2+3} reaching margin nearer pterostigma. First and second sections of Cu_{1a} about equal in length. Third section running towards wing margin obliquely and meeting margin at an angle. In hind wing Rs and M fused for a length. Genitalic features unknown.

Distribution: Paraguay, Brazil.

* *Psocidus* Pearman (121 species)

Psocidus Pearman, 1934. *Stylops* 3: 122.

Type species: *Psocus zanzibarensis* Pearman.

This genus cannot be defined.

Note: Pearman (1932a) redefined the genus *Psocus* Latreille in a narrow sense. For many years species with diverse characters falling within the family Psocidae had been assigned to *Psocus*. It had thus become a genus without any limitations. Owing to Pearman's redefinition a very large number of species were excluded from *Psocus* and Pearman (1934b) established the genus *Psocidus* for these with the intention that it become a "holding" genus. The included species, on further study, could be transferred to recognizable and definable genera. At present there are about one hundred and twenty species in this genus, including a few species from amber. Owing to the heterogeneous nature of the content of

this

this genus it is of little value to discuss it at present. All that can safely be done is to leave it as a "holding" genus and include it in the family Psocidae without attempting to discuss the relationships of its members or their classification until such time as they can be adequately restudied (see also note under Psocus).

Oreopsocus Roesler (1 species)

Oreopsocus Roesler, 1939. Zool. Anz. 125: 165.
Type species: Psocus montanus Kolbe.

Antennae not much longer than fore wing. Fore wing (fig. 4.783) with pterostigma smoothly rounded behind. Rs and M meeting in a point. Areola postica as in Trichadenotecnum, almost triangular. Hypandrium (fig. 4.784) almost symmetrical. Phallosome (fig. 4.785) prolonged apically by a small apophysis. Subgenital plate (fig. 4.786) with a small median lobe. Gonapophyses (fig. 4.787). Ventral valves pointed with some apical spinules. Dorsal valve broad, fleshy, terminating in a spinulate point and bearing some spinules postero-ventrally on the lobe. External valve with lobe, reduced somewhat in comparison with other valves.

Distribution: Europe.

Pearmania Badonnel (7 species)

Pearmania Badonnel, 1946. Rev. Zool. Bot. afr. 39: 192.
Type species: Psocus usambaranus Badonnel.

Fore wing (fig. 4.788) with basal Sc ending in R. Pterostigma long, with rounded angle at apex. Second section of Cu_{1a} long, third section slightly curved. Hypandrium (fig. 4.789) symmetrical with a median longitudinal basally broadening band flanked by depressions. Terminal ornamentation in the form of spines, granules or papillae. The depressions sometimes papillate. Phallosome (figs. 4.790, 4.791) simple, with some aedeagal sclerification, of varying shape. Subgenital plate (fig. 4.792) with a long median posterior lobe with apical setae. Gonapophyses (fig. 4.793) with ventral valves continuously narrowing to point. Dorsal valves fleshy, broad, bearing chitinous papillae on the internal surface. External lobes very well developed, transverse, with a large lobe. Spermathecal entrance with an annular sclerite (fig. 4.794).

Distribution: Congo, South Africa, East Africa, Angola, Mozambique, Rhodesia.

Atlantopsocus Badonnel (4 species)

Atlantopsocus Badonnel, 1944. Rev. franc. Ent. 11: 48.
Type species: A. chopardi Badonnel.

Fore wing (fig. 4.795) with pterostigma smoothly curved behind. Basal Sc ending free in membrane. Rs and M meeting in a point or fused for a short length. Second section of Cu_{1a} shorter than first. Discoidal cell with subparallel sides. Hypandrium (fig. 4.796) almost symmetrical with a longitudinal band, broadest basally, the band bearing a row of denticles on either side along its length. Band flanked by depression. Phallosome (figs. 4.797, 4.798) prolonged by an apical process; open proximally. Subgenital plate (fig. 4.799) with a median lobe with strong terminal setae. Gonapophyses (fig. 4.800) with ventral valves long and pointed, apically with spinules. Dorsal valve broad, fleshy, narrowing gently to blunt point, spinulate near point and elsewhere. External valve slightly lobed, large.

Distribution: Canary Islands, Azores, Morocco, Southern Ireland.

Ghesquierella Badonnel (3 species)

Ghesquierella Badonnel, 1949. Bull. Inst. Sci. nat. Belg. 25: 61.

Type species: G. ealensis Badonnel.

Antennae longer than fore wing. Fore wing (fig. 4.801) with basal Sc ending free. Pterostigma subtriangular. Discoidal cell almost rectangular. Cu_{1b} very short so that the corner of the discoidal cell is almost at the wing margin. Hypandrium slightly asymmetrical (fig. 4.802) with a strongly sclerified basal transverse bar; a longitudinal sclerotized band, bordered with a row of teeth on each side; a median apical piece bears two lateral apophyses. Phallosome (fig. 4.803) simple, rounded proximally pointed distally; penial bulb with two terminal dilatations covered with pointed, chitinous papillae (not shown in figure 4.803). Females not known.

Distribution: East Africa, Congo, Guatemala.

Note: The Guatemala species is probably not a Ghesquierella.

Hyalopsocus Roesler (3 species)

Hyalopsocus Roesler, 1954. Beit. zur Ent. 4: 572.

Type species: Psocus contrarius Reuter.

Antenna a little shorter than fore wing. Fore wing (fig. 4.804) with basal Sc ending in R. Pterostigma fairly broad, with distinct angle at apex. Sometimes a short spur-vein present. Rs and M meeting in a point or are joined by a short crossvein. Stem of Rs fairly short. Branches of radial fork parting in a sharp angle. Areola postica long. Angle between first and second sections of Cu_{1a} slight with the second a little shorter than the first. Hypandrium (fig. 4.805) a little asymmetrical with median sclerotized band, tapering posteriorly, curving to the left; a depression on each side. Hypandrium laterally sclerotized near base. Phallosome (fig. 4.806) with a symmetrical frame, transverse posteriorly, narrowing anteriorly. Posteriorly, arise various asymmetrical processes, rugose bulbs and spines. Subgenital plate (fig. 4.807) with elongate, tapering posterior lobe. Gonapophyses (fig. 4.808) with ventral valve with preapical dilatation. Dorsal valve broad, tapering to a terminal curved point. External valve narrowly transverse with a small lobe. Spermathecal opening (fig. 4.809) with circular sclerite.

Distribution: North America, Europe.

Camelopsocus Mockford (2 species)

Camelopsocus Mockford, 1965. Folia ent. mex. 11: 3.
Type species: Camelopsocus monticolus Mockford.

Strongly sexually dimorphic. Males macropterous, females micropterous. Females with middle abdominal segments raised into a conspicuous hump; males with more normal abdomen, hump represented by a small protuberance near base of abdomen. Antennae longer than body. Subgenital plate (fig. 4.810) with short posterior lobe, rounded apically, pigmented area Y-shaped. Gonapophyses (fig. 4.811) with external valve with conspicuous lobe. Dorsal and ventral lobes terminate in long slender process. Male fore wings (fig. 4.812) with shallow pterostigma, curved smoothly behind, no clearly defined apex. Rs and M fused for a short length. Areola postica and M fused for a fairly long length. Hypandrium (fig. 4.813) with median scletotized tapering band, bending to left near apex, depressions on each side of band. Phallosome (fig. 4.814) with a long anterior median fusion of parameres; the fused length greater than the rest of the phallosome. Parameres apically fused and a little extended posteriorly; laterally a small apophysis on each side; some sclerification of penial bulb.

Distribution: Mexico, Arizona, Colorado.

CHARACTERS OF THE THYRSOPHORIDAE

Belonging to the Psocomorpha. Lacinia with a few apical teeth (an inner tooth and a broader subdivided outer tooth). Ocelli very close together on a tubercle. Antennae long, with thickened first flagellar segment. Fore wing with pterostigma broadest in basal half. R_{2+3} and R_{4+5} long. Rs and M joined by a crossvein, fused for a short length or meeting in a point. R_{4+5} also meeting it in a point or joined by a crossvein, or fused. Areola postica tall, joined to M for a length. Cu_{1a} usually straight from apex of areola postica to wing margin. Wings glabrous. Hind wing with Rs and M joined by a crossvein or fused for a length. M unbranched. Hind wings glabrous. Tarsi 2-segmented. Claws with preapical tooth. Male paraproct with strong spine-like process and a trichobothrial field. Hypandrium lobed, symmetrical, with or without chitinous projections, tubercles or papillae in various degrees of complexity. Phallosome simple, closed anteriorly and with a posterior median projection formed by fused parameres. A little sclerification of penial bulb present. Female genitalia as in Psocidae. Subgenital plate with a median posterior lobe. Gonopophyses complete. Ventral valve pointed; dorsal valve broad, fleshy, with pointed apex, sometimes whole valve longitudinally folded; external valve large, setose, transverse, wrapping around other valves and base of apical lobe of subgenital plate.

GENERA INCLUDED IN THE THYRSOPHORIDAE

<u>Thyrsophorus</u> Burmeister, 1839

<u>Thyrsopsocus</u> Enderlein, 1900

<u>Dictyopsocus</u> Enderlein, 1901

Thyrsophorus Burmeister (6 species)

Thyrsophorus Burmeister, 1839. Handbuch. Ent. 2 (2): 781.
Type species: T. speciosus Burmeister.

Antennae with first flagellar segment strongly thickened and setose. Fore legs with femur and tibia strongly broadened. Fore wing (fig. 4.815) with pterostigma long, broadest in basal third and tapering to a fine distal extremity. Basal Sc present, ending in membrane. Rs and M joined by a crossvein. Stem of radial fork short. R_{4+5} fused with M for a length between M_3 and areola postica. Areola postica fused with M. There results two closed cells, the discoidal cell and a more distal cell in the midwing. Hind wing (fig. 4.816) with Rs and M joined by a crossvein, meeting it in a point or fused for a short length. M simple.

Distribution: Brazil, Peru, Colombia.

Dictyopsocus Enderlein (1 species)

Dictyopsocus Enderlein, 1901. Zool. Jb. Abt. Syst. 14: 543.
Type species: Thyrsophorus pennuicornis Burmeister.

Characters as for Thyrsophorus but with normal fore legs, with a network of anastomosing veins in the forewing in the area bounded by Rs, basal section of M after its separation from Cu_1, Cu_1, Cu_{1a} and Rs + M, that is, the area of the discoidal and additional cell in Thyrsophorus is here covered by an anastomosing network (fig. 4.817). In hind wing Rs and M fused for a length.

Distribution: Brazil, Argentina.

Thyrsopsocus Enderlein (12 species)

Thyrsopsocus Enderlein, 1900. Zool. Jb. Abt. Syst. 14: 140.
Type species: T. peruanus Enderlein.

Fore legs normal. Fore wing as in Thyrsophorus but R_{4+5} and M are joined by a crossvein or fused for a length in Thyrsophorus. Pterostigma long and thin (as in Thyrsophorus) or short and broad (fig. 4.818). When R_{4+5} and M are fused for a length, the wing is also very long and narrow (fig. 4.819).

Distribution: Ecuador, Brazil, Honduras, Peru, Barro Colorado Island, Panama.

CHARACTERS OF THE PSILOPSOCIDAE

Belonging to the Psocomorpha. Lacinia with broad apex with several teeth. Fore wings glabrous. Pterostigma strongly broadened; R_1 before apex curved giving a strongly concave hind border to the pterostigma. Apex with a spur-vein. Rs and M meeting in a point. Areola postica large; Cu_{1b} long, Cu_{1a} curved so that the forking of Cu_1 is well basad of the point which Cu_{1b} reaches the wing margin. Hind wing with Rs and M fused for a short length. Tarsi 3-segmented, claw with preapical tooth, pulvillus broad. Male paraproct with broad, pointed, apical process. Hypandrium simple; with slightly thickened margin. Phallosome closed anteriorly and posteriorly, ring-like without apically free parameres. Subgenital plate with elongate posterior lobe bearing few strong setae, symmetrically arranged. Gonopophyses complete. Ventral valve long, pointed; dorsal valve broad, narrowing to a long pointed process; external valve broad, strongly setose. Entrance to spermatheca with sclerifications.

Nymphs of remarkable facies with posterior abdominal segments fused and sclerotized forming a hard capsular posterior section to the abdomen. Epiproct, paraprocts and anus in postero-ventral position, sclerotized; the epiprocts and paraprocts capable of closing together and sealing off the anus.

GENERA INCLUDED IN THE PSILOPSOCIDAE

Psilopsocus Enderlein, 1903

Psilopsocus Enderlein (3 species)

Psilopsocus Enderlein, 1903. Ann. hist. -nat. Mus. hung. 1: 305.
Type species: P. nigricornis Enderlein.

Characters as for family. Fore wing (fig. 4.820).

Lacinia (fig. 4.821). Subgenital plate (fig. 4.822). Gonapophyses (fig. 4.823). Sclerifications of spermathecal opening (fig. 4.824). Phallosome (fig. 4.825).

CHARACTERS OF THE MYOPSOCIDAE

Belonging to the Psocomorpha. Lacinia with a small outer tooth and a broad inner cusp divided into several teeth. Fore wings with venation as in Psocidae; without setae. Colour pattern of wings consisting of a mottling of irregularly confluent small, dark marks. In hind wing Rs and M fused for a length or joined by a cross vein. Glabrous. Strong patterning absent. Tarsi 3-segmented. Claw with preapical tooth; pulvillus broad. Male epiproct frequently armed with processes or flaps, sometimes anteriorly directed. Paraprocts with one or two pointed processes. Hypandrium strongly sclerotized, symmetrical. Phallosome anteriorly closed, closed posteriorly or not, frequently with a median longitudinal sclerotized bar. Female subgenital plate with an elongate tapering posterior lobe bearing terminal setae. Gonapophyses complete. Ventral valve fine and pointed; dorsal valve broader, terminating in a long slender pointed process; external valve broad, rounded, setose. Entrance to spermatheca with sclerifications. Eggs laid in groups, covered with an encrustation.

GENERA INCLUDED IN THE MYOPSOCIDAE

Myopsocus Hagen, 1866
Lophopterygella Enderlein, 1907
Phlotodes Enderlein, 1910.

Myopsocus Hagen (32 species)

Myopsocus Hagen, 1866. *Verh. zool. -bot. Ges. Wien* 16: 210.
Type species: *Psocus* *unduosus* Hagen.

Characters of the family; in hind wing Rs and M joined by a crossvein. Fore wing margin without incurving between branches of veins. Fore wing (fig. 4.826). Subgenital plate (fig. 4.827). Sclerification of spermathecal opening (fig. 4.828). Phallosome (fig. 4.829). Gonapophyses similar to Phlotodes.

Distribution: Australia, New Zealand, Philippines, Guam, Java, Sumatra, Ceylon, Japan, Thailand, Fiji, Argentina, Brazil, Paraguay, Hong Kong, India, North America, Santo Domingo, Congo, Cameroon, Angola, French Guinea, Sierra Leone, South Africa, Southern Rhodesia, Ivory Coast.

Note: In only a small proportion of the species described in Myopsocus and its relatives is the nature of the relationship between Rs and M in the hind wing known. The distribution records given for Phlotodes and Myopsocus can, therefore, be of only limited reliability.

Phlotodes Enderlein (25 species)

Phlotodes Enderlein, 1910. S.B. naturf. Freunde Berl. 1910: 67.
Type species: Myopsocus kolbei Enderlein.

Characters of the family but with Rs and M in hind wing fused for a length. No incurving of wing margin between branches of veins. Fore wing (fig. 4.830). Subgenital plate (fig. 4.831). Gonapophyses (fig. 4.832). Phallosome (figs. 4.833, 4.834). Hypandrium (figs. 4.835, 8.836).

Distribution: Angola, Natal, Congo, Madagascar, East Africa, Southern Rhodesia, Seychelles, Europe, New Guinea, Java, Borneo, Sarawak, Samoa, Paraguay.

Note: See under Myopsocus.

Lophopterygella (3 species)

Lophopterygella Enderlein, 1907. Notes Leiden Mus. 29: 121.
Type species: L. camelina Enderlein.

Characters as for Myopsocus but with incurving wing margin in fore wing between branches of veins.

Distribution: Haiti, Java, Tonkin, Philippines, Formosa, East Africa, Japan.

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The following genera cannot be recognized from the descriptions well enough to enable them to be placed in a family.

Allopsocus Banks (1 species)

Allopsocus Banks, 1920. Bull. Mus. comp. Zool. Harv. 64: 312.
Type species: A. marginatus Banks.

Valenzuela Navas (1 species)

Valenzuela Navas, 1924. Publ. Junta Cienc. nat. 4: 20.
Type species: V. marianus Navas.

CHAPTER V. FOSSIL PSOCOPTERA

1. OCCURRENCE OF FOSSIL PSOCOPTERA

Tillyard (1926b) made a major contribution to the study of fossil Psocoptera when studying the insects from Lower Permian deposits in Kansas; Martynov (1928) subsequently described material from Upper Permian deposits in Russia. Carpenter (1926, 1932, 1933, 1938, 1939) studied further material from the Kansas beds and Tillyard (1935) described material from Upper Permian deposits in Australia. More recently Becker-Migdisova (1953, 1962) and Becker-Migdisova and Vishnyakova (1962) have studied Lower and Upper Permian as well as Triassic material from Russia. Martynov (1926) and Handlirsch (1906) have described a little Upper Jurassic material from Russia and Germany and Scudder (1890) has described a psocid from the Eocene of Colorado.

There is a considerable amount of material from Oligocene Amber which has been studied by several workers (e.g. Enderlein, 1900a; Enderlein, 1911b; Kolbe, 1883e; Navas, 1914c; Cockerell, 1916, 1919).

As is usual with fossil insects, most of the remains of fossil Psocoptera consist of wings or wing fragments. In a few species remains of the bodies and appendages other than wings have been found. In the case of Dichentomum tinctum Tillyard, from the Lower Permian of Kansas, Carpenter (1933) has studied a very large series and has been able to provide a fairly full description of the species. Becker-Migdisova and Vishnyakova (1962) have studied very well-preserved material of D. sojanense B. -M.

Below is given a list of the genera of fossil Psocoptera, arranged in the currently accepted classification.

A reference to the generic definition is given and the type species and deposits in which the genera have been found are mentioned. Genera which include species from amber are included in the list of Recent genera already given because, as might be expected, their affinities lie with recent psocids rather than with fossil forms.

In that list those which include species from amber are marked with an asterisk (*).

Becker-Migdisova and Vishnyakova (1962) have placed the Dichentomidae, Permopsocidae and Martynopsocidae in a suborder, the Permopsocida, and have placed the Surijokopsocidae, Lophioneuridae, Zygopsocidae, Asientomidae and Archipsyllidae with all the modern families in a second suborder the Parapsocida. The general tendency, however, has been to group all the fossil families in the Permopsocida.

Of the families of the Permopsocida, the Dichentomidae are by far the best known, the Martynopsocidae and Permopsocidae being known only from wings whereas the body structure of the Dichentomidae is relatively well known. The remaining families are known only from wing characters, in most cases only the fore wings are known.

2. ARRANGEMENT OF THE GENERA OF FOSSIL PSOCOPTERA IN GENERAL USE

ORDER PSOCOPTERA

Suborder PERMOPSOCIDA

Family DICHENTOMIDAE

Austropsocidium Tillyard, 1935. Proc. Linn. Soc. N.S.W. 60: 267.
A. pincombei Tillyard. (Upper Permian - Australia).

Dichentomum Tillyard, 1926. Amer. J. Sci. 11: 320.
D. tinctum Tillyard. (Lower Permian - U.S.A.; Upper Permian - U.S.S.R.).

Megapsocidium Tillyard, 1935. Proc. Linn. Soc. N.S.W. 60: 268.
M. australe Tillyard. (Upper Permian - Australia).

Stenopsocidium Tillyard, 1935. Proc. Linn. Soc. N.S.W. 60: 270.
S. elongatum Tillyard. (Upper Permian - Australia).

Family PERMOPSOCIDAE

Lithopsocidium Carpenter, 1932. Amer. J. Sci. 24: 14.
L. permianum Carpenter. (Lower Permian - U.S.A.).

Orthopsocus Carpenter, 1932. Amer. J. Sci. 24: 15.
O. singularis Carpenter. (Lower Permian - U.S.A.).

Permopsocus Tillyard, 1926. Amer. J. Sci. 11: 339.
P. latipennis Tillyard. (Lower Permian - U.S.A.).

Progonopsocus Tillyard, 1926. Amer. J. Sci. 11: 337.
P. permianus Tillyard. (Lower Permian - U.S.A.).

Family MARTYNOPSOCIDAE

Martynopsocus Karny, 1930. Treubia 12: 446.
Dinopsocus arcuatus Martynov. (Upper Permian - U.S.S.R.).

Family SURIJOKOPSOCIDAE

Surijokopsocus Becker-Migdisova, 1961. Pal. Ins. Kuznetsk. p. 284.

S. radtshenkoi B.-M. (Upper Permian - U.S.S.R.).

Family LOPHIONEURIDAE

Austrocypha Tillyard, 1935. Proc. Linn. Soc. N.S.W. 60: 277.

A. abrupta Tillyard. (Upper Permian - Australia).

Cyphoneura Carpenter, 1932. Amer. J. Sci. 24: 18.

C. permiana Carpenter. (Lower Permian - U.S.A.).

Cyphoneurodes Becker-Migdisova, 1953. Dokl. obsch. Sobr. Ak. Nauk. SSR. 90: 281.

Cyphoneura reducta Carpenter. (Lower Permian - U.S.A.).

Lophiocypha Tillyard, 1935. Proc. Linn. Soc. N.S.W. 60: 274.

L. permiana Tillyard. (Upper Permian - Australia).

Lophioneura Tillyard, 1921. Proc. Linn. Soc. N.S.W. 46: 417.

L. ustulata Tillyard. (Upper Permian - Australia).

Lophioneurodes Becker-Migdisova, 1953. Dokl. obsch. Sobr. Ak. Nauk. SSR. 90: 280.

L. sarbalensis B. - M. (Lower Permian - U.S.S.R.).

Zoropsocus Tillyard, 1935. Proc. Linn. Soc. N.S.W. 60: 273.

Z. delicatus Tillyard. (Upper Permian - U.S.S.R.; Australia).

Family ZYGOPSOCIDAE

Zygopsocus Tillyard, 1935. Proc. Linn. Soc. N.S.W. 60: 271.

Z. permianus Tillyard. (Upper Permian - Australia).

Family ARCHIPSYLLIDAE

Archipsylla Handlirsch, 1906. Die Fossilen Insekten 4: 503.
A. primitiva Handlirsch. (Upper Jurassic - Europe (Germany, U.S.S.R.)).

Family ASIENTOMIDAE

Asientomum Martynov, 1926. Bull. Acad. Sci. U.R.S.S. 1926: 1365.
Lithopsocus praecox Martynov. (Upper Jurassic - U.S.S.R.).

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Parapsocus Scudder, 1890. Tert. Insects p. 118.
P. disjunctus Scudder. (Eocene - U.S.A.).

Psococicadellopsis Becker-Migdisova, 1962. Paleont. J. 1962 (1): 101.
P. primitiva B. - M. (Triassic - U.S.S.R.).

Surijokocypha Becker-Migdisova, 1961. Pal. Ins. Kuznetsk. p. 280.
S. surijokovensis B. - M (Upper Permian - U.S.S.R.).

Vitriala Becker-Migdisova, 1961. Pal. Ins. Kuznetsk. p. 282.
V. nigriapex B. - M. (Lower Permian - U.S.S.R.).

3. CHARACTERS OF GENERA AND SUPRAGENERIC CATEGORIES OF FOSSIL PSOCOPTERA

Family DICHENTOMIDAE

Head relatively large, extended anteriorly into a short rostrum and with large compound eyes. Antennae long, filiform, of more than fifty segments, the first and second shorter and broader than the remaining segments. Antennal socket in a pit with an adjacent ridge. Maxillary palps long, apparently 3-segmented; labial palps shorter, but evident as segmented appendages. Prothorax short and collar-like. Meso- and metathorax large; division into lobes not evident. Legs long and slender; tarsi 4-segmented, the first segment longest; claws short and strongly curved. Fore and hind wings almost homonomous, apically rounded. Wings comparatively long, one-third to one-fourth as wide as long. Sc long, terminating on R_1 with a distal section sometimes forming the proximal margin of the distinct pterostigma, sometimes fused basally with R. R_1 curved, giving a rounded hind margin to the pterostigma or straight, giving a narrow triangular pterostigma. Rs 2- or 3-branched, sometimes connected to the pterostigma by a cross-vein; branches of Rs arising distad of the pterostigma; Rs straight before bifurcation; stem of Rs long. M approaching R basally. M at least 4-branched; a cross-vein sometimes present between Rs - M in midwing but M otherwise free of R after initial basal separation. Cu_1 branched, to form the areola postica; Cu_{1a} usually only slightly curved giving a low triangular areola postica; areola postica free; Cu_{1b} continuing almost in same line to wing margin; apex of areola postica always well basad of end of Cu_{1b}. IA usually straight. Cu_2 and IA ending well apart at wing margin; 2A present. Hind wings very similar to fore wings and only a little smaller. Abdomen 10-segmented. Cerci absent.

Lower Permian (U.S.A.), Upper Permian (Australia, Russia).

Dichentomum Tillyard 1926

Fore wing (figs. 5.1, 5.2) with Sc forked distally. R_1 bounding well formed pterostigmal area. Rs 2-branched. Basal parts of M and Cu separate from R. M 4-branched. IA close to Cu_2. 2A present. Cross-veins absent except for a pterostigmal spur-vein reaching Rs. Areola postica long and low, free. Fore and hind wings similar to one another with hind wing barely shorter and broader. (Genitalia have been described and figured (Becker-Migdisova and Vishnyiakova 1962, fig. 678) but examination of the specimen leaves me unconvinced as to the nature of the structures involved; it seems doubtful whether they form part of the specimen).

Lower Permian (U.S.A.); Upper Permian (U.S.S.R.).

Austropsocidium Tillyard 1935

Fore wing (figs. 5.3, 5.5) elongate-oval. Costa gently curved. Sc ending on R_1. Pterostigma triangular. R well removed from costa. Branches of Rs arising distad of level of end of R_1. Rs 2- or 3-branched; branches short. M 4-branched, joined to Rs by a cross-vein. Cu_1 arising behind M. Areola postica flat, long free. 2A present. IA almost straight, close to Cu_2. 2A slightly sinuous.

Hind wing (fig. 5.4) without pterostigmal area, Rs removed from R. Rs 2-branched. M 4-branched. Rs-M cross-vein present. Areola postica long, low and free. Cu_2 straight. 2A absent.

Upper Permian (Australia).

Stenopsocidium Tillyard 1935

Fore wing (fig. 5.6) narrow-elongate. Costa nearly straight to end of R_1. Sc ending on R_1 with a branch vein to costa. R not far removed from costa, simple. Rs 2-branched, branches short. M 5-branched (4-branched in hind wing). Areola postica long, fairly flat, Cu_{1a} curved. Cu_2 and IA nearly straight. 2A absent.

Upper Permian (Australia).

Megapsocidium Tillyard 1935

(Described from an incomplete distal section of a wing).

R_1 and Rs connected by a crossvein behind a forking of R_1. Rs forked at this crossvein; anterior arm probably forking before wing margin. M probably 4-branched.

Upper Permian (Australia).

Family PERMOPSOCIDAE

Antennae shorter than in Dichentomidae. Fore wing moderately broad, broader than in Dichentomidae. Sc terminates either on R_1 or on costa. Sc and R close together and parallel. Pterostigma well developed, with curved hind margin. At least one crossvein between R_1 and Rs. Rs 2-branched. M approaching or fusing with R basally. M 4-branched; sometimes a cross-vein present in midwing between Rs and M. Areola postica strongly arched, nearly always shorter than high; joined to M by a crossvein. Cu_{1a} present. Hind wing similar to fore wing but a little smaller. Body structure little known.

Lower Permian (U.S.A.).

<u>Permopsocus</u> Tillyard 1926

Fore wing (figs. 5.7, 5.8), broad, Sc sometimes ending in R_1 sometimes in costa, always long. Two crossveins between R_1 and Rs. Rs forking distad of forking of M_1 and M_2. Rs 2-branched. M 4-branched. Crossvein present between M_2 and M_3. Areola postica tall, joined to M_{3+4} by a crossvein. 2A present.

Lower Permian (U.S.A.).

<u>Progonopsocus</u> Tillyard 1926

Fore wing (fig. 5.9) well rounded apically. Sc ending on costa, connected with R_1 just before end. R_1 enclosing pterostigmal area. Only one crossvein between R_1 and Rs; one between Rs and M close to fork of M. No crossvein between M_2 and M_3. Areola postica tall, joined to M_{3+4} by a crossvein. Cu_{1a} curved. 2A present.

Lower Permian (U.S.A.).

<u>Lithopsocidium</u> Carpenter 1932

Fore wing (fig. 5.10, 5.11) with ridge of unknown homology running from R to Cu_1 in basal part of wing. Sc terminating on R_1, near pterostigma. Pterostigma joined to Rs by a crossvein. Rs arising about half way along wing. Origin of M indistinct. Areola postica joined to M by a crossvein. Crossvein present between M_2 and M_3.

Lower Permian (U.S.A.).

<u>Orthopsocus</u> Carpenter 1932

Similar to <u>Permopsocus</u>. Hind wing (fig. 5.12) with

Sc terminating on R_1, near pterostigma. Rs arising near wing base. Rs - M crossvein present. Areola postica triangular, joined to M_{3+4} by a crossvein.

Lower Permian (U.S.A.).

Family MARTYNOPSOCIDAE

Known only from fore wing (fig. 5.13). Sc terminating on R_1. Pterostigma slender. Rs and M both 3-branched. Two crossveins present between R_4 and M_1 and one between R_2 and R_3. Areola postica low, joined to M by a crossvein.

Upper Permian (U.S.S.R.).

Martynopsocus Karny 1930

Characters as for family.

Upper Permian (U.S.S.R.).

Family SURIJOKOPSOCIDAE

Fore wing (fig. 5.14) apparently much broader distally than proximally. Costal area fairly wide at base. Sc close to R. M 5-branched. Basal parts of Cu_1 and R + M thickened, forming cell at wing base. Distal branches of Cu_1 recurved. Anal area narrow. Areola postica long, subrectangular, joined to M by a crossvein. Hind wings and body unknown.

Upper Permian (U.S.S.R.).

Surijokopsocus Becker-Migdisova 1961

Characters as for family.

Upper Permian (U.S.S.R.).

Family LOPHIONEURIDAE

Head broad. Antennae reaching only to midwing. Fore wing with Sc short, extending at most a little beyond level of origin of Rs and terminating on costal margin. Rs 2-branched. Base of M coalesced with R. M 2-branched. Cu_{1b} very weak or Cu_1 not branched. Hind wing about two-thirds as long as fore wing. IA sometimes absent. 2A, when present, reduced to small basal spur.

Lower Permian (U.S.A.); Upper Permian (Australia, U.S.S.R.).

Lophioneura Tillyard 1921

Fore wing (fig. 5.15) elongate, oval, about three times as long as broad. R and Cu_1 much stronger than other veins. Sc short, ending on costal margin. R, M and Cu_1 arising from same basal stem. Rs with wide-angled distal fork. R_{4+5} terminating behind wing apex. M arises a little basad of Rs, widely forked distally. M forks basad of forking of Rs. M 2-branched. Areola postica sometimes absent, low. Cu_{1b} faint. IA absent.

Upper Permian (Australia).

Cyphoneura Carpenter 1932

Fore wing (fig. 5.16) nearly oval. R_1 curved towards costal margin. No pterostigmal area. Branches of M directed posteriorly to end behind wing apex, sometimes strongly so. Cu_1 not branched, sinuous. 2A absent.

Lower Permian (U.S.A.).

Austrocypha Tillyard 1935

Fore wing (figs. 5.18, 5.19) sometimes without Sc. R_1 far from costal margin. R_1 strongly bent anteriorly to wing margin. Rs, M and Cu_1 arise close together from R_1 and run almost parallel to one another. Cu_1 strongly sinuous. Cu_2 connected to Cu_1 by a basal crossvein. Areola postica absent. Hind wing (fig. 5.20) about half as long as fore wing. Base narrow. Sc absent. Rs and M simple. R_1, Rs and M only present; Rs and M forked.

Upper Permian (Australia).

Lophiocypha Tillyard 1935

Fore wing (figs. 5.21-5.23). Similar to Lophioneura but with Rs arising further from wing base. IA present. 2A reduced to small spur-vein. Areola postica absent. Hind wings (fig. 5.23) shorter than fore wings. R_1 very short. Rs forked. M simple. Head hypognathous. Eyes round and wide apart. Meso- and metathorax fused.

Upper Permian (Australia).

Zoropsocus Tillyard 1935

Fore wing (figs. 5.24, 5.25) narrow at base. Costal and posterior wing margin fairly straight. Sc long, ending in costa. R_1 simple. Branches of Rs directed anteriorly. Cu_1 independant of R plus M, arising from common Cu stem; connected to M by a short crossvein. M forking at level distad to that of forking of Rs. Areola postica absent. 2A absent.

Upper Permian (Australia).

Cyphoneurodes Becker-Migdisova 1953

Fore wing (fig. 5.17) almost triangular. R_1 not as strongly curved as in *Cyphoneura*. Cu_1 straight.

Lower Permian (U.S.A.).

Lophioneurodes Becker-Migdisova 1953

Fore wing (fig. 5.26) with both branches of Rs directed anteriorly. Rs forked basad of forking of M. Cu_1 arising from stem of R plus M.

Lower Permian (U.S.A.)

Family ZYGOPSOCIDAE

Fore wings (fig. 5.27) broad, membranous, rounded apically, with heavy veins. Sc terminating on R_1 about half way along wing. Rs 4-branched, arising near base. Rs connected to R_1 by crossvein behind end of Sc. Rs to M crossvein present, M 2-branched. Cu_1 strongly curved towards margin near apex, not branched. Wing margin thickened. IA fused distally with Cu_2. Areola postica absent.

Upper Permian (Australia).

Zygopsocus Tillyard 1935

Characters as for family.

Upper Permian (Australia).

Family ARCHIPSYLLIDAE

Fore wings (fig. 5.28) elongate, oval, about three times as long as broad. Sc reduced to a small basal section joining costa and a distal section at base of pterostigma.

Pterostigma short and broad, angled behind. Vein from angle of pterostigma to Rs. Rs arising near wing base. Rs forked distally. Rs to M crossvein present in midwing. M fused basally with R, 4-branched. Cu_1 forked; areola postica long and low. Cu_{1b} short. Anal area reduced.

Upper Jurassic (U.S.S.R.).

Archipsylla Handlirsch 1926

Characters as for family.

Upper Jurassic (U.S.S.R.).

Family ASIENTOMIDAE

Fore wing and hind wings only known imperfectly. Fore wing (fig. 5.29) with pterostigma about four times as long as broad. Rs joined to R_1 by an oblique cross-vein at base of pterostigma. Rs forked. M dividing well basad of radial forking. Cu_1 not branched; no areola postica. Hind wing (fig. 5.30) with Rs and M apparently 2-branched. Cu_1 simple.

PSOCIDA AGNOTA

The four fossil genera listed under this heading are very little-known.

Parapsocus Scudder is described from the Eocene (U.S.A.) and is probably a psocopterous insect.

Psococicadellopsis Becker-Migdisova is known from a wing with Rs probably unbranched found in Triassic strata (U.S.S.R.).

Surijokocypha Becker-Migdisova is known from wings from the Upper Permian (U.S.S.R.). Rs is forked more deeply than M and Cu_1 is simple.

Vitriala Becker-Migdisova is based on a Lower Permian (U.S.S.R.) wing in which M is simple.

These fossils are so incomplete that no advantage can be gained from considering them any further.

4. DISCUSSION OF FOSSIL PSOCOPTERA

From the definitions given above it can be seen that the fossil Psocoptera differed in many ways from the Recent forms. Their classification raises some problems but as we are dealing here primarily with the classification of the Recent forms it is in relation to these that the fossils will be mainly discussed. In this regard they are valuable from two points of view. First, they can be used to provide an indication of the age of the order Psocoptera and, secondly, they can be used to give an indication of the relatively plesiomorphous and apomorphous conditions of characters used in classification. The latter is the more important for present purposes.

The fossil genera currently accepted have been listed. There are twenty four genera grouped into eight families plus the four genera too poorly known to warrant discussion.

Owing to the fragmentary nature of fossils generally and particularly of much of the Psocoptera material extreme caution needs to be exercised in their study and in arriving at conclusions drawn therefrom. Without entering into detail it can be said that there is some evidence that sufficient caution has not been exercised by some workers in the past.

The attitude adopted here is that anything which is of dubious or doubtful value should be discarded rather than that haphazard guesswork replace logical conclusion. As a result it will be necessary to remove from the fossil Psocoptera certain genera without placing these in any other group. This is not considered unwarranted when dealing with material which is fragmentary. In fact, it is considered that it would be preferable not to describe such poor material in the first instance rather than increase the already voluminous entomological literature with unusable or possibly misleading data.

Dichentomidae. The excellent series of specimens of Dichentomum tinctum Tillyard available to Carpenter (1933) has made possible a remarkable reconstruction for such a small insect. The general form of the species is well known and although some features not characteristic of modern psocids are present the general characteristics are what would be expected in a "primitive" psocid. For example, the prolongation of the head into a rostrum and the origin of the antennae in pits are not psocid features. Many of the other characters are simple in a somewhat plesiomorphous condition relative to their modern apomorphous homologues. The modern state of a character, as so frequently happens in insect groups and as has been happening since the origin of the groups, is that of a reduced condition. For example, the antennae and maxillary and labial palps have fewer segments in modern forms. The heteronomous wings of modern species can be derived by a greater or lesser degree of reduction in size of the hind wings with concurrent reduction and specialization of venation from the homonomous state. The venation, in particular, is already reduced in Permian Psocoptera but had not yet reached the degree of reduction and specialization of modern forms. For example, M was still 4-branched and the presence of a second anal vein was usual. It is present in a few modern forms. Relationship to modern Psocoptera is clear in the genera Dichentomum, Austropsocidium and Stenopsocidium which differ from each other in minor venational features. Megapsocidium, however, is known only from an incomplete apical part of a wing and its reconstruction and any suggestion as to its relationship would be guesswork. It cannot, therefore, be reasonably discussed as even its ordinal position cannot be established.

Permopsocidae. The venation of the Permopsocidae is fundamentally very similar to that of the Dichentomidae. The crossvein from the pterostigma to Rs is a more constant feature and the areola postica is joined to M by a crossvein. Both of these features are present in a few modern families. There is a strong tendency for a crossvein (Rs - M) to be present in midwing as in Permopsocus and Progonopsocus or in the distal part of the wing as in Orthopsocus. This crossvein is absent in Lithopsocidium. These genera clearly have psocopteran affinities. A wing very similar to that found in the Dichentomidae is arrived at by reduction in crossveins of a Permopsocid. The tall areola postica is now, however, a Dichentomid feature nor is the greater degree of reduction in the hind wing.

Martynopsocidae. In this monotypic family the wing venation is very similar to that of the Permopsocidae but Rs and M are both 3-branched.

Surijokopsocidae. Comparatively little information can be gleaned from the little material known of this family. The distal broadening of the wing is not psocid-like nor is the presence of a basal cell bounded by strong veins. Details of the wing apex are not known. It is questionable whether Surijokopsocus really has any psocopteran affinities even though there appears to be an areola postica joined to M by a crossvein.

In any case, this genus is far removed from both the Dichentomidae and the Permopsocidae on the one hand and the modern Psocoptera on the other. It provides little information on their relationships and at most, on presently available data, may be retained in the Permopsocida with reservation.

Lophioneuridae. The insects included in this family had wings which broadened apically and which had Rs, M and Cu_1 all arising from a common stem with R and running more or less parallel with one another. An areola postica is lacking. The hind wings were considerably smaller than the fore wings. There was no suggestion of a pterostigmal area and both Rs and M are 2-branched. These insects seem to have had little in common with either modern Psocoptera or the fossil forms most resembling modern forms. Their association with those in the order does not seem justified. Certainly the inclusion of the Lophioneuridae in a suborder also including modern species is not justified on any grounds using presently available data.

Zygopsocidae. In Zygopsocus Rs is 4-branched and M is 2-branched. There is no areola postica and the wing is membranous with strongly thickened veins. These characters suggest a strongly modified and specialized line of development and one not resembling modern Psocoptera nor the other fossil families. It is difficult to support a suggestion that they be included in the Permopsocida. The position of the family is problematical and it is better not to assume psocopteran relationships for it.

Archipsyllidae. The single genus Archipsylla is very similar in venational features to the Dichentomidae. The main difference is in the lack of Sc and in the apparent absence of the anal vein. Cu_2 is evanescent. The available information, although the material is very limited, indicates psocopteran affinities.

Asientomidae. The available material of this family is insufficient to render considered opinion possible. The basal section of the fore wing is not known and the vein referred to in the descriptions as an unbranched Cu_1 might well be M_3. Its basal origin is not visible. The condition of Cu_2 and the anal veins and, indeed Cu_1 if M_3 is 3-branched, are unknown. In the hind wing Rs and M appear to be 2-branched and Cu_1 simple. The placing of Asientomum in the Psocoptera cannot be adequately supported at present.

From the foregoing it is apparently necessary to eliminate some genera from further consideration for one of two reasons. First, it is necessary to disregard some because of insufficient information. These include the four genera already listed under "Psocida Agnota", Megapsocidium and Asientomum. Secondly, some must be disregarded owing to their apparent lack of real affinity with either modern Psocoptera or with other fossil groups included in the Permopsocida. These include Surijokopsocus, the Lophioneuridae and Zygopsocus.

If, in fact, these latter groups are in any way related to the Psocoptera they exhibit a degree of apomorphism in many characters greater than that of Recent groups relative to the Permopsocida and hence must constitute a strongly apomorphic line (or lines) which have evolved from the Permopsocid stock in a manner different and further from that of modern forms. Because of this they can, in any case, throw little light on the phylogeny and classification of the monophyletic group here considered as constituting the order Psocoptera. At most they could be considered as the sister group of the Permopsocida plus the Recent Psocoptera.

The groups remaining in the Permopsocida after the removal of the dubious groups are the Dichentomidae, Permopsocidae, Martynopsocidae and Archipsyllidae.

Table 3 includes the genera discussed and the geological periods from which they are known. Genera in brackets are here not considered to be true Psocoptera.

The age of the Psocoptera. The earliest specimens of undoubted Permopsocida come from the Elmo limestone of Kansas. These insects were clearly well on the way to being Psocoptera as we know them now although it is not suggested, for reasons given below, that they were the direct forerunners of the present forms. It is likely, as the Elmo limestone is of Lower Permian origin and the forms show some strongly apomorphic features, that the origin of the group took place during the Carboniferous.

Phylogeny of the Permopsocida. Sóme of the principles involved in phylogenetic study are discussed later but in order to dispose of the only partially relevant question of phylogeny in the fossil Permopsocida anticipation of the acceptance of the principles is made here.

So far as fossil forms are concerned we are restricted to consideration of largely haphazardly preserved morphological characters on which to base discussion.

The earliest of the Lower Permian specimens are members of the Dichentomidae and Permopsocidae. In each of these families can be found some relatively apomorphous features. The rostrum on the head in Dichentomum is clearly one such feature; the reduction in the number of crossveins, of which in Dichentomum (fig. 5.1) the only remaining one is the vein between R_1 and Rs, is another. In the

Permopsocidae, on the other hand, there are usually a few crossveins present but the hind wing has become reduced in size and venation. This latter is clearly apomorphous relative to the condition of almost wing homonomity in the Dichentomidae; the hind wing of Austropsocidium (figs. 5.3, 5,4) however, is apparently smaller than the fore wing and has fewer veins. Also, in Austropsocidium even the R_1 to Rs crossvein has disappeared. On morphological grounds the Dichentomidae can be said to exhibit some strongly apomorphous features, especially in the head, where Dichentomum is concerned and in wing features where the other genera are concerned, whereas the Permopsocidae are seen to be relatively plesiomorphous in most features except that they all show reduction of hind wings.

In the Martynopsocidae we have fewer characters known to us for consideration but we find a condition similar to that of the Permopsocidae in the fore wing but with Rs having an additional branch and M one fewer. It would seem that the Martynopsocus wing (fig. 5.13) is easily derivable from a primitive Permopsocid wing by comparatively little change, for example, from Permopsocus itself (figs. 5.7, 5.8).

The Archipsyllid venation (fig. 5.28) is similar to that of Dichentomum but a midwing crossvein is retained and the anal area reduced. In addition to the crossvein from R_1 to Rs there is a midwing crossvein from Rs to M.

It is possible on morphological grounds to suggest what the relationships of these four families might be, bearing in mind the relatively little material available and its nature; it is clearly impossible to do other than suggest broad relationships; detailed and intricate plylogenies based on such material must inevitably be illogically constructed.

The most primitive family is the Permopsocidae, with a series of genera known, some of which (e.g. Permopsocus (figs. 5.7, 5.8)) are more plesiomorphous than others (e.g. Progonopsocus (fig. 5.9)).

On a somewhat different line of development are the overall more apomorphous Dichentomidae within which the most plesiomorphous genus is the homonomous-winged Dichentomum (figs. 5.1, 5.2). Stenopsocidium (fig. 5.6) is probably the most apomorphous of the genera. From a Permopsocus - like group can be derived the apomorphous Martynopsocus and from a Dichentomum - like group can be derived Archipsylla (fig. 5.28).

Determination of the relationships of these four groups is a comparatively simple phylogenetic problem; the simplicity of the situation may well be a result of lack of data on intermediate or other forms; in fact, it probably is so considering the time intervals involved between the appearance of groups concerned in the fossil record. The availability of material, however, is beyond our control and we can but consider that data which we have.

Beginning with the clearly primitive Permopsocidae, we find that they share some apomorphous features (e.g. condition of Rs and Sc) with all other groups except Martynopsocus which does, however, have a 3-branched Rs. It seems likely that Martynopsocus (fig. 5.13) is an apomorphous remnant of a sister group to the remaining fossil forms. A primary dichotomy in the evolutionary history of the group seems to be represented by the Martynopsocidae on the one hand and all the other genera on the other. Amongst the remaining forms the Dichentomidae and the Archipsyllidae share apomorphous features not present in the Permopsocidae (e.g. crossvein arrangement). The Dichentomidae and Archipsyllidae together represent a sister group to the Permopsocidae. We can thus establish a second dichotomy, the Permopsocidae on one hand and the Dichentomidae plus Archipsyllidae on the other. The Archipsyllidae represent a modified line of development of the Dichentomidae.

The broad relationships suggested here can be indicated graphically (fig. 5.31). They have been arrived at purely on morphological grounds, without consideration of the known ages of the various groups.

If we now take the time factor into consideration we find that the evolutionary sequence suggested accords well with it, the Martynopsocidae representing a line which died out, leaving its sister group to continue into the Triassic in the form of Archipsylla.

Concluding comment.

A perusal of the fossil material provides some indication of the state of the characters of early psocids and what changes these characters were undergoing in the early history of the order. We find that in common with most insect groups the trend in wing venation is one from a condition in which there are numerous crossveins to a condition in which these are reduced to a few or none. It is interesting to note that where, in fossil psocids, there remain only one or two such crossveins that these occupy the positions in which these veins sometimes occur in modern groups, even though they may do so now exceptionally rather than as the rule.

Also, there is a tendency to reduce the number of branches of some veins.

The third clear tendency is for the hind wings to become much smaller and have fewer veins than the fore wings. The general conditions of reduction are more advanced than in the fore wing. There is some suggestion (although only a few specimens are available) that reduction in antennal length was sometimes carried to a conspicuous level in the fossil forms.

We shall find later, in considering the modern forms as against the fossil forms, that the tendency is frequent for other characters to become reduced during their evolutionary history, e.g. as seen in tarsal segmentation. It is with such background information, obtained from the fossil material that we can now proceed to discuss in more detail the Recent Psocoptera.

TABLE 3. OCCURRENCE OF FOSSIL PSOCOPTERA

GEOLOGICAL PERIOD	U.S.A (KANSAS)	AUSTRALIA	U.S.S.R.	GERMANY	U.S.A. (COLORADO)
EOCENE					(Parapsocus)
CRETACEOUS					
JURASSIC			Archipsylla (Asientomum)	Archipsylla	
TRIASSIC			(Psococicadellopsis)		
(UPPER)		(Zygopsocus) (Austrocypha) (Lophiocypha) (Lophioneura) (Zoropsocus) Austropsocidium (Megapsocidium) Stenopsocidium	Martynopsocus Dichentomum (Surijokopsocus) (Zoropsocus) (Surijokocypha)		
PERMIAN					
(LOWER)	Dichentomum Lithopsocidium Orthopsocus Permopsocus Progonopsocus (Cyphoneura) (Cyphoneurodes)		(Lophioneurodes) (Vitriala)		

CHAPTER VI. PHYLOGENY AND EVOLUTION IN THE PSOCOPTERA

1. INTRODUCTORY COMMENTS

The stagnation from which systematics has been suffering over the past few decades and from which it is now emerging has been due to several factors. Some were historical, others were directly related to lack of data, data of a kind which could only be provided by other disciplines (e.g. genetics and ecology) and still others were due to lack of fresh appraisal of the methods of study and techniques in use. These matters have been discussed extensively in the literature and many arguments, accusations, counter-arguments and denials fill the pages of recent journals and special works devoted to the subject. One has only to peruse such works as those of Bigelow (1956, 1958, 1959), Hennig (1953, 1957, 1966) Simpson (1944, 1945, 1951, 1953, 1959a, b) Zimmerman (1943, 1953), Mayr (1958) and Mayr, Linsley and Usinger (1953) and some of the references given by these authors to find a wealth of discussion on the practical and theoretical aspects of systematics. It is often the case in a discipline which is about to make new advances that apparently irreconcilable viewpoints are built up until discussion almost ceases to be discussion and comes to the point of almost being an expression of contempt for holders of a viewpoint opposite to that of the author concerned. In the case of systematics the view has been held by many, amongst them some systematists, that the tasks of the science have ended at the descriptive and cataloguing stage and that thereafter systematists has nothing to offer to the rest of biological science. Bertalanffy (1932) considers the goal of systematics to be the production of as complete a species catalogue as possible. Hertwig (1914) suggests that the aims of systematics are primarily practical, inferring that little of theoretical value can come from systematic studies. Heintz (1939) goes so far as to suggest that the relation between systematics and biology is similar to that between a library catalogue and a library. On the other side have been those who hold the view that systematics can and should provide an evolutionary or phylogenetic picture in its classification (Hennig, 1966, Zimmerman, 1937). A point had been reached when these two viewpoints were so firmly held and held as diametrically opposing viewpoints, that systematics and systematists were becoming somewhat ridiculous in the eyes of more "practical" biologists and those engaged in disciplines more remotely connected to biology.

One major criticism of systematic work has been that the criteria for selecting characters to be used in defining categories has been subjective and that the grouping of species into higher categories has been biased by the uncritical weighting of characters chosen subjectively. This has been a major and justified criticism by the protagonists of numerical taxonomy as a tool for use in systematics.

Another criticism has been that the hierarchic system of presentation of classification, although giving the appearance of indicating phylogeny, was not, on logical grounds, necessarily capable of doing so. This problem is discussed at length by Hennig (1966) and also by Gregg (1954) and need not be discussed here.

Hennig (1950, 1957, 1965, 1966) has presented a critical analysis of the methods of phylogenetic systematics whereby a classification of groups can be presented which will indicate relationship and phylogeny as well as provide a practical classification. The methods advocated to achieve this are discussed by Bock (1969), Schlee (1969), Brundin (1966), and Colless (1967, 1969).

In brief, it is necessary to determine, in the characters of groups under consideration, which are in a plesiomorphous and which in an apomorphous condition, remembering that these conditions are relative to one another within the group under consideration. To take an extreme example, aptery in the Thysaunra is plesiomorphous in relation to the presence of wings in the Diptera but aptery in the Siphonaptera is apomorphous in relation to the relatively plesiomorphous winged condition of the Diptera. It is also important to establish beyond reasonable doubt that the groups under consideration are monophyletic, a condition dependant on the possession of synapomorphous characters and not on symplesiomorphous characters, i.e. common possession of "primitive" characters does not necessarily imply monophyly. Phylogenetic relationships of groups must be considered in relation to conditions of their characters; overall similarity is not considered a justfiable criterion for establishing relationships, degree of overall similarity does not necessarily indicate community of descent. A monophyletic group is a group descended from a single species; it must include all the species which are descended from that species. This species is sometimes referred to as the "stem" species.

It is also necessary to ensure that the characters being considered in relation to each other within a transformation series are homologous. Whilst most cases are clear, there are some which are not. In determining the direction of the transformation series, which is not always self-evident, it may be necessary to use palaeontological data, information on geographical distribution or ontogenetic data. Precedence of one character condition relative to another in the geological sequence would imply that the earlier is the more plesiomorphous. In general terms it can be said that there is a relationship between apomorphy and apochory. Apomorphy being the presence of apomorphous character conditions. The tendency is for a species which has departed furthest geographically (apochorous) and ecologically from its parent species to be most apomorphic, hence the relationship between apomorphy and apochory. The relationships between ontogeny and phylogeny have been discussed extensively in the literature and whilst the theory of recapitulation should clearly not be too rigidly applied so far as details of ontogeny are concerned, its complete rejection is unjustified. Also, it sometimes happens that the transformation series of groups of characters are correlated. Where the direction of the transformation series of one or more of the series is known that of the remainder of the series may be inferred. Loss of characters must be taken into consideration. The end of a transformation series in which a character is progressively reduced may be complete loss of the character, which is the same as the condition which prevailed before the appearance of the character in the first place. It is also necessary to bear in mind the possibilities of convergence and parallelism in evolution.

Attempts at establishing the phylogeny of a group and setting up a phylogenetic classification should not be based only on morphological data. Any feature of the physiology, ecology or ethology of the organisms may be used, in fact, any aspect of the biology of the organism which has been subject to selection and, hence, evolution, is potentially a taxonomic character. Theoretically, this means that virtually any feature can be considered. In the past justifiable criticism has been levelled at systematists for using a limited range of characters; modern systematists have tended to use non-morphological features where available to support findings based on morphological studies. It is important, however, that the approach to and handling of any feature is the same as that applicable to morphological features. It is necessary to attempt to establish the manner in which non-morphological features have evolved, for example, a specialized feeding habit will usually be considered to have been derived from a generalized one.

For most groups of animals until knowledge of their biology becomes as detailed as knowledge of their morphology, the latter must remain the main source of data on which considerations of phylogeny can be based. This will always be so for fossils. In any event, morphological features are the most easily seen, described and studied characters and they reflect well those adaptations to environmental change which are the essence of evolution. In many groups of animals, there is considerable supplementary data from fields of study other than descriptive and comparative morphology, such as genetics, ecology, and physiology. In the case of the Psocoptera, unfortunately, such supplementary data are available from few fields, and even then it is not consistently available. In addition to morphological features or those which may be handled as such in reasoning out the problems of phylogeny, the general tendency for sister-groups of organisms to occupy different geographical areas can be used to indicate such sister-group relationship. Sister groups are groups of species which have arisen by divergence at the same point in the evolutionary history of the monophyletic group to which they belong.

Palaeontological data may be available for consideration. The main drawback with such data lies in its incompleteness. Provided the limitations set by the nature of the material and the data which can be derived from it are borne in mind and reasoning carried on within this framework and not allowed to extend beyond it, palaeontological data remains useful within and despite its obvious limitations.

In dealing with the problem of phylogeny and classification of a particular group we are faced with the task of grouping species into groups of higher category in a hierarchic system based on the evolutionary history of the group. The first step (p.256) is necessarily the establishment of the transformation series of the characters to be used, that is, in determining the plesiomorphous and apomorphous conditions of the characters. This is followed (p. 290) by the determination of which are the monophyletic groups and what are the relationships which they bear to each other. The taxonomic ranking of the groups in a hierarchy must then be determined (p. 349).

In order to arrive at a phylogenetic classification which is as satisfactory and as accurate as possible, it is necessary to utilise the data on as many aspects of the biology of the animals concerned as possible.

The characters available for use in a phylogenetic study of the Psocoptera, such as that presented later, can now be discussed.

2. CHARACTERS AND CHARACTER CONDITIONS

In broad terms there are three sources from which data can be taken for consideration when discussing phylogeny and classification.

1. Palaeontology provides a certain amount of information.
2. Geographical distribution of living species and groups of species provides information on the likely relationships of the organisms since apomorphy and apochory bear some relation to each other.
3. Morphology and biology (in its widest sense) of living species is the main source of data, potentially being able to provide information on every aspect of the organism's existence.

The fossil Psocoptera have been dealt with and reference to fossil forms will be made subsequently in discussion of morphological features.

The subject of the geographical distribution of Psocoptera will be left until later. I shall first discuss the phylogeny of the group on the evidence available from morphological, biological and ecological data and then subsequently review our knowledge of geographical distribution patterns and, if possible, use these as a check on conclusions drawn from the other data.

Here we shall first discuss the characters, both morphological and otherwise, other than zoogeographical, which provide information likely to be useful in phylogenetic study.

It is unfortunate that the biology of only a very few species of Psocoptera has been investigated in detail. Also, detailed ecological work has been reported on for very few species. The Psocoptera are not easy to rear in captivity. They feed on fungal hyphae and spores, algae, lichens and yeasts and are extremely sensitive to the temperature and humidity conditions of the microhabitat. Detailed biological requirements cannot, therefore, consistently be used as adjuncts to morphological data when considering the classification of the Order. Nevertheless, in addition to morphological features some data is available on habitat preferences and sometimes on other ecological factors. Oviposition habits are known in quite a large number of genera, enough for some generalizations to be made, and parthenogenesis and viviparity can be taken into account as well as immature stages and sometimes the behaviour patterns of nymphs.

MORPHOLOGY

A superficial perusal of the literature gives the impression that many characters are in use. Unfortunately, many useful characters have been mentioned only once or a few times and inconsistency in descriptions has in the past made comparisons difficult. In order to be able to define the genera adequately enough for the present study, a wide range of characters has been presented in the definitions. As is the case in most groups of animals their significance at the generic level varies; in some cases characters which may be considered as being of significance at the generic level in some families may be of significance at the family level in other groups. That is, when many characters are taken into consideration it becomes apparent that in some cases a given character has varied more when associated with some characters than it has when associated with others.

In order to make any assessment of the relationships of the genera, families and higher groupings of the Order, it is essential, first, to attempt to establish which are the plesiomorphous and which the apomorphous conditions of characters. We are fortunate in having some reasonable amount of knowledge of the morphology of fossil Psocoptera; so far as most modern genera are concerned we now have fairly detailed knowledge. Within the order homologies can be easily recognized in most organs; occasionally problems arise in connection with some features of the male phallosome and the hypandrium as these organs are particularly liable to develop complex adventitious structures but these usually range over a few related genera and are not a problem in the Order as a whole. So far as the directions of the transformation series are concerned most instances are reasonably clear and where these are not, there are often other correlated apomorphous characters for which the transformation direction is apparent. We have here, of course, the assistance of the fossil material in determining the likely direction of transformation of many of the characters (especially wing venation characters). There are certain characters in which there is a tendency for parallelism to be apparent. Which characters are involved will become clear as the individual characters in their various forms are discussed.

The epicranial suture is usually clearly defined, especially the median part which crosses the vertex (figs. 4.1, 4.2). The anterior arms are often absent but their position is indicated by a feature of the colour pattern. Sometimes even the median section is somewhat abbreviated and restricted to the upper part of the vertex. Becker-Migdisova and Vishnyakova (1962, fig. 684) have illustrated a species of Zoropsocus showing cephalic sutures but the nature of these is difficult to decide on from their position and, in any case, this group is thought here not to be related to the Psocoptera. The same comments would apply to Tillyard's illustration of Lophiocypha (Tillyard 1935, fig. 7A). Although Permian fossil Psocoptera do not show any signs of the epicranial suture some amber species have clearly defined anterior arms. It can be confidently stated that progressive reduction in extent of the epicranial suture, always involving first the loss or reduction of the anterior arms, is an apomorphous tendency.

The vertex (figs. 2.1, 2.2, 4.495) is very variable in form. It is usually smoothly rounded; the degree of curvature varies considerably. Sometimes the head is shortened with consequent steepness of the front of the head. In such cases the vertex may be ridge-like, falling away steeply in front and behind. The ridge may drop down into a depression in the midline so that the median epicranial suture comes to lie in a groove. A steep vertex and a median groove occur together in some genera. The epicranial plates are, in a few genera, raised into processes which, in the extrme form become antler-like. The vertex may, on the other hand, be flattened giving a broad, flat top to the head or it may be drawn out laterally with adjacent parts of the head capsule to form eyestalks. The presence of adventitious structures, excessive flatness or sharpness of the vertex and the presence of a strong median groove are clearly departures from the plesiomorphous rounded condition of the top of the head capsule as seen in fossil forms.

The hairs on the vertex may be fine or coarse or even be strong bristles. They may be widely spaced or closely packed. A tendency to stabilisation of the positions in the setae has not been found and the arrangement of bristles, even in those species with a limited number of large bristles, appears not to be regular nor of any taxonomic value. The transformation series in this character is probably from one in which there is general, heavy cover, through stages of increasing size of bristle with reduction in number to one in which there are very few, large, widely spaced setae. The final reduction is to glabrosity which condition would represent the most apomorphous state. In some genera the setae become specialized and glandular or they may be apically knobbed or divided. In some cases extraneous material adheres to such hairs, in others not. Such setal specializations are clearly apomorphous developments from simple setae.

The frons is often ill-defined owing to the evanescence of the anterior arms of the epicranial suture but its posterior angle bears the median ocellus.

The postclypeus is one of the most characteristic of the superficial characters of the psocopteran head and plays a large part in giving the insects their characteristic facies (figs. 2.1, 2.2). It usually bulges strongly forwards and is often marked with anteriorly converging stripes. In those genera which have a sharp vertex and shortened head the postclypeus is flattened and this flattening is the major factor in the shortening. The degree to which the postclypeus bulges varies from group to group and may differ between closely related species.

This sclerite is not clearly differentiated in fossil material but the head was sometimes extended into a rostrum. Amber species agree with living forms in having a bulbous postclypeus but this could be an apomorphous condition in relation to other species with a normal, flattened front to the head. It is likely that some groups have reverted to a flattened postclypeal form (e.g. Calopsocus) whereas other groups are plesiomorphous in that condition.

The anteclypeus is a transverse sclerite, nearly always lightly sclerotized, lying anterior to the postclypeus. It shows little variation and appears never to present any feature of taxonomic importance.

The labrum is usually a fairly simple, slightly convex broader-than-long structure. The anterior margin is often concave in the median section. In certain genera (e.g. Caecilius) the labrum carries a pair of styli, one near each disto-lateral angle; they are quite small. In the Epipsocetae the labrum bears a pair of chitinized bands on its inner surface which transverse the labrum from posterior to anterior border. These are sometimes conspicuous and are readily visible from the front of the insect. The presence of styli and the transverse bands appear to apomorphous specializations occurring in restricted groups.

The antennae are always filiform. The first and second segments are short and thick, whereas the remaining segments (flagellar segments) are long and narrow, becoming progressively shorter distally. The fossil forms had extremely long antennae with more than fifty segments. Some living groups also have long, many-segmented antennae. Apomorphically, however, this number is reduced and most species have thirteen segments. A further specialization and more apomorphous feature appears to be the increase in length of the basal flagellar segments relative to the length of the more distal segments. That is, the greater discrepancy in size between the proximal flagellar segments and the distal ones is an apomorphous condition. In some groups which have antennae with more than thirteen segments, some of the segments are sculptured in such a manner as to give the impression that the segments are secondarily annulated. There is no evidence to suggest that fossil forms were so sculptured. Some thickening of flagellar segments occurs apomorphically in a few genera.

The genae are usually without taxonomically significant features; they are usually glabrous but in a few forms they bear scattered setae.

The compound eyes vary from large, conspicuous orbs to small organs consisting of only one or two facets. They are usually glabrous but may have setae between the facets. The dimensions of the eyes in relation to the distance between them has been found to be a valuable taxonomic character at the species level but not for genera or other groups. The eyes are usually larger in the male than in the female, but not always so, and the degree of prominence varies; in extreme cases they are carried on eyestalks which protrude from the upper angles of the head. The compound eyes in fossil forms were well-developed and reduction is clearly an apomorphous condition. Compound eyes are present in most adult hemimetabolous insects. Reduction has probably occurred several times in the evolutionary history of the order as there are several groups which have only this feature in common. Also, reduction in compound eye development is frequently associated with brachyptery or aptery. The extreme development of eyestalks and the somewhat less prominent lateral expansion of the dorso-lateral part of the head (seen, for example in some species of Psocidae) are clearly apomorphous conditions. This development, too, has clearly taken place more than once, it occurs in clearly distinct families the members of which have no other apomorphous features in common. It seems that the pilose condition of the compound eyes is relatively plesiomorphous whereas the

the loss of eye setae is apomorphous. It is not possible to make a decision on this point by reference to the eyes alone. This transformation series is inferred from the fact that in many other features, such as in the wings, body and other appendages, the tendency is always from a condition of considerable hairiness to one in which the number of hairs is reduced and at the same time apparently become more specialized in function and less variable in position. Eventually, many organs are glabrous in their most apomorphous condition. This is a tendency which can be traced in many insect groups.

The ocelli, of which there are normally three, may be widely spaced on the head (fig. 4.1) or grouped closely together around the bifurcation of the epicranial suture (fig. 2.1), the group may be raised on a tubercle. The median ocellus is frequently smaller than the lateral ocelli. Reduction in size and number is frequent and they may be absent altogether, as they always are in nymphs. It is clear from the fossil forms and amber species that three widely spaced ocelli represents the plesiomorphous condition and that grouping, raising on a tubercle or loss are apomorphous conditions.

The mandibles (fig. 2.3) are asymmetrical and the outer edge may be obtusely angled or smoothly curved.

The lacinia is probably the most characteristic feature of the order (figs. 2.4, 4.28, 4.138, 4.631). Its peculiar form and the relationship which it bears to the other parts of the maxilla resulted in some doubts as to the homology of the so-called maxillary "pick". The work of Badonnel (1934), however, makes it quite clear that the "pick" is a highly modified lacinia; Badonnel (loc. cit.) also discusses the previous literature. It may be straight, curved or twisted; it may be broad or narrow distally and its apex may be pointed, divided into two or more lobes or teeth or the end may be broad and subdivided into numerous teeth. At the specific level the lacinia provides excellent characters in some genera whereas in other groups its form is fairly uniform for a number of species. The lacinia, so characteristic of psocids appears to be plesiomorphous in the condition where it has a broad apex, usually subdivided into many small teeth; the specialized state probably involves narrowing of the apex, reduction of teeth to two or the apex may be simple; it is not possible to be dogmatic on this matter as we do not know what form this organ took in fossil forms.

The maxillary palp is four-segmented; in some genera the fourth segment may depart from the usual elongated, apically-rounded form and become round or hatchet-shaped. In some groups there is a conspicuous conical sensillum on the second segment.

The apical segment is spindle-shaped in fossil and amber forms; departure from this represents the apomorphous condition.

The labium bears reduced paraglossae which flank a reduced glossa. The labial palps are also reduced to small one-or two-segmented lobes, the apex of the palp being rounded. On the other hand the palps are prominent in fossil forms and of an undetermined number of segments. Reduction of palpal segments is apomorphous, with the apical segment rounded. Lateral extension of the single palpal segment is a continuation of that transformation series.

The hypopharynx is complex and includes two ovoid sclerites which are joined to a median sitophore sclerite by chitinous filaments. The relationships which these filaments bear to each other appears to be a useful character for distinguishing higher groupings within the order. They may run free individually to the sitophore sclerite or they may fuse. The separated condition seems to be an unspecialized, plesiomorphous state.

The prothorax is reduced in winged forms, in some groups more so than in others but it is relatively better developed in apterous forms. In some genera it is lobed; the arrangement and form of its marginal setae are occasionally useful taxonomic characters at the specific level.

The meso- and metathorax are developed in accordance with powers of flight. The former is always the better developed segment in winged forms and the two segments are strongly fused. The pleura are well-developed and the sterna reduced in winged forms. On the other hand, flightlessnessoften involves greater independance and more nearly equal development of the meso- and metathorax. Where the body is flattened, the pleura are reduced but the sterna are broad; in some groups the arrangement of the setae of the sterna afford useful taxonomic characters at the species level.

The meso- and metathorax are fused in fossil forms with wings but well developed lobing is not apparent. Reduction of the pterothoracic segments is apomorphous for the Order as a whole. As the development of the thorax is linked closely with wing development and function and other features associated with polymorphism care needs to be exercised in its use as a systematic feature. Reduction and independance of segments can be regarded as apomorphous conditions. Reduction of the pleura and extension of the sterna associated with flattening of the body are apomorphous conditions. Wing reduction occurs in a high proportion of the families and parallelism and convergence in characters associated with it are to be expected.

<u>The coxae</u> of the metathoracic leg may bear an organ (Pearman's organ or coxal organ) which is apparently stridulatory in function (fig. 2.5). Each organ consists of two parts, a rounded dome-like portion of the integument which is variously roughened and an adjacent membranous area of integument (typanum). In its simpler form the organ lacks the typanum and so consists only of the rugose dome, which varies in size. The stridulatory organ tends to occur in its simpler form in the Trogiomorpha and tends to be so in those forms of the Troctomorpha and Psocomorpha which are apterous, or strongly brachypterous. It appears in its most complex forms in those groups of Psocomorpha which are fully winged. It tends to be absent altogether in the wingless forms of the Trogiomorpha and in some of the wingless Troctomorpha and Psocomorpha. This organ is clearly an apomorphous structure for the order as a whole. It is plesiomorphous in its simple form and apomorphous in its more complex specialized form; its loss or reduction is a character which is correlated with wing reduction or loss and it may be strongly reduced in apterous genera which in every other way resemble specialized winged genera. In general it is better developed in males than in females and is absent from nymphs.

<u>The femora</u> are normally cylindrical; occasional departures from this condition to a slight extent are sometimes found. Fossil forms had cylindrical femora and departure from this appears to be an apomorphous state.

The tibiae are also usually cylindrical and are armed with a variable array of spines and ctenidiobothria. These become larger and arranged in more definite fields in some groups. The tibiae bear apical spines, reduction in size and number or loss occurs and seems to represent an apomorphous condition.

The tarsi are 2- or 3-segmented in adults and 2-segmented in nymphs. They usually bear a row of ctenidiobothria along the inner side, especially on the basal segment or the first two segments in 3-segmented forms. In 2-segmented tarsi the first segment is usually the longer; in 3-segmented tarsi the first is usually the longest and the second the shortest. The tarsi in fossil forms were 4-segmented, which is apomorphous, relative to most other fossil groups, which had more than four segments. The reduction in the transformation series has been continued in living forms leading to the modern 2- or 3-segmented condition. In many brachypterous or apterous genera the tarsi are 2-segmented although these genera are clearly closely related to other 3-segmented alate genera when many other features are considered. Reduction in number of tarsal segments may, therefore, be the result of parallelism or convergence and in some cases appears in genera which are neotenic (see page 284).

The claws (figs. 2.6, 4.11, 4.110) may be strongly curved near the apex or may be almost straight; they may be long or short and they may or may not have a preapical tooth. The ventral edge may carry a series of fine points giving a comb-like structure instead of or as well as having a preapical tooth. Proceeding from the more generalized to the more specialized condition the transformation series probably runs from a plesiomorphous condition in which there is a series of spinules through one in which there are a few or only one preapical tooth to one in which there are no preapical teeth. It seems, also, that the curvature of the claw increases and relative length decreases through the same transformation series. The presence of one preapical tooth or its absence appears to be closely connected to habitat preferences in that leaf-dwelling forms tend to lack the tooth whereas bark-dwellers tend to retain it.

The wings, which have been used so extensively in the past as taxonomic characters must receive careful consideration; we have more information available on wings in the fossil forms than any other organs (figs. 2.7, 4.4, 4.317, 4.330, 4.366). The usual number in the order is four. They are usually membranous, but may be hardened and elytriform. All degrees of development from macroptery to aptery occur and venational variation is great; in some cases the veins are hardly distinguishable and in others there is such a multiplicity of branches and cross-veins that homologies are not immediately apparent. The hind wings are always smaller and their venation more reduced than in the fore wings. The wings may be broad or narrow, rounded or pointed. They are usually held roof-wise over the abdomen but in a few groups they are held with their flat surfaces almost horizontal. The surface of the wing membrane may be glabrous or bear setae or scales; microtrichia are usually present and more or less evenly distributed. The veins and wing margin are setose or glabrous. The degree of development and the arrangement of wing setae are important taxonomic characters. Certain venational features are useful, sometimes at the species level and sometimes for higher category definition.

In the fore wing the subcosta is reduced, one section is sometimes evident in the basal half of the wing and there is a distal remnant forming the proximal border of the pterostigma. The pterostigma is bounded behind by R_1 and its membrane may be thickened or not. At the point of origin of the distal section of Sc is the stigmapophysis, an organ for holding the hind wing in position when not in use; it varies in form and degree of development. Rs is usually forked into two branches; multiplication of the branches is found in some genera. Rs may be fused to the media at a point or for a length or may be joined to it by a cross-vein; it is also sometimes joined to R_1 by a cross-vein which may be represented only by a variably developed rudiment arising from the hind angle of the pterostigma. M is usually fused with Cu_1 for a length basally; it is normally three-branched, but its branches subdivide in some genera or it is unbranched. Cu_1 is usually forked, the area between the fork forming the very characteristic psocopteran wing feature termed the areola postica. The point of bifurcation and the degree of curvature of the branches result in variation in the form of the areola postica. Cu_{1a} may be fused with M at a point or for a length or be joined to it by a cross-vein. The fusion or contact so established determines whether cell M is open to the wing margin or closed. In the latter case a closed cell is formed termed the discoidal cell. The shape and proportions of this cell vary. Cu_2 runs to the wing margin and may meet the end of IA at the margin, the point of junction being termed the nodulus. The end of Cu_2 carries a wing coupling organ of variable form. Vein 2A is present in the fore wing in few genera.

The hind wings are smaller than the fore wings and the venation more reduced. Sc is usually not evident and R_1 runs to the fore margin of the wing about three quarters of the way along the wing. Rs is usually divided the ends of the branches embracing the wing apex. M + Cu is usually fused basally with R diverging from R near the wing base as a single vein which divides. The anterior branch (M) may be fused with Rs for a length, may meet it in a point or be joined to it by a cross-vein. M_1 after its separation from Rs may run to the wing margin as a single vein or may divide. Cu_1 and Cu_2 are usually not branched and there is usually only one anal vein.

There are two cross veins which appear frequently in the fore wing in various families of the order. One runs from the hind margin of the pterostigma to Rs and the other from the areola postica (from Cu_{1a}) to M.

Wing buds are evident in the nymphs of forms with winged adults from the second instar but venational or other features are not usually discernible until after the final moult.

In general terms it can be said that the psocopteran wing has undergone reduction in relative size of the hind wing and that the venation has become reduced and more specialized in the evolutionary sequence of events. Other modifications, such as sclerification of the membrane to form an elytriform structure or an alteration in proportions to produce a strap-like wing, have occurred from time to time; these changes are obvious when encountered and clearly represent apomorphous states. These insects are, in fossil forms, fully winged; brachyptery and aptery are clearly apomorphous in living forms. The general occurrence of these phenomena in families clearly not closely related within the order represents parallel evolution. Loss of veins has been carried to extremes in some genera without too excessive a degree of wing reduction; in others, vein reduction has been accompanied by wing reduction and also in some instances, by hardening of the membrane. Cases of an increase in the number of branches of veins are fairly frequent and represent an apomorphous condition in modern species. The general change from wing homonomy to wing heteronomy is apomorphous; the Dichentomidae are virtually homonomous so far as wings are concerned.

The wing form, apart from size, in Permian species has been modified in modern species. The anal area tends to be reduced and the wing to narrow somewhat. It is pointed or narrowly rounded in some groups. These changes from the broad, rounded form of wing are clearly apomorphous.

It is not known whether the wings of Permian species were hairy or glabrous. It seems reasonable to suppose that they were hairy and that the general tendency exhibited by most insect groups to move from a hairy towards a glabrous condition or towards a condition in which hairs become specialized in form, function and position, was also followed by the Psocoptera. If this is so, membrane hairs seem to have disappeared early in the sequence, followed by reduction in number of vein hairs and hairs of the margin to a single row; the final stage is complete glabrosity. Specialization of setae into scales has occurred in two families.

In the forewing of fossil species Sc is usually well developed (fig. 5.1) and ends in R_1; in a few species it ends on the wing margin; reduction of this vein is apomorphous as is the ending of the remnant on the wing margin in some recent forms. The division of the vein into two, leaving an apical section to form the proximal border of the pterostigma is an apomorphous feature.

There is no evidence to suggest that the pterostigmal area in the fossils was thickened; it is so in many modern groups.

In fossil forms Rs is usually 2-branched (fig. 5.2) with a long stem before the bifurcation and this is the condition in the majority of Recent forms; departure from this condition by reduction or increase in number of branches can be considered an apomorphous state.

In Dichentomum (Permian) R and M are widely separated at the base of the wing; M arises within the membranous area of the wing without any basal connections (fig. 5.2). This also occurs in some Permopsocidae. Fossil forms frequently have Rs and M connected by a crossvein near the midwing (fig. 5.8) and other crossveins may be present. A transformation series can be established for the relationships between Rs and M from a condition in which the two veins are completely separate, through one in which they are connected by a cross-vein to one in which there is greater or lesser fusion for a length before they separate again. The variability seen in the Rs - M relationship in some species suggests that those occasions on which the connection does not conform to that of related species need careful consideration. Rs is connected by a cross-vein in some living and in many fossil forms to the apex of the pterostigma (fig. 5.1) which must be considered as a plesiomorphous condition as a whole in the living forms. In many living forms this cross-vein is reduced to a rudiment of a vein, frequently being referred to in the literature as a "spur-vein" arising at the hind angle of the pterostigma (fig. 4.421). Reduction and, finally, loss of this feature may be considered, in general, to be apomorphous. This feature may return to some extent in groups in which apomorphous vein bifurcation is excessive, and occasionally when it is not.

M is 4-branched in fossil forms; reduction in number of branches or increase in branching are apomorphous features. It is most frequently 3-branched in living forms. M and Cu_1 are fused basally in living forms; this lengthy basal fusion is an apomorphous condition as compared with that found in fossil forms where fusion may be short (figs. 5.2, 4.426).

Cu_1 is usually forked, in both living and fossil forms. In general, branching nearer the wing base (fig. 4.4) is plesiomorphous in relation to more distal branching (fig. 4.158). Also, the tendency for Cu_{1a} to curve after leaving Cu_{1b} (fig. 6.77) is apomorphous in relation to a straighter condition (fig. 4.158). The angle of divergence of Cu_{1a} and Cu_{1b} varies and a narrower angle (fig. 4.4) is generally plesiomorphous in relation to a wider angle (fig. 4.158). In some forms Cu_{1b} becomes indistinct (fig. 4.455) in a few Cu_{1a} has been lost (fig. 4.575). The relations between Cu_{1a} and M vary from no contact, through connection by a cross-vein to a condition of fusion for a length; this sequence probably represents the transformation series. The presence of a nodulus is apomorphous in relation to separate junctions of Cu_2 and IA with the wing margin, as found in fossil forms. Where a nodulus is present, the form of the wing-coupling apparatus presents a transformation series from or in which there is a series of hooks to a condition in which the hooks are fused into a single specialized hook arising from one point near the end of Cu_2. It is doubtful whether Permian Psocoptera had coupled wings. The presence of a second anal vein is a plesiomorphous condition; in most Recent forms only IA is present.

Progressive reduction and specialization in hind wings appear to have been along similar lines to the fore wing but to have been carried to greater extremes.

The abdomen usually shows but few features of taxonomic importance apart from the genitalia and the terminal structures surrounding the anus. There are nine abdominal segments, usually poorly sclerotized, plus a median dorsal epiproct and two lateral paraprocts.

The abdomen is 10-segmented in fossil forms, although in most fossil specimens the abdomens are poorly preserved. In Dichentomum sojanense Becker-Migdisova, however, the abdomen is very well known. The integument is usually fairly thin except for the terminalia. Some species have thickened tergites on the abdomen.

The paraprocts (figs. 2.8, 4.6, 4.651) may carry a great variety of sclerotized adventitious structures in the form of hooks, spikes, papillae or other structures. There is usually a well-defined field of setae, each of which arises from a rosette-shaped base, of varying extent, termed the trichobothrial field; this field may be reduced to a small group of setae or may be absent. There are no cerci in either fossil or living forms. In many groups considered as "primitive" the trichobothria are poorly developed or may be represented by a group of hardly specialized setae; the presence of a trichobothrial field may well, therefore, be a relatively recent development.

The loss of the cerci took place prior to the Permian and it seems reasonable to suppose that, by the time of appearance of modern forms, or those resembling them, the remnants of cerci would have disappeared altogether. The function of the trichobothria is not known; in groups exhibiting many characters known to be strongly apomorphous they occur in their most highly developed state, being numerous and grouped into distinct fields with specialized integumentary sculpturation between the "rosette" like bases of the individual trichobothria. They are reduced or lost in correlation with brachyptery and aptery and they do not occur in nymphs. The available evidence suggests, therefore, that they are apomorphous features not homologous with cerci. Structures of similar superficial appearance occur in distantly related insects (e.g. some Neuroptera) but true homology is doubted. Simple, rounded paraprocts probably represent the plesiomorphous condition in relation to those which bear complex structures such as the hooks, spines and processes found in the Psocidae and Hemipsocidae.

The hind margin of the paraproct may carry a small cone, simple or bifurcate, with or without attendant setae. Similar cones are found in nymphs. The strong spine found in the Trogiomorpha may represent an apomorphically strongly developed cone. In other groups the cone may remain or be lost.

The epiproct (figs. 4.498, 4.537, 4.584) is a dorsal flap which is usually simple and setose but which may be ornamented. The epiproct is probably, like the paraproct, simple in a plesiomorphous condition and an apomorphous condition is suggested by the presence of the complex structures of unknown homology which sometimes occur; they appear to be adventitious structures arising from unspecialized epiprocts several times in the history of the order.

<u>The female subgenital plate</u> arises from the

seventh sternite and covers the bases of the valves of the ovipositor (figs. 2.11, 4.189, 4.652, 4.773). It may be a simple plate or its hind margin may carry a median lobe, a pair of lateral lobes or be emarginate. The subgenital plate is usually generally setose but certain areas may bear characteristically arranged groups of setae; marginal setae may be very specifically situated. An internal, variously developed sclerite occurs on the inner surface of the subgenital plate in a few genera; this frequently, but not always, is T-shaped. It is referred to in the literature as the "T-shaped sclerite" irrespective of its actual shape.

The homologies of the lobes are not easy to determine. It is tempting to homologize them with rudimentary appendages but evidence to support such a conclusion is lacking. In no species do they assume more than the appearance of lobes. Fossil forms give no assistance here; the structures illustrated by Becker-Migdisova and Vishnyakova (1962) as gonapophyses appear, on my reexamination of their material, to be extraneous matter not to be associated with the specimen. The sex of the individual is thus in doubt and the structure illustrated as a subgenital plate may be a hypandrium. In any case, it is not as clearly definable as in the illustration and may not, in fact, have had the form illustrated. Returning to the question of the significance of the subgenital plate structures it seems that we can only assume that these in their variety of forms and specialized structures developed in relation to copulation or oviposition. If such is the case, the simple, unspecialized form of subgenital plate can be considered plesiomorphous with the lobed forms being apomorphous. The highly specialized forms with a strongly developed median lobe would be at the end of one line of development with the bilobed forms representing another line. In some groups fusion of two lobes to form a central lobe has clearly taken place. The subgenital plate has probably been subject to strong selection in the evolutionary history of several families and is an organ in which we can expect to find strong morphological modification in response to variation in functional requirements. Under such circumstances we can expect parallelism and convergence. In some groups the setal arrangement on the subgenital plate becomes specialized. From a general distribution of setae there may develop a condition in which setae of a particular area become more regularly spaced and larger; the areas involved may be of any shape and their arrangement usually involves some symmetrical pattern of occurrence. Marginal setae tend to become regular in arrangement in specialized forms even to the point of being very few and specifically or generically constant in numbers and arrangements. This specialized setal arrangement is apomorphous in relation to a generalized arrangement; setal loss is apomorphous. The so-called "T-shaped sclerite" which occurs internally on the subgenital plate in some groups appears to be a peculiar apomorphous structure.

The female gonapophyses consist, when fully developed, of three pairs of valves (fig. 2.12). The ventral valves (fig. 2.12, v.v.) arising from the eighth segment are usually styliform and glabrous but they may bear a preapical lobe and apical spinules. The dorsal and external valves arise from the ninth segment. The dorsal valves (fig. 2.12, d.v.) are usually in the form of fleshy lobes but they may be pointed and may or may not carry a preapical subsidiary lobe. The external valves (fig. 2.12, e.v.) are variously shaped, short, broad and strongly setose. Setal arrangement may be haphazard or characteristically fixed. The gonapophyses may be reduced in various ways or even absent altogether. They provide useful taxonomic characters at nearly all levels; in some groups they are useful at the higher levels and in others at the specific level. In the plesiomorphous state there are three pairs of valves. Reduction in valve development and numbers is an apomorphous condition. Such reductions have taken place in several different transformation series in the Psocoptera. The ventral valves are usually long and pointed. This appears to be the plesiomorphous state. In most cases the valve consists of a sclerotized pointed bar from which is suspended a ventral, tapering, membranous flap. Setae are absent, but apical spinules may be present as an apomorphous development. The dorsal valves are similar in the plesiomorphous condition but are prone to greater changes, with a tendency to become broader, more membranous or fleshy, and to develop spinules. A preapical membranous lobe is frequently developed. The dorsal valve also lacks setae. The external valve occurs in a great variety of forms. Presumably the simple lobe is plesiomorphous and the many other conditions (simple, bilobed, rounded, square or pointed) all indicate an apomorphous condition. The external valve is nearly always setose; in fact, in one group of genera a simple seta on a sclerified area is all that remains of the strongly reduced external valve. It is not easy to decide whether a setose condition in the external valve is plesiomorphous or apomorphous.

It could be assumed that, in keeping with the general rule within the order, the setose condition is plesiomorphous and the glabrous condition apomorphous. On the other hand, the groups which have glabrous external valves are the bearers of plesiomorphous characters in comparison with the groups which have setose external valves and which carry many apomorphous characters. The possibility that the external valves in groups which have them glabrous are not homologous to the same organs called external valves in groups which have them setose, should not be overlooked. The ventral valve (arising from the eighth segment) and the dorsal valve (arising from the ninth segment) are serially homologous. The external valves, of both types, appear to arise as basal, lobar outgrowths and it is conceivable that such lobes have arisen more than once in the group; in some of the Amphientometae the glabrous external valve is bilobed itself.

In the present interpretation of the homologies of the valves however, the conventional view is taken and it is considered that the ventral valves are true glabrous gonapophyses (outgrowth of a coxite) of the eighth segment, the setose stylus having disappeared. The dorsal valve represents the gonapophyses of the ninth segment and the external valve the setose stylus of that segment. If the setose external valves are not homologous with the glabrous external valves the latter would have to be considered as an additional gonapophysis-like organ, in lobar form, which is replacing the setose external valve which is, in the setose forms, the stylus of the ninth coxite.

There is inadequate evidence at present to solve the problem of the homologies of the ovipositor valves in the Psocoptera beyond all doubt. For the present, the weight of indirect evidence suggests that in the plesiomorphous condition the external valve is setose.

<u>The eighth sternite</u> carries the entrance to the spermatheca; this may be surrounded in its apomorphous state

by sclerifications of various forms, sometimes simple, sometimes complex (figs. 4.173, 4.809).

The male hypandrium is formed by the ninth sternite (figs. 2.9, 4.609, 4.805, 4.796). It may be anything from a simple plate with a rounded hind margin to a complex plate adorned with a variety of apophyses, hooks or other structures which may be symmetrical or not. It is clearly simple in its plesiomorphous state; the complex adventitious structures which suddenly appear and of which the homologies can seldom even be guessed at, are indicators of apomorphy.

The male phallosome (figs. 4.8, 4.67, 4.166, 4.282, 4.376, 4.543, 4.678, 4.791, 4.803) is a structure associated with the eversible end of the ejaculatory duct. It frequently appears as a sclerified ring the posterior apex of which forms the aedeagus. Arising from either side of the ring, on the outer side, is a posteriorly projecting process; these are the parameres. Within the circle of the phallosome the penial bulb may be simple or its walls may be thickened by sclerifications which sometimes assume an extremely complex and often irregular but characteristic form. The aedeagus and parameres are also found in a great variety of forms of greater or lesser complexity. The phallosome may be considerably reduced, in some or all of its parts.

In its simplest form the phallosome consists of rod-like structures supporting the walls of the ejaculatory duct (fig. 4.9). These rods may be fairly complex but are usually not attached to each other anteriorly, nor posteriorly. These are the parameres. They frequently have "sensory pores" at their distal ends. Additional sclerification, attached or not to the parameres, may be present between them near their distal ends. These sclerifications, of various forms, form the aedeagus ("inner parameres" of some authors (fig. 4.86)). The wall of the ejaculatory duct anterior to the aedeagus may develop complex sclerifications and the anterior ends of the parameres approach each other and fuse (fig. 4.515).

The stages outlined above represent the stages in the transformation series leading from a simple to complex intromittant organ. Reduction of some, or most, of the parts has taken place in one or other group, representing further stages in the transformation series (e.g. Myopsocus, fig. 4.829).

The general body form found in the order is usually robust. In some genera apomorphic flattening has occurred with associated broadening of the sternal regions. In some the abdomen is short and stout giving a rotund appearance to the insect.

POLYMORPHISM

Badonnel (1938b, 1948c, 1949b, 1959a) and Mockford (1965) have discussed polymorphism in the Psocoptera. Many other authors have mentioned it in passing or described polymorphic species. All degrees of polymorphism are to be found in the Order from simple size differences to considerable intraspecific morphological differences involving a range of characters. The occurrence of polymorphism within a group can be considered as a taxonomic character per se and is used as such in discussion of generic characterization and relationships later in this work. The occurrence of polymorphism involving morphological features which are themselves used as taxonomic characters raises certain problems. A character may vary from group to group in a fixed fashion and its variation be used in defining distinct taxonomic groups; the same variation may occur intraspecifically. For example, degree of wing development varies but is constant at a given form for a given group; some may be fully winged and some may be brachypterous. In some polymorphic species fully winged and brachypterous forms occur, sometimes in one and sometimes in both sexes. Fortunately, this does not render invalid the use of characters which are fixed in some species, but involved in polymorphism in others. In the study of polymorphic species it is always found that some characters, e.g. genital characters, remain constant and definitions can be formulated and relationships discussed on the basis of these as well as those characters which are variable within the range of polymorphism.

Care must be exercised when dealing with polymorphic groups because it is obvious that polymorphism has appeared many times in the order. Mockford (1965) records alary polymorphism in sixteen families and eighty eight species of Psocoptera.

CORRELATION OF CHARACTERS IN POLYMORPHISM

The most obvious form of polymorphism is that involving wing development i.e. so-called alary polymorphism. The wings are considered macropterous when they are fully functional and reaching beyond the end of the abdomen when not in use. The wing venation is usually fully developed as in non-polymorphic species of the same group. Brachypterous forms have the fore wings at least somewhat reduced in comparison with macropterous specimens of the same group, not reaching the end of the abdomen and usually having at least some venational differences; the hind wings are also reduced. Micropterous forms have the forewings reduced to small non-functional vestiges and the hind wings may be correspondingly further reduced or absent. Apterous forms lack both fore and hind wings. In practice, it is often difficult to make a decision as to whether some forms are to be regarded as brachypterous or micropterous and precise classification is neither possible nor, usually, necessary; the variation is sometimes continuous. As the wings of psocids become reduced in development the tendency is for the more distal parts of the wings to be affected to a relatively greater extent than the more proximal parts. Thus, the branches of the veins tend to be shortened or distorted, moreso than the main basal veins and the radial and median cells tend to become relatively more reduced than the cells towards the base of the wing.

It is usually found that a species in which alary polymorphism occurs also exhibits polymorphism in other characters. These can be divided into thoracic polymorphism and polymorphism in other characters. The variations found in the thorax are to be expected and are a direct result of differences in thoracic development correlated with wing development and ability or inability to fly. The development of meso- and metathoracic antedorsal and lateral lobes is reduced according to the degree of wing reduction and may reach the point where the parapsidal sutures disappear. The mesothoracic precoxal bridge may be narrower in brachypterous forms than in the macropterous forms of the same species.

Polymorphic characters other than those directly related to flight are surprisingly diverse. The ocelli, which are usually well developed in macropterous forms, are reduced in brachypterous forms and may be absent altogether when wing reduction is carried to extremes. The compound eyes are usually smaller with wing reduction and may be considerably reduced in apterous forms. The ctendiobothria on the tarsi are frequently reduced or disappear as wing reduction proceeds. Tarsal segmentation is not normally involved in polymorphism as most species have either 2- or 3-segmented tarsi in the adults. One species is known, however, in which winged females have 3-segmented tarsi and apterous females have 2-segmented tarsi. Some winged genera with 3-segmented tarsi have closely related brachypterous or apterous genera with 2-segmented tarsi. The antenna are often shorter in short-winged forms. The trichobothrial field may be quite large in macropterous individuals and may disappear with aptery, brachypterous forms having a reduced trichobothrial field. The cone on the hind margin of the paraproct tends to be present in brachypterous adults of groups in which it is usually absent in the winged adults. It is usually present in nymphs. As a character for use in systematic studies, polymorphism is an apomorphous phenomenon.

<u>The causes of polymorphism in the Psocoptera</u>

Very little experimental work has been done with a view to elucidating the physiological mechanisms which result in psocid polymorphism. Badonnel (1948c, 1949b, 1951) suggested that control of polymorphism in most cases was environmental, operating through hormonal influence. It was pointed out above that of the characters involved in polymorphism some were thoracic and clearly directly associated with flight ability and that the others were more widely dispersed on the organism. These latter have, however, one feature in common, that is, in one of the forms in which they occur they are nymphal features and this form is the one which is found correlated with wing reduction or aptery. Ocelli are absent from nymphal psocids. Compound eyes are relatively smaller in nymphs than in adults. The tarsi of nymphs lack ctenidiobothria. The nymphs always have 2-segmented tarsi (adults may be 2- or 3-segmented). Nymphal antennae are shorter than adult antennae. Nymphs lack a trichobothrial field on the paraprocts but nymphs do have a marginal cone. A consideration of the characters in which changes take place correlated with wing reduction shows them to be retaining their nymphal form. Characters which usually alter when the insect becomes an adult (reproductive) are being retained in the unaltered form to a later stage in ontogeny than is usual for the group. This phenomenon has been termed neoteny and it is in this sense that the term is used here.

There have, unfortunately, been various applications of the term neoteny. Wigglesworth (1961, p. 54) uses the term for the phenomenon more often referred to as paedogenesis (with reference to Dixippus). He also uses it as a synonym of metathetely (loc. cit. p. 56) and of prothetely (loc. cit. p. 63). A point has now been reached where it is necessary to make clear how this term is being applied when it is used. It is to be hoped that physiologists will clarify the situation by more careful use of the word. When alary polymorphism occurs in the Psocoptera there is a tendency for nymphal features to be carried over into the adult instars. Polymorphism in psocids appears to be neotenic in the sense indicated above.

FEEDING HABITS

With the limited knowledge of the biology of the Psocoptera it is not possible to suggest, with any certainty, a transformation series so far as feeding habits is concerned. Some species are general fungus feeders whereas other groups include species with very specialized feeding habits, e.g. some will only feed on the apothecae of lichens. It is of some value to bear in mind this specialization, which would indicate an apomorphous condition in comparison with that of general feeding.

HABITAT PREFERENCES

In the long history of a group such as the Psocoptera there must inevitably have been many invasions of new habitats as these became available and the insects would have evolved with changing habitats. Obviously, we cannot determine "transformation series" in habitat preferences within the group as a whole but at present certain genera or higher groups are typically found in certain habitat types. Where possible these habitat preferences have been here considered in conjunction with morphological features.

OVIPOSITION

Oviposition habits vary in the Psocoptera. The eggs may be laid singly or in groups; they may be covered with an encrustation formed by particles of excrement cemented together by a rectal secretion. They may or may not be covered by silken threads; the density of the threads varies from a thick mat to a few loose strands. The eggs themselves may be ovoid or ellipsoidal with a smooth chorion or they are somewhat narrowed at the anterior end and have the chorion sculptured with ridges and pits. When considering oviposition habits and eggs the original mode is very probably that in which a hard sculptured egg is laid bare and singly; later developments include a smooth chorion, grouping of eggs and the provision of special devices such as webbing and covering the eggs with an encrustation indicating more specialized ovi-position habits.

PARTHENOGENESIS

Parthenogenesis, facultative or obligatory, occurs in many species. Although the phenonemon has clearly arisen several times in the order in widely different evolutionary lines, it is nevertheless sometimes of value as an indicator of relationship when considered in con-junction with other characters. Parthenogenesis is an apomorphous attribute in relation to bisexuality within the Psocoptera.

3. MONOPHYLETIC ORIGIN OF THE PSOCOPTERA

Before proceeding to discuss the classification and phylogeny of the Order in detail it is necessary to make a decision as to whether or not the Order as a whole is monophyletic. Hennig (1966) has discussed and strongly stressed that a set of groups can be monophyletic only if they have corresponding characters which are apomorphous, that is, if their similarity is the result of synapomorphy. If the group is monophyletic the relationships of its various genera may be discussed. If it is polyphyletic, each line must be separated and discussed as a separate entity.

An examination of the Psocoptera reveals that they all have certain characters which can be regarded as synapomorphous and that those characters do not appear in any other order of insects. In fact, the definition of the group rests largely on such characters.

The presence of the rod-shaped lacinia of the maxilla is a clearly apomorphous character shared by all species and which only occurs elsewhere, probably by convergence, in a few Mallophaga. The form of the postclypeus is apomorphous and is a distinctly psocopteran feature; the labium is reduced in characteristic fashion not appearing in other orders. In the whole order, wing venation, which is reduced in its apomorphy, follows or can be derived from a basic pattern not shared by forms other than fossil Psocoptera. The lack of cerci is both characteristic and constant, even in fossil forms. The genitalia are derivable from a definite pattern peculiar to the order.

The indications are, clearly, that the Psocoptera as an order are monophyletic. The presence of the fossil forms recognizable as Psocoptera (Permopsocida) in the Permian suggests an origin for the group not later than the Upper Carboniferous.

The view that the Psocoptera form a monophyletic group is contrary to that expressed by Hennig (1966) although the presently expressed view is arrived at by following the approach and methods of that author. The characters mentioned above, as well as many others, such as male and female genitalia, are synapomorphous in the Psocoptera and appear nowhere else in the form in which they appear in the Psocoptera. These are the very criteria laid down by Hennig (loc. cit.) by which monophyly may be detected. His statement that the characters are synplesiomorphous is plainly false according to his own definition as is his statement that the Permopsocida are plesiomorphous fossils. They are, in fact, apomorphous when compared with many other fossils and are plesiomorphous only in comparison to modern psocids. This sequence of plesiomorphous leading to apomorphous characters is a requirement according to his own criteria of monophyly; the Permopsocida have, indeed, many of the characters in an apomorphous condition in the transformation series towards the extremely apomorphous condition in living forms. There is no doubt that the Psocoptera, as a group, are monophyletic. They can, therefore, as is done in the following sections of this work, be subjected to study according to the criteria required by Hennig in a phylogenetic systematic study.

4. RELATIONSHIPS AND PHYLOGENY WITHIN THE PSOCOPTERA

We are now armed with the main requirements for a study of the generic relationships within the order; from such a study we may hope to establish a classification which is both of practical use and which also reflects the relationships and phylogeny within the order. We now have:

1. Information on most of the genera and higher groupings at present accepted.

2. An indication of the plesiomorphous and apomorphous conditions of the characters involved.

3. Knowledge that we are dealing with a monophyletic group in the order as a whole.

We shall now embark on a discussion of the currently accepted genera and suprageneric groups. By searching for the groups with synapomorphous features common to them alone we should be able to establish which groups within the order represent the monophyletic groups and subgroups. It should be possible to establish where the dichotomies in the evolving lines have taken place by the detection and recognition of the subgroups with synapomorphous features or with progressively more specialized conditions in the transformation series. At the same time it should be possible to detect and recognize the sister group relationships of the groups concerned. The work thus becomes essentially a task of seeking out and recognizing monophyletic sister groups within the evolutionary history of the order and of establishing the evolutionary changes common to members of the groups. Investigation of relationships between groups will provide information on the sequence of events which has taken place during the evolutionary history of the groups. The status of the groups within the hierarchy is a different problem and although they may be discussed together it is important to bear in mind that there are two quite distinct problems, that of establishing relationships and that of establishing the equivalence of groups in the hierarchy.

We must, of necessity, discuss present groupings as at this stage we have knowledge only of the limits of these. During the following discussion it will be necessary to reassess the extent and equivalence of some of them and this will result in changes in the present classification.

In such a study the starting point chosen is of little importance as by working through the groups the end result, if it be logically arrived at, must be the same, irrespective of the starting point. We may start at the lower or higher end of the hierarchy, at the specific (or generic) level or at the ordinal level. It is convenient to start by seeking out the group which has a large array of plesiomorphous conditions in its characters and to work from that to those exhibiting many apomorphous features. A perusal of the suborders and suprafamily groups rapidly leads one's attention to the Atropetae and, in particular, to the Psoquillidae as a starting point for discussion. It should be noted that in this discussion "Psocoptera" means living Psocoptera unless fossil or amber forms are specified. The groups of genera are here referred to their present categories in the hierarchy, that is, the terms "Trogiinae", "Lepidopsocinae" and so on are used in their current sense. The question of the proper status of these groups within the hierarchy and their equivalence and relationships to other groups of Psocoptera will be discussed.

It is important to note that in the discussion only the salient features of each group will be mentioned in order to avoid extensive repetition of listing of morphological and other characters of the categories; it is clear from the generic diagnoses and the discussion of the apomorphous and plesiomorphous characters (Chap. 6, Sect. 2) which apomorphous features occur in each group. If each character were mentioned for each group this discussion would become so voluminous as to be incomprehensible and impossible to handle.

RELATIONSHIPS OF THE ATROPETAE

The group Atropetae is at present made up of the families Lepidopsocidae, Trogiidae and Psoquillidae. The Psoquillidae exhibit most of their characters in a condition plesiomorphous to that of other groups but certain characters are apomorphous in a manner not found in most other families of the order. This is so for the female gonapophyses, which are reduced to the setose external valve in the form of a long lobe. There is no second anal vein, an apomorphous feature present in most Psocoptera. The vein is retained in the Amphientomidae and some other genera. There are accessory bodies associated with the female spermatheca. The apomorphous features of the Psoquillidae which are found in other families are few, and they are found in the Lepidopsocidae and Trogiidae. The female genitalia are similar in all three families, the lacinia is similar and the female spermatheca has accessory bodies in the Trogiidae but not in the Lepidopsocidae. The Lepidopsocidae differ in having scales and in having pointed wings as well as in other apomorphous features in certain genera, such as wing sclerification, wing reduction and reduction in venation. The Lepidopsocidae, Psoquillidae and Trogiidae can clearly be considered to form a monophyletic group. They carry certain synapomorphous features not found in other groups, amongst a large number of plesiomorphous characters, which set them apart from the rest of the Psocoptera.

The fossil groups can be set off as a sister group of the Recent Psocoptera; the latter share obvious apomorphous features, e.g. wing specializations, reduction in number of tarsal segments, which indicate monophyly of the Recent forms. The relationships between fossil forms, the Atropetae and the remainder of the Psocoptera can be expressed very simply in a diagram, as in fig. 6.1.

RELATIONSHIPS WITHIN THE ATROPETAE

The ancestral group of the Atropetae clearly had an abundance of characters which were plesiomorphous to the remaining Psocoptera but had, as its main apomorphous features, the reduction of the female genitalia to the setose, lobar external valve. This condition is present in the amber genus Empheria, which is plesiomorphous in most features. It has but few setae on the wing membrane but Trichempheria, which is very similar in most respects to Empheria, has very setose wing membranes. These two genera seem to represent conditions in the transformation series in which increasing wing glabrosity is achieved.

The Atropetae can be divided into those forms which have apomorphous accessory bodies to the spermatheca and those which do not. The former include the Trogiidae and Psoquillidae and the latter the Lepidopsocidae. If we inspect the Trogiid-Psoquillid line, there is a division into those with the apomorphous condition of strong wing setae reduction and those without. These are the Trogiid and Psoquillid groups respectively, if one does not include Empheria and *Trichempheria* in the Trogiidae. These two genera, as we know, show few apomorphous features which are not common to all the Atropetae and they clearly must have arisen near the origin of the lines giving rise to the other genera of the Atropetae. The Trogiidae (again without *Empheria* and *Trichempheria*) can be divided into two groups, those with a male abdominal brush and those without (only one genus so far known, *Anomocopeus*). The genera which do have an abdominal brush in the male are similar to one another in many respects (*Trogium*, *Lepinotus*, *Cerobasis* and *Myrmecodipnella*) and with *Anomocopeus*, constitute the present Trogiinae. *Myrmecodipnella* has been described as having a remnant of a dorsal valve to the gonapophyses; the females of *Anomocopeus* are not known and it would be interesting to know whether *Anomocopeus* retains a dorsal valve remnant or not. It is not necessary to follow through this discussion to the point of considering the relationships of the genera within the Trogiinae as they form a compact group of genera which can be considered as a unit for present requirements.

Returning to consider the Trogiid-Psoquillid line of development, it is unfortunate that we do not know the condition of the female spermatheca in *Trichempheria* and *Empheria*; they have wing features (venation and wing form) more in keeping with Psoquillids than with Lepidopsocids and on this evidence, without having information on the spermatheca, we may consider that they are appropriately placed within the Trogiid-Psoquillid line rather than in the Lepidopsocid line. We know, also, that *Empheria* is apomorphous relative to *Trichempheria* in wing membrane setation and the other genera of Psoquillidae continue this tendency to glabrosity. Early Psoquillids must have been *Empheria*-like. Wing reduction marks the *Psoquilla* line of development and other wing characters in apomorphous condition characterize the other genera, Rhyopsocus, Eosilla and Balliella. As in the case of the Trogiin genera these form a compact group of genera whose precise relationships need not concern us here as they throw no light on the major evolutionary trends within the group.

We may now turn our attention to those genera which have the characteristically reduced gonapophyses but which do not have accessory spermathecal bodies, that is, to the Lepidopsocidae. In this group the wings have retained a setose condition of the membrane. They cannot, lacking the two most obvious apomorphous conditions in the Psoquillidae, be considered within that group.

Three features play an important part in providing information on the relationships within the Lepidopsocidae. These are the basal cell in the hind wing, the wing shape and the presence of setae modified into scales. The presence of the basal cell in the hind wing is a plesiomorphous condition and its loss by fusion of the adjacent veins is apomorphous and is the condition found generally elsewhere in the Psocoptera. The modification of setae into scales is clearly apomorphous as is the tendency for the apex of the wing to become pointed or strongly narrowed. In some cases the whole wing has a tendency to become narrow. The Thylacellinae retain the plesiomorphous condition of the wing membrane being setose, without scales, whereas the remaining genera have scales. If one considers the genera with scales, we find that the Perientominae and the Lepolepidinae have retained the hind wing basal cell, whilst the Lepidopsocinae have lost it. With regard to the Lepolepidinae it must be remembered that in only one of the three described species (L. occidentalis Mockford) is the hind wing well enough developed to make the cell apparent. The distinctions between the Perientominae and Lepidopsocinae are, essentially, that the Lepidopsocinae have lost the hind wing basal cell but retained thirty to fifty segments to the antennae whereas the Perientominae have antennae reduced to at most twenty four segments but have retained the basal cell. The Lepolepidinae have long antennae. The wisdom of retaining the group may be questioned but a closer investigation of the group at the specific level is required before its inclusion in the Perientominae or the Lepidopsocinae is warranted. Perhaps Lepolepis should be split into two genera. The relationships of the genera within the Lepidopsocinae, Perientominae and Lepolepidinae need not concern us here as the genera within each are characterized by small differences in venational features.

The relationships of the main groups of genera within the Atropetae as established above by considering the relative plesiomorphy and apomorphy in various characters can be summarized as in figure 6.2. From this it will be seen that the arrangement within this group does not differ greatly from that at present accepted but Empheria and Trichempheria are associated with the Psoquillidae rather than the Trogiidae; mainly on the evidence of wing form and venation.

RELATIONSHIPS OF THE PSOCATROPETAE

In the classification at present in use the Psocatropetae are given sister group equivalence with the Atropetae, the two family groups being divisions of the Trogiomorpha. The two family groups, therefore, should have some apomorphous features in common if they have arisen from some common stock and form part of a monophyletic group. It is, in fact, very difficult to find any such features common to the Atropetae and Psocatropetae. It is true that the female genitalia are reduced but inspection of the Psocatropetae reveals that the reduction and the form of the remaining valves is somewhat different in the Atropetae from that found in the Psocatropetae. In the latter group there is frequently a dorsal valve remnant present and sometimes even a ventral valve, indicating that the degree of reduction is not as great as in the Atropetae and the external valve is always broad, membranous and bears a few long setae, frequently bearing also some specialized large setae near the broad, rounded end. The Psocatropetae also have a few apomorphous features of their own such as the loss of the sensillum on the maxillary palp and the presence of a nodulus. They share some venational features such as fused Rs and M with many groups. It is not easy to justify the view that the Atropetae and the Psocatropetae bear a sister group relationship to one another. The Psocatropetae appear to form a monophyletic line of development in which there has been parallel development with other distant groups in several features. Such characters as the Rs-M relationship, the nodulus, the reduction in wing setae, secondary antennal annulation and the reduction of the female gonapophyses seem to be parallel apomorphous developments to the conditions found in other groups. The Psocatropetae retain many plesiomorphous character conditions, such as a basal cell in the hind wing; a well developed Sc in some genera, branching M in the hind wing and long antennae, the form of eggs and mode of egg laying are plesiomorphous. The relationships between the Psocatropetae and the other suprafamily groups is admittedly a difficult problem to solve; that they form a separate line of development is a possible conclusion. On the other hand, the reduction in female gonapophyses would suggest community of origin between the Atropetae and the Psocatropetae. If this is taken as a sufficient basis on which to regard them as sister groups then it must be assumed that the nodulus has developed more than once in the evolutionary history of the group; this seems not unreasonably the result of wing and venation reduction in which the ends of Cu_2 and IA become approximated at the wing margin.

Egg laying habits assist us little in making a decision of the above alternatives. The method of laying and the egg form are clearly plesiomorphous.

These conclusions have been arrived at by a study of the morphological data. It is interesting to consider such ecological data as is available. The Lepidopsocidae are mainly bark and leaf litter inhabitants; the Trogiidae are mainly found on bark and rocks and the Psoquillidae are inhabitants of dried leaves, bark and birds' nests. In general these insects can be said to be found on dried leaf material, whether on the ground (litter), on the trees (dried leaves) or in birds' nests (material of leaf or fibre origin) and on rocks. On the other hand, the Psyllipsocidae and Prionoglaridae are essentially cave dwellers, occur under stones or are found in houses (which in an ecological sense can be considered as a cave). The two groups, the Psocatropetae and the Atropetae have, therefore, some degree of habitat preference and each line of development has evolved some specialization in habitat choice. In both groups a clearly plesiomorphous condition has been retained in the sculptured eggs and the habit of laying them singly without any additional protection (details not known for Prionoglaridae).

The Psocatropetae are essentially cave dwellers or associated with human habitation; two habitats which are really similar to one another in many ways. The Atropetae are found in human habitations, caves, under stones, in leaf litter, birds' nests and on and under bark. They too, are essentially inhabitants of secluded situations. In many genera there is a range of habitat choice, suggesting relative lack of specialization in habitat paralleling relative lack of morphological apomorphy.

The conclusion here is that the Atropetae and the Psocatropetae can be considered as two diverging evolutionary lines of one stock; they form two sister groups derived from the same stock.

The relationships between these groups and the rest of the Psocoptera are indicated in figure 6.1.

RELATIONSHIPS WITHIN THE PSOCATROPETAE

Of the two families at present included in the Psocatropetae, the Psyllipsocidae and the Prionoglaridae, the genera of the Psyllipsocidae are clearly a monophyletic group of closely related genera, connected by the apomorphous condition of the female gonapophyses of a form not found in quite the same condition elsewhere in the order. Other apomorphous features already mentioned when discussing the relationships of the Psocatropetae indicate monophyly for the genera. The Prionoglaridae includes only one genus, which is quite remarkable in the order in that the lacinia is lost at the final moult and the mandibles become sickle-shaped. The phallosome of the male is also of peculiar form of which the homologies, even in relation to the rest of the Psocatropetae, cannot be determined. The genera of the Psyllipsocidae have apomorphous venational and other features, such as secondary annulations on the antennal segments, a reduced basal section of Sc; Rs and M is fused for a length. They also exhibit various degrees of wing reduction and polymorphism occurs in *Psyllipsocus*. Clearly, *Prionoglaris*, with plesiomorphous venational features and some apomorphous features peculiar to itself forms a line of evolution of its own in a sister group relationship with the Psyllipsocidae. It remains now to discuss the relationships of genera within the Psyllipsocidae. The genus *Speleketor* exhibits the most plesiomorphous wing vein condition but shows apomorphous features in the strong reduction of the female genitalia, in the hairless wings and in the development of the phallosome. The venation of *Speleketor* and *Prionoglaris* are very similar and are clearly the most plesiomorphous genera of the Psocatropetae in this respect. In all other genera more apomorphous wing features are found. *Dorypteryx* and *Dolopteryx* are similar but *Dorypteryx* has more reduced, narrower, wings with fewer veins remaining. In genitalia features the genera are very similar to one another. The wings of *Psocatropos* are reduced but not to the extent of those of *Psyllipsocus* (macropterous forms) although *Psyllipsocus* is polymorphic in some species. There is considerable reduction in the general amount of body and wing setation in *Psyllipsocus*. The relationships of the genera other than *Speleketor*, to which they all collectively form the sister group, can be described as follows. The genera *Psocatropos*, *Dorypteryx* and *Dolopteryx* form a group having in common strong wing reduction and retaining a degree of setation not found in *Psyllipsocus* and these genera form a sister group to *Psyllipsocus*. *Dolopteryx* and *Dorypteryx* together form a group synapomorphous in the extent of wing reduction which is greater than in *Psocatropos*. The probable relationships of the groups of the Psocatropetae can be diagrammatically indicated as in figure 6.3.

RELATIONSHIPS OF THE TROCTOMORPHA

In the present classification the Troctomorpha are given subordinal rank with two included family groups, the Amphientometae and the Nanopsocetae. The relationships of the Amphientomidae (sens. lat.) (divided into several families) to the Nanopsocetae and other Psocoptera have recently been discussed by Mockford (1967). This is the only attempt, other than the present one, of which I am aware in which any of the Psocoptera have been dealt with from a phylogenetic point of view using the principles set out by Hennig; it deals primarily with the position of genera related to Electrentomum.

The Amphientometae and the Nanopsocetae are united by several apomorphous features. The T-shaped sclerite of the subgenital plate, the tympanum of the hind coxae, the secondary annulations of the antennae, the tendency to reduction in number of antennal segments and the lack of setae on the external valve of the gonapophyses and the habit of laying smooth eggs encrusted with debris are all apomorphous conditions. The male phallosome is interesting in that it is closed anteriorly or nearly so, with an anteriorly directed point; the two main longitudinal elements, so conspicuous in the phallosomes of the groups treated so far, which are usually divergent anteriorly, have here approached one another or fused to give, in some cases, a wishbone-like framework to the phallosome. This is an apomorphous condition relative to that found in the Trogiomorpha. It is noteworthy that a somewhat similar form is found in the Ptiloneuridae, in fact, this apomorphous condition of closure of the anterior end of the phallosome appears to be of considerable significance and unites the Troctomorpha and Psocomorpha in opposition to the Trogiomorpha. Mockford (loc. cit.) when discussing the relative status of the groups Nanopsocetae and Amphientometae concluded that the Nanopsocetae could not be subordinate to the Amphientometae, that the Trogiomorpha could not be subordinate to the Nanopsocetae and that both the Trogiomorpha and Nanopsocetae are monophyletic lines not included within the Amphientometae. The monophyly of the Trogiomorpha has been discussed above. The Amphientometae, in addition to the apomorphous features which they share with the Nanopsocetae, have a nodulus, which is undoubtedly an apomorphous feature. Mockford (loc. cit.) reasonably concludes that the nodulus has arisen more than once in the order. Its presence in the Amphientometae but not in the Nanopsocetae marks out the two main troctomorph lines of development. The Amphientometae have tarsal ctenidiobothria and an enlarged postclypeus, both apomorphous features. These are not, however, here considered to be of vital importance in indicating monophyly of the Amphientometae and Psocomorpha as the ctenidiobothria could well have arisen more than once and the form of the postclypeus varies considerably within quite narrow limits in many parts of the order, in some cases within what are clearly generic limits. Although its bulbous form is apomorphous relative to a flattened condition in general within the order, it has clearly reverted to a flattened condition in many cases and this character is considered reliable only within narrow group limits. The Troctomorpha, therefore, appear to represent a monophyletic line of development arising from a group which had retained many plesiomorphous characters, including the second anal vein, Rs and M joined by a crossvein, setose wing membrane and a full set of gonapophyses with a setose external valve but which had developed the apomorphous features mentioned above. With the closure of the phallosome there was development of sclerotization of the penial bulb. From such a group are derivable the Troctomorpha on the one hand and the Psocomorpha on the other.

In both Amphientometae and Nanopsocetae the eggs, where known, are smooth, laid singly but covered with an encrustation of debris. This is in strong contrast to the sculptured, uncovered egg of the Trogiomorpha. This synapomorphous egg character and habit is additional evidence for regarding the Nanopsocetae and Amphientometae as being derived from the same line. The Epipsocetae also have this egg character and it will be shown on morphological grounds that this group includes, in some features, the most plesiomorphous Psocomorpha which, it is suggested, also arose from the line from which the Troctomorpha developed.

So far as habitat preferences are concerned the Musapsocidae and Troctopsocidae are predominantly dry leaf inhabitants; the Compsocidae and the Amphientomidae are found mainly on bark on or under rocks with a few species of the latter family occurring in termites' nests.

The Liposcelidae are bark dwellers, living on or under bark, but also occurring in leaf litter and invading houses and stored products. The Pachytroctidae are essentially dried leaf inhabitants whereas the Sphaeropsocidae live in moss, in caves, under stones and in leaf litter. It would seem, therefore, that in general the habitats occupied by the Troctomorpha are similar to those of the Atropetae but that some specialization has taken place towards rocky habitats in the Amphientomidae and towards a bark habitat in the Liposcelidae. It is not without significance that these two families are also considered the most apomorphous of the Amphientometae and Nanopsocetae respectively on purely morphological grounds.

The relationships of the major groups so far discussed are indicated in figure 6.4.

RELATIONSHIPS WITHIN THE TROCTOMORPHA

The two main lines of development suggested above correspond to the two presently accepted family groups, the Nanopsocetae and the Amphientometae; the Nanopsocetae have the apomorphous conditions of wing membrane glabrosity and the loss of M_3 (or even greater vein reduction) and the second anal vein in the fore wing as well as such modifications as flattening of the body and shortening of legs in some genera; the Amphientometae have the apomorphous nodulus (cf. Mockford, loc. cit.) as well as such features as development of scales in some genera.

RELATIONSHIPS WITHIN THE AMPHIENTOMETAE

Prior to the work of Mockford (1967a) the Amphientometae consisted of two families, the Amphientomidae and the Plaumannidae (now Troctopsocidae). The former family consisted of four subfamilies, two of which, the Amphientominae and the Tineomorphinae, contained scaly-winged species; the others contained a variety of genera including some forms from amber, many of which were poorly known. Mockford (loc. cit.) rearranged the genera into five families and discussed their relationships. In brief, he concluded that they could be considered a monophyletic line which included also the Psocomorpha as a final line of development arising from the same line that gave rise to the Amphientomidae. This conclusion was based on the common possession of ctenidiobothria, enlarged postclypeus and a nodulus. As pointed out above, these features probably do not necessarily indicate community of origin and the presence of scales in the Amphientomidae (apomorphous feature) and loss of setae from the external valve of the gonapophyses (also apomorphous) make it unlikely that the

Psocomorpha, which have these latter features in plesiomorphous condition, could have arisen after the development of these characters within the line which gave rise to the Amphientometae and, more especially, the Amphientomidae. Consideration of relationships within the Amphientometae should not, therefore, include the Psocomorpha. Mockford's conclusions regarding the relationships within the Amphientometae are considered correct as far as present knowledge permits; he was justifiably unable to place the genera Electrentomum and Parelectrentomum. It is not necessary to repeat his discussion here; it is sufficient to reproduce that part of his phylogenetic diagram which indicates his conclusions so far as the Amphientometae are concerned (figure 6.5).

RELATIONSHIPS WITHIN THE NANOPSOCETAE

The Nanopsocetae is the sister group to the Amphientometae. It arose, like the Amphientometae, from a stock in which the glabrosity of the female genitalia, the T-shaped sclerite of the subgenital plate and the habit of laying smooth, encrusted eggs were already established.

The Nanopsocetae have also lost the second labial palp segment; they did not develop the nodulus; the meso- and metanota are often fused and various degrees of venational reduction, wing reduction or modification by sclerification are common. The families involved are the Sphaeropsocidae, Pachytroctidae and Liposcelidae.

The Liposcelidae exhibit a wealth of apomorphous characters over and above those common to other Nanopsocetae. The body is strongly depressed and the legs are relatively short; the labial palps are characteristically shaped and bear external, subapical papillae; the pronotum is divided into lobes; the venation, when wings are present at all, is reduced to indistinct thickenings of the membrane and M and R_1 when recognizable, are not branched in the fore wing. There is a tendency for fusion of abdominal tergites and the meso- and metanota are fused in apterous forms. Investigation of the Sphaeropsocidae reveals that, when wings are present, they are elytriform with incomplete venation. There is some tendency for fusion of abdominal terga and the phallosome is anteriorly closed (in Liposcelidae some species still retain a small anterior gap) by convergence of the longitudinal bars; the meso- and metanota are fused in apterous forms.

In the Pachytroctidae apterous forms have separate meso- and metanota and other relatively plesiomorphous characters but they have lost M_3 in the fore wing.

The Sphaeropsocidae and the Liposcelidae have some apomorphous features in common, such as wing reduction with fusion of meso- and metanota and abdominal tergites; each family has some apomorphous features of its own such as body depression and labial palp shape in the Liposcelidae and elytriform wings in the Sphaeropsocidae. It appears that the Liposcelidae and Sphaeropsocidae are two sister groups which together form the sister group of the Pachytroctidae. The Pachytroctidae have no apomorphous features in common with either the Liposcelidae or the Sphaeropsocidae which they do not have in common with the other family. The Liposcelidae and Sphaeropsocidae, however, have some common apomorphous features shared with the Pachytroctidae as well as some common to them only. The relationships between the families, therefore, are such that the Liposcelidae and Sphaeropsocidae form one line of development and the Pachytroctidae another. The first two families each represent an independant line arising from their common stock. These suggested relationships are indicated in figure 6.6.

RELATIONSHIPS OF THE PSOCOMORPHA

We have so far considered two of the three currently recognized suborders. In terms of the proportion of known species, however, they constitute only about 20% of the order. The remaining 80% are placed in the Psocomorpha. Reasons for regarding the Psocomorpha as a monophyletic assemblage are given below. The group exhibits many apomorphous features in various stages of their transformation series and with such a high proportion of the species sharing these it is not surprising that between them they show considerable variety of apomorphous features in the subordinate groups and that many of them would retain plesiomorphous features. The suborder as a whole, therefore, appears superficially as a very varied group.

The main features which point to the Psocomorpha as being a monophyletic group are:- the antennae are reduced to thirteen segments (occasionally less) and these tend to have the segments progressively shorter towards the apex; the labial palps are unsegmented and relatively small; winged forms have ctenidiobothria and trichobothria and the pterostigma is thickened; Pearman's organ is usually well developed and strongly chitinized, its reduction usually being associated with loss of wings; the hypopharynx has the chitinous filaments separated only at the posterior extremity; a nodulus is present and the wing coupling apparatus is in the apomorphous form of a single hook and not a series of separate hooks; the phallosome is closed anteriorly (or apparently reduced from such a condition).

We have, in effect, so far followed the probable evolutionary history of the order and have established the transformation series within the more "primitive" parts of the order and find that prior to the diversification of the Psocomorpha, which we shall now discuss, the most recent psocopteran had the features enumerated above in apomorphous form whilst retaining others in plesiomorphous condition. A second anal vein was present, Rs and M were connected by a crossvein, the tarsi were still 3-segmented, the female gonapophyses consisted of three pairs of valves with the dorsal valve divided or lobed and the lacinia had a broad apex; there were other plesiomorphous features, such as heavy setal covering. The development of apomorphous conditions from these and other plesiomorphous conditions and the further modification of those considered already apomorphous in relation to the other suborders constitute the changes which took place during the diversification and evolution of the Psocomorpha to give the present variety of subordinate groups within the suborder. As before, our task is that of establishing which groups are monophyletic within the suborder, basing our conclusions on the possession of synapomorphous features peculiar to the subordinate groups. Within this suborder apomorphy has been carried to its extremes.

RELATIONSHIPS WITHIN THE PSOCOMORPHA

In order to find a starting point for discussion it is convenient to seek out a group which has the apomorphous characters which permit its inclusion in the Psocomorpha but which has also as many plesiomorphous features as possible. Two groups can be considered, the Epipsocetae and the Pseudocaeciliidae. The former group has retained a Rs-M crossvein, 3-segmented tarsi, a second anal vein in some genera and a plesiomorphous phallosome. The Pseudocaeciliidae, although retaining plesiomorphous male and female genitalia, share other apomorphous features with a large proportion of the genera in the suborder. It is preferable, therefore, to start by considering the Epipsocetae. As pointed out previously, the choice of starting point does not affect the final conclusion.

It is necessary to decide whether the Epipsocetae is a monophyletic group. They have elongated heads, with long genae, transverse chitinized bars traversing the labrum, the outer margin of the mandibles rather strongly angled, the setose external valves of the gonapophyses are basally fused to the elongate dorsal valves. In extreme cases, the gonapophyses are further reduced to the fused external and dorsal valves the resultant compound "valve" being setose but extended into a distal point which represents the apex of the original dorsal valve. This combination of apomorphous features is found in no other group of Psocomorpha; the Epipsocetae constitute a monophyletic line.

By far the greater proportion of genera of Psocoptera have Rs and M fused or the relationship between these veins can be derived from such a condition even when there is a short crossvein present (see below). This fusion is considered an apomorphous feature which indicates monophyly for all groups other than the Epipsocetae, Polypsocidae and Calopsocidae. Each of these groups has apomorphous features of its own which prevent inclusion in any of the groups which have Rs and M fused.

The Polypsocidae have strongly reduced female genitalia. The reduction is superficially similar to that found in the Caecilietae but if we consider the Polypsocidae to be a sister group to the Caecilietae it is necessary to agree that fusion of Rs and M has taken place many times during the evolution of the Psocomorpha. It seems more reasonable to suppose that reduction of the female gonapophyses to leave only the dorsal and ventral valve had occurred independantly in the Polypsocidae and Caecilietae. It is clear from the variety of forms in which they are found that reduction of gonapophyses has occurred many times in various ways and two separate reductions of the external valve seems more likely to have occurred than many independant fusions of Rs and M in groups which are otherwise somewhat different in their apomorphous features. Additional evidence for not associating the two occasions on which reduction has taken place is to be found in the egg laying habits and habitat preferences of the Caecilietae. The Polypsocidae have in the past been united with the Caeciliidae; the latter group has a strongly apomorphous method of egg laying in that they lay smooth eggs in groups, covered with silken threads. Also, they inhabit, in general, living leaves. Unfortunately, we do not have information on egg laying in the Polypsocidae. If it should be found that they lay smooth eggs in groups and cover them with silk it may be necessary to reconsider their affinities. If they lay eggs singly, encrusted with debris, this would be additional evidence for separating them from the Caecilietae and placing their origin prior to the development of those Psocomorpha in which Rs and M are fused.

The main apomorphous features of the Epipsocetae have been listed above. It seems that the lines of development arose prior to the time when fusion of Rs and M took place, one line including the Epipsocetae and the other the Polypsocidae and Calopsocidae. This is indicated in figure 6.7. We shall discuss relationships within these before proceeding to the rest of the suborder.

RELATIONSHIPS WITHIN THE EPIPSOCETAE

At present within the Epipsocetae there are recognized three families. Of one of these, the Callistropteridae, we know little other than wing and tarsal characters. The other two families each appear to represent monophyletic lines within the Epipsocetae. They share the apomorphous features which are peculiar to the other Epipsocetae but each has apomorphous features of its own. On the one hand the Epipsocidae have 2-segmented tarsi, more strongly modified female genitalia than the Ptiloneuridae, a simplified phallosome, reduced setation of the veins and wing margin and only one anal vein. The Ptiloneuridae have many and various adventitious apophyses, hooks and spines on the hypandrium and the paraproct is also frequently ornamented to a varying extent. The relationship of the monotypic Callistopteridae to the other two families cannot be established although its apomorphous wing venation, involving fusion of R_1 with R_{2+3} and the separation of R_{4+5} into two veins prevent its inclusion in either. The loss of the second anal vein and the loss of a tarsal segment suggest epipsocid rather than ptiloneurid affinities and this relationship is tentatively suggested and indicated in figure 6.8.

The loss of the second anal vein has probably occurred several times in the history of the order. In general, in the whole class Insecta, there is a tendency within each order for the hind portion of the wing to be reduced with resultant narrowing of the wing, especially in the basal areas, as part of the process of increasing flight efficiency.

The genera within the Ptiloneuridae form an interesting complex. The group from which the Epipsocetae (and the Psocomorpha) arose had a branched media in the hind wing. The genera in the Ptiloneuridae appear to have become apomorphous in this character in two ways; one group of genera (*Triplocania*, *Cladiopsocus* and *Euplocania*) have an unbranched media in the hind wing (as have most of the Psocomorpha) whereas *Ptiloneura* and *Ptiloneuropsis* have this vein multibranched. With this latter development there has, in both genera, been an increase in the number of branches of M in the fore wing and the areola postica has become tall in *Ptiloneuropsis* being joined to M by a crossvein. *Ptiloneura* and *Ptiloneuropsis* are very similar and the wisdom of maintaining them as separate groups could be questioned. In any case, these two genera clearly form one line of development in the Ptiloneuridae and the remaining three genera another.

Of these, *Cladiopsocus* stands apart with its strongly apomorphous wing vein reticulation. In *Triplocania* the paraproct bears rugose areas, an apomorphous feature; in *Euplocania* the fore wing has only one row of setae on the veins whereas *Triplocania* has two. These two genera seem to form a sister group to *Cladiopsocus*. The relationships of the genera of Ptiloneuridae are indicated in figure 6.8.

There are four genera in the Epipsocidae. *Goja* is known only from one incomplete specimen, which Roesler (1946) considers to be an Epipsocid. The multiplicity of branching of the wing veins, a tendency common in this group of families, separates the genus from the others. *Neurostigma* is remarkable in its apomorphous development of a multiplicity of crossveins traversing the pterostigma although in other features it is similar to *Epipsocus*. *Epipsocus* and *Epipsocopsis* are closely related genera but differ in the greater reduction of female gonapophyses in *Epipsocopsis* in which the dorsal and external valves are fused and the ventral valve lost altogether. Also, in some species in which this condition occurs the lacinia exhibits apical modifications into a sharp point. If the genitalic characters are used for the basis of generic definition in this part of the Epipsocidae, some redistribution of species between Epipsocus (Epipsocidus) and Epipsocopsis becomes necessary. This is minor rearrangement at species level which need not concern us in this account and does not affect the suggested relationships between the genera. Goja is the sister group to the other genera of Epipsocidae with its unique apomorphous multiplicity of veins; Neurostigma resembles Epipsocus and Epipsocopsis but is more strongly setose and has peculiar crossveins in the pterostigma. Epipsocus and Epipsocopsis constitute the two most apomorphous genera in the family and have few setae and more specialized genitalia, especially Epipsocopsis. The latter genus also exhibits some degree of alary polymorphism in some species. These relationships are indicated in figure 6.8.

RELATIONSHIPS OF CALOPSOCIDAE AND POLYPSOCIDAE

The Epipsocetae arose from a stock in which a second anal vein was present; in the course of evolution of the Epipsocetae this was lost. The remaining genera of the Psocomorpha have also lost the second anal vein. The Calopsocidae and Polypsocidae have also lost the second anal vein and retained the Rs-M crossvein. They cannot, however, be included in the Epipsocetae as that group has definitely apomorphous features not found in the groups mentioned. They arose, however, before the fusion of Rs and M in the line which gave rise to the rest of the Psocomorpha and they have reduced tarsal segmentation. In Polypsocidae alary polymorphism occurs and the reduction in tarsal segments is probably associated with this; the

Calopsocidae also tend to have short wings and a similar reason for the 2-segmented tarsi may be postulated. The question of the distribution of 2-segmented tarsi through the Psocomorpha is discussed below. The Polypsocidae show apomorphous reduction in genitalia analogous to that in the Caecilietae. The Calopsocidae have apomorphous head characters and venational features and appear as the sister group to the Polypsocidae. The relationships of these groups are indicated in figure 6.7.

RELATIONSHIPS WITHIN THE CALOPSOCIDAE

The relationships of the three genera of Calopsocidae are fairly clearcut and are shown by the relative degree of apomorphous condition in the transformation series leading from that of little vein anastomosis to a complex reticulation of veins. Also, in the same line is a transformation series from a normal wing to a broad, shortened, bent wing. Dirla is the most plesiomorphous of the series with normally elongate wings and but little anastomosis of veins immediately behind the pterostigma. This line is extended to Neurosema where the anastomosis is carried to extremes but with little change in wing form; from the line which gave rise to Neurosema must have arisen Calopsocus as the most apomorphous genus with complex anastomoses and broadening and bending of the wing.

RELATIONSHIPS WITHIN THE POLYPSOCIDAE

There are only two genera in the Polypsocidae, Polypsocus and Monocladellus. The family arose near the point of origin of the Psocomorpha and both genera have reduced venation, in Polypsocus M is 2-branched and in Monocladellus simple. These two genera are simply sister groups (figure 6.7).

SOME GENERAL COMMENTS ON THE REMAINING PSOCOMORPHA

Rs and M relationship in the fore wing

All of the remaining genera of the Psocomorpha have Rs and M fused for a length or have a condition which can reasonably be derived from such. Some genera do, in fact, have Rs and M joined by a crossvein and as this may appear to contradict what has been written above, some explanation is necessary here. It seems that the condition in which Rs and M are joined by a crossvein can be either plesiomorphous or strongly apomorphous in genera which have arisen from stocks in which these two veins were fused. The presence of a crossvein can occur in genera with many plesiomorphous features or occasionally in genera which are highly apomorphous in many features; it is in the latter cases that its appearance seems to be secondary and highly apomorphous, in fact, in such cases more advanced in the transformation series than the fused condition. *Amphigerontia*, for example, has Rs and M joined by a short crossvein. The family to which it belongs, Psocidae, has many strongly apomorphous features and can be seen to belong to a strongly apomorphous complex of families including the Myopsocidae and Psilopsocidae in which the Rs and M relationship is fundamentally one of apomorphous fusion. In *Amphigerontia* the Rs - M crossvein is clearly secondary and not plesiomorphous. *Amphigerontia* itself has many apomorphous features in common with the other members of its family which would make its inclusion in any of the groups with a plesiomorphous crossvein impossible. Other similar situations exist in other groups (e.g. in the Caecilietae), where one or two genera (e.g. *Stenepipsocus*) have an Rs to M crossvein but have many apomorphous features which prevent the conclusion that the feature is plesiomorphous.

Comparison of the venation of genera in which the crossvein is considered plesiomorphous with those in which it is considered apomorphous reveals that, in general, where it is thought to be plesiomorphous it is usual for the veins to bifurcate soon after Rs - M crossvein or to divide near the wing margin so that long, uninterrupted veins come to lie more or less parallel to each other along the wing length. In those cases where the crossvein is a strongly apomorphous condition Rs and M tend to diverge or become sinuous distad of the crossvein and the positions of subsequent divisions are variable. Also, those genera with a plesiomorphous crossvein usually have the pterostigma and areola postica flattened and long even sometimes with Cu_{1a} arising basad of the point at which Cu_{1b} reaches the wing margin (e.g. Calopsocus). In those genera in which the Rs - M crossvein is apomorphous these cells are of different, apomorphous shapes, usually tall and narrow in the case of the areola postica and frequently broad or with a more or less idstinct hind angle to the pterostigma. It seems that the fusion of Rs and M in the fore wing is an important apomorphous character possessed through true synapomorphy and not convergence by many Psocomorpha genera. The event itself seems to have been one in a series leading from a generalized to a specialized condition of the wing; the same event occurred much earlier in the history of the hind wing and is probably a consequence of wing narrowing with resultant approximation of the main longitudinal veins near midwing.

Number of tarsal segments

The number of tarsal segments is reduced in the transformation series and tarsi are never more than 3-segmented in the Recent Psocoptera. The psocomorph genera other than those included in the Epipsocetae, Polypsocidae and Calopsocidae, that is, those with Rs and M fused or with a condition derived from fusion, include some with 2-segmented and some with 3-segmented tarsi. This feature indicates a dichotomy in the evolution of the group, the genera with 2-segmented tarsi being apomorphous in this feature relative to the others. The groups with two segmented tarsi include the Hemipsocidae, Pseudocaeciliidae, Caecilietae, Ectopsocinae, Lachesillidae, Trichopsocidae and Archipsocidae. The groups with 3-segmented tarsi include the Philotarsidae, Mesopsocidae, Elipsocidae, Psilopsocidae and Myopsocidae. There are, however, some groups which clearly share apomorphous features with genera having 3-segmented tarsi which have 2-segmented tarsi. These include a few genera of Elipsocidae, the Psoculidae, Thyrsophoridae, Psocidae and Archipsocidae. The apomorphous reduction of tarsal segments appears to have taken place more than once. Once it lead to the Pseudocaeciliidae, Caecilietae and related groups having 2-segmented tarsi on another occasion occurred at the base of the Psocidae-Thyrsophoridae line; other occurrences are found in the Elipsocidae, Archipsooidae and Lachesillidae. In some cases the reduction is found in whole families and involves mainly fully winged or mainly non-polymorphic genera. This is so in the Lachesillidae, Pseudocaeciliidae, Caecilietae and related families on the one hand and the Psocidae and Thyrsophoridae on the other. The possession of 2-segmented tarsi is here regarded as being a synapomorphous feature for these two lines; they all possess it because the original stocks from which each came had it. In the case of the Elipsocidae and Archipsocidae reduction is found associated with polymorphism, brachyptery or aptery in one or both sexes and has associated with it other morphological changes such as loss of trichbothria and ocelli. This has already been discussed and the conclusion reached that these changes are essentially neotenic, involving some genera of groups which otherwise have 3-segmented tarsi.

Other transformation series

As in the case of the Epipsocetae and other groups already discussed, it is possible to follow certain other transformation series in both the "2-segmented tarsi" line and the "3-segmented tarsi" line. There is a general tendency for loss of setae to occur; there is modification of the phallosome, the subgenital plate becomes apomorphous in various ways as does the hypandrium and there is specialization in habitat selection and egg laying habits.

It may be well here to indicate the degree of apomorphy which had been reached in the order at the time of the major dichotomy into the "2-segmented tarsi" line and the "3-segmented tarsi" line. The main features are as listed previously for the stock from which the Psocomorpha as a whole arose but in addition there were further apomorphous conditions. The second anal vein had been lost, Rs and M were now fused in both wings. The male phallosome had retained plesiomorphous complex sclerifications of the penial bulb; the eggs were covered with an encrustation and the subgenital plate was simple as was the hypandrium. The "2-segmented line" and the "3-segmented line" of development referred to above are broadly equivalent to the Caecilietae (without the Polypsocidae and Calopsocidae), Hemipsocidae, Peripsocinae, Ectopsocinae, Pseudocaeciliidae and Trichopsocidae on the one hand and the Homilopsocidea families with 3-segmented tarsi plus the Lachesillidae, Psilopsocidae, Myopsocidae and Psocidae, on the other.

We shall first discuss the relationships of the groups in the "2-segmented tarsi" line.

RELATIONSHIPS WITHIN THE "2-SEGMENTED TARSI" LINE

Two small groups which have in the past been associated with other families in this line present special problems. These are the Hemipsocidae and the Peripsocinae.

The Hemipsocidae have somewhat simplified female genitalia with broad external valves almost devoid of setae. The epiproct bears rugose areas (somewhat reminiscent of some Caecilius spp.), the phallosome is simplified with peculiar sclerifications of the penial bulb; the paraprocts bear protuberances (probably not homologous with those characteristic of Psocidae), M_3 has been lost and the areola postica joined to M by a crossvein and the wing vein setae arise from conspicuous alveolae (a character found in some other unrelated genera). The position of the family cannot be determined with certainity; the features given above are apomorphous and occur nowhere else in the combination nor in quite the same forms as in the Hemipsocidae. Habitat preference (dried leaves) and egg laying habits (eggs encrusted with debris) are of no help as they are both relatively plesiomorphous characters within the Psocomorpha. The family seems to represent a strongly apomorphous line of unknown origin; they are here tentatively regarded as a separate line arising from the main line of evolution of the "2-segmented tarsi" groups (figure 6.9).

The Peripsocinae have been associated with the Ectopsocinae in the Peripsocidae by virtue of only two features in common, neither of which are peculiar to the Peripsocidae, namely, the lack of an areola postica and the possession of 2-segmented tarsi.

A perusal of the morphological features of the genera of the Peripsocidae gives some indications of probable relationships.

Peripsocus is a well known genus. Kaestneriella agrees with Peripsocus in all of the male features which have been described except that the veins and margin of the fore wing are setose in Kaestneriella. It is interesting to note that the setae are in a double row on the branches of the veins. Peripsocus and Kaestneriella are clearly very closely related and the former can be derived from the latter simply by loss of setae; these are absent from the hind wing of Kaestneriella and are found on the fore wing margin only in the basal half of the wing.

Ectopsocus and Ectopsocopsis are very similar in most features. They differ in that the structures on the ninth abdominal tergite of the male are a little more complex in Ectopsocopsis than in Ectopsocus. In females the subgenital plate in Ectopsocus is bilobed and in Ectopsocopsis the lobes are reduced to produce a simple subgenital plate or the plate has a suggestion of a median lobe (see below). In Ectopsocus the gonapophyses are complete with a characteristic form to the somewhat weakly sclerotized external valve. In Ectopsocopsis the gonapophyses are reduced with only the rudimentary setose external valve remaining. Interpsocus agrees with Ectopsocus and Ectopsocopsis in most features but is generally less apomorphous. The ninth tergite and epiproct of the male do not carry specialized structures and the phallosome is somewhat simpler. The gonapophyses are complete and the subgenital plate is bilobed. Ectopsocus and Ectopsocopsis can be fairly easily derived by specialization from an Interpsocus-like form.

If we compare the Ectopsocus - Ectopsocopsis - Interpsocus group of genera with Peripsocus - Kaestneriella group we find that in many important characters the two groups differ. These may be tabulated as follows:

	"*Peripsocus*" group		"*Ectopsocus*" group
1.	Claws with tooth	1.	Claws without tooth
2.	Pulvillus narrow	2.	Pulvillus dilated
3.	Pterostigma normal	3.	Pterostigma rectangular
4.	Fore wing with Rs and M fused	4.	Fore with with Rs and M meeting in a point
5.	Hind wing with Rs and M fused	5.	Hind wing with Rs and M connected by a cross-vein (except *Interpsocus*)
6.	Hind wing glabrous	6.	Hind wing margin setose between R_{2+3} and R_{4+5}.
7.	Male epiproct simple	7.	Male epiproct with "comb" (except in *Interpsocus* and some *Ectopsocopsis*, latter with more complex abdominal structures).
8.	Phallosome with external parameres fused and pointed posteriorly; internal parameres separate posteriorly. Penial bulb sclerifications symmetrical, rod-like.	8.	Phallosome with external parameres separate posteriorly; internal parameres fused. Penial bulb sclerifications irregular and asymmetrical, complex
9.	Subgenital plate with median posterior lobe	9.	Subgenital plate bilobed or with lobes reduced or with median lobe (see below)
10.	Ventral valve strong and pointed	10.	Ventral valve pointed, usually weakly sclerotized (absent in *Ectopsocopsis*).
11.	Dorsal valve broad, basally dilated and apically setose.	11.	Dorsal valve broad, weakly sclerotized, without setae (absent

"Peripsocus" group

12. External valve somewhat reduced, setose.

"Ectopsocus" group

in Ectopsocopsis).

12. External valve subparallel-sided and setose (only setose rudiment in Ectopsocopsis).

The two groups of genera have somewhat similar lacinia. The setation of the veins is similar amongst the "Ectopsocus" genera but differs considerably in Peripsocus and Kaestneriella. The ninth abdominal tergite in the male frequently has a "comb". In Peripsocus this is in the form of a series of small papillae along the posterior margin of the tergite; the papillae may be grouped on a curved section of the margin. In Ectopsocus and Ectopsocopsis the "comb" is more definitely formed of stronger spurs. The "combs" in the two groups of genera seem not to be homologous. Likewise the median lobe of the subgenital plate in Peripsocus is a strongly developed structure; in some species of Ectopsocopsis which have a median lobe it appears to be a structure resulting from the fusion of two lobes and appearing rather as a bulging of the posterior margin of the subgenital plate than a distinct lobe; in other species the median lobe appears to arise internally basad of the simple margin of the subgenital plate proper. The lobes, as in the case of the "combs", do not appear to be homologous in the two groups of genera.

Anomopsocus has been associated with the Peripsocidae. The affinities of this genus appear to lie with Lachesilla and it will be dealt with under the Lachesillidae.

Notiopsocus has a combination of characters such that it is difficult to associate it with either generic group mentioned above. The apex of the lacinia is cup-shaped and the lacinia is laterally asymmetrically dilated before the apex. The claws are without preapical teeth but the pulvillus is slender. The pterostigma is of more or less usual form, but M is only 2-branched. The fore wing has Rs and M fused for a length but the setal arrangement of the veins and hind wing is similar to that of Ectopsocus. The subgenital plate is simple. The gonapophyses are reduced, but in a manner different from the reduction in Ectopsocopsis. In Notiopsocus it is the ventral and external valves which are reduced, the dorsal valve remains the best developed valve but even this is a little reduced and is a membranous structure reinforced by a sclerotized ventral margin. The rudimentary external valve bears only one seta. The male of Notiopsocus is unknown, but the combination of characters in the female (apart from lack of areola postica, form of pulvillus and 2-branched media) suggest affinities with the Caeciliidae. Notiopsocus appears not to be particularly closely related to the other genera at present in the Peripsocidae.

The genera at present placed in the Peripsocidae have been grouped in the past mainly because of one common venational feature i.e. lack of areola postica. Genera in other families (e.g. Nepiomorpha in the Elipsocidae) also lack the areola postica; this one feature should not be taken alone as indicative of close relationships. The following tentative conclusions are here reached, based on morphological features. The genera of the Peripsocidae fall into two groups, with Notiopsocus not being closely related to either group, as follows:

1. Peripsocus and Kaestneriella
2. Ectopsocus, Ectopsocopsis and Interpsocus
3. Notiopsocus.

These groups are not particularly closely related. Groups 1 and 2 are sufficiently different to be placed in separate "families", their common features e.g. "combs" on ninth tergite in the male and median lobe of subgenital plate, and loss of areola postica appear to be analogous rather than homologous. Notiopsocus is not includable in either and is probably more closely related to the Caecilietae having only superficial venational similarity with the other genera without an areola postica.

Two pieces of non-morphological evidence to support the above-suggested groupings are forthcoming.

The eggs and method of laying are entirely different in the two "families". In Peripsocus the eggs are laid singly, are rough, with somewhat pointed apex and are covered with an encrustation of debris. Eggs of Kaestneriella are unknown. In Ectopsocus and Ectopsocopsis eggs are laid in groups, are ovoid, without an encrustation of debris and are covered with silken threads. In Interpsocus they are laid in groups, encrusted and covered with a light silken covering.

Peripsocus is usually an inhabitant of bark of trees and shrubs; Ectopsocus, Ectopsocopsis and Interpsocus usually inhabit dried leaves, leaf litter and birds' nests. Notiopsocus is a lichen dweller. Eggs and egg laying and habitat preferences are in marked contrast in the two groups, supporting separation on morphological grounds.

The Peripsocinae is a group which seems to have arisen sometime after the fusion of Rs and M and the reduction of tarsal segments in the line which gave rise to the Psocidae. The female genitalia, in which both the dorsal and external valves are setose, are unique in this respect. It appears to have arisen from the stock which gave rise to Lachesilla and will be dealt with with that genus.

The remaining groups with 2-segmented tarsi can be grouped into (a) those in which the female genitalia have been modified and in which the habit of encrusting the eggs has given way to one in which silk is used to cover the eggs and (b) those in which a full set of genitalia is retained and in which the habit of encrusting the eggs is retained. The former is the Caecilietae and Ectopsocidae and the latter the Pseudocaeciliidae and Trichopsocidae.

The Pseudocaeciliidae and the Trichopsocidae are sister groups in which the Trichopsocidae are relatively more apomorphous in having only one row of setae on the veins of the fore wings and the hind wing veins glabrous; there is specialization of marginal setae longer and shorter setae occurring alternately on some parts of the margin. The Pseudocaeciliidae have many plesiomorphous features but have a strongly apomorphous hypandrium and a subgenital plate with a divided median lobe, and, in some groups, apomorphous simplification of the phallosome. The Pseudocaeciliidae and Trichopsocidae share apomorphous features of the epiproct, in which there is strong development of a chitinized edging to the plate and setal specialization along the margin and on the body of the plate.

In those groups in which the female genitalia have undergone strong modification two lines can be distinguished. In one the modification has involved the loss or extensive reduction of the setose external valve to leave the dorsal and ventral valve (usually as slender, tapering, pointed structures) (Caecilietae). In the other accent has been on the development of the external valve into a setose lobe with various degrees of reduction of the dorsal and ventral valve (Ectopsocinae).

The uniformity of genital and labial palp structure singles out the Caecilietae as a monophyletic group as does the development of the external valve and apical dorsal abdominal structures in the male in the Ectopsocinae. In the Caecilietae the phallosome is modified into a simpler form with varying degrees of reduction of the penial bulb sclerifications whereas in the Ectopsocinae strongly individualistic modifications of the penial bulb sclerifications have occurred. The suggested relationships between the groups within the "2-segmented tarsi" line are indicated in figure 6.9.

RELATIONSHIPS WITHIN THE PERIPSOCINAE

It has been shown that the Ectopsocinae and Peripsocinae do not share apomorphous features peculiar to them alone and that their traditional association in a family is not warranted. Also, it was suggested that Notiopsocus was not appropriately associated with Peripsocus. The Peripsocinae, therefore, consists only of Peripsocus and Kaestneriella. These two genera are clearly closely related with Peripsocus having a more apomorphous condition in wing and other features. The wings in Kaestneriella are setose whereas those of Peripsocus are glabrous. The phallosome of Peripsocus is more apomorphous than that of Kaestneriella in some respects. A simple sister group relationship appears to exist between the two as indicated in figure 6.10. They are both associated with Lachesilla and its relatives.

RELATIONSHIPS WITHIN THE HEMIPSOCIDAE

The position of Anopistoscena is not clear. Little is known of this genus, the fore wing resembles that of Hemipsocus but has the distal section of Cu_{1a} missing so that the "areola postica" is open. If these two genera are closely related they must bear a simple sister group relationship to one another with Anopistoscena having a relatively apomorphous venation (see figure 6.11).

RELATIONSHIPS WITHIN THE TRICHOPSOCIDAE

The Trichopsocidae are very similar to the Pseudocaeciliidae; the main significant differences have already been mentioned above.

The amber genus Palaeopsocus has been grouped with Trichopsocus, but in a tribe of its own, by Roesler (1944). The venation of the fore wing and the venation and setal characters of the hind wing do not seem to indicate close relationship with Trichopsocus. The information available on Palaeopsocus makes it impossible to place the genus with any degree of certainty. Enderlein (1911) placed it in the Caeciliinae of the family Caeciliidae. Karny (1930) placed it with a wide variety of genera in the tribe Lachesillini in his very broad family Lachesillidae. The key characters used by Roesler (i.e. venation, tarsal segmentation, setae on wings, and claw characters) lead to the genera Fulleborniella, Trichopsocus, Chaetopsocus and Palaeopsocus being placed together. Fulleborniella is an Amphipsocid and Chaetopsocus has been found to be a synonym of Ectopsocus. It seems likely that Palaeopsocus should also be dissociated from Trichopsocus.

The fact that Cu_{1a} does not reach the wing margin and the form of the lacinia suggest that Palaeopsocus may be part of the group which gave rise to the Ectopsocinae, the lack of a tarsal claw suggests that Palaeopsocus may also have been a leaf dweller. The unbranched Rs would, however, prevent its inclusion in the direct line of Ectopsocin development. For the present, it is retained in the Trichopsocidae with reservation (figure 6.12).

RELATIONSHIPS WITHIN THE PSEUDOCAECILIIDAE

The main apomorphous features which unite the Pseudocaeciliidae are the presence of a divided lobe on the hind margin of the subgenital plate, each division bearing apical setae and the presence of variously complex adventitious hooks, spines and apophyses of the hypandrium. There are also stages present within the family from a complex phallosome to a simplified form and increasing glabrosity is evident.

The other groups within the "2-segmented tarsi" line of evolution (Ectopsocinae, Caecilietae) each have their own apomorphous features which leaves the Pseudocaeciliidae as one of the most generally plesiomorphous families in the Psocomorpha. The wingmembrane is setose in some genera or some membrane setae at least are retained in modified scale-like form near the wing base. Prior to the work of Lee and Thornton (1967) there were seven genera in this family. Scytopsocus and Ophiodopelma were considered as subgenera of Cladioneura and Pseudocaecilius respectively. Lee and Thornton (loc. cit.) gave Ophiodopelma and Scytopsocus generic rank and erected five new genera, giving a total of fourteen genera. The five new genera of Lee and Thornton appear from the adequate descriptions and illustrations to be very similar to one another.

They may, for present purposes be considered as belonging to Heterocaecilius. The genera to be considered here, therefore, are Pseudocaecilius, Cladioneura, Ophiodopelma, Mesocaecilius, Scottiella, Pseudoscottiella, Trichocaecilius, Electropsocus and Heterocaecilius sens. lat.

Electropsocus (from Prussian amber) was placed by Roesler (1940) in the subfamily Pseudocaeciliinae. In his discussion of the genus, however, he compares it to Mesopsocus which is a genus only very distantly related to Pseudocaecilius. Electropsocus seems to differ from Pseudocaecilius in almost all features except in having 2-segmented tarsi. Roesler (1944) placed Electropsocus in a subfamily Electropsocinae but retained it in the Pseudocaeciliidae. Electropsocus appears to be a genus which could be placed near the Mesopsocidae. Pseudocaecilius and Trichocaecilius share with Scottiella and Pseudoscottiella the apomorphous condition of a simple elongate phallosome. The latter two genera, however, are synapomorphous in the structure of the hypandrium in that instead of having small lateral hooks and processes the hypandrium has broad, strong processes nearer the midline. Scottiella and Pseudoscottiella also share the synapomorphous character of having a 2-branched media. They differ from one another in the thickness of the costa. Trichocaecilius differs from Pseudocaecilius in the form of theventral valve which is broad and membranous supported by a longitudinal sclerified rod in Trichocaecilius. These four genera share with Heterocaecilius and Cladioneura the apomorphous condition of a complex hypandrium; this is relatively simple in Ophiodopelma. The relationships of the genera of Pseudocaeciliidae therefore, as indicated in figure 6.13, can be described as follows. Ophiodopelma does not share the apomorphous complex hypandrium and stands as a sister group to the rest of the family. Heterocaecilius and Cladioneura stand in sister group relationship to the four genera Pseudocaecilius, Trichocaecilius,Scottiella and Pseudoscottiella all of which share the apomorphous simple phallosome. In each case the members of the pairs of genera Pseudocaecilius and Trichocaecilius, Scottiella and Pseudoscottiella, Heterocaecilius and Cladioneura stand in sister group relationship to one another. The condition of the male genitalia in Mesocaecilius is not known and its position within the family cannot be established; its small areola postica may indicate affinity with Ophiodopelma. Scytopsocus is typically Pseudocaeciliid in every way, with a complex phallosome and hypandrium. It retains, however, an Rs - M crossvein which is probably of secondary origin and, amongst the Pseudooaeciliidae, is found only in Scytopsocus. It forms a sister group to the other two genera with a complex phallosome, that is, to Heterocaecilius and Cladioneura.

The position of the amber genus Ptenolasia should be mentioned here. It is currently considered to be a Caeciliid. It would appear, however, to have more in common with the Pseudocaeciliidae. Hagen (1882) regarded Ptenolasia as being a Caecilius. Enderlein (1911) erected a new genus for it on account of its fore wing membrane being setose. He pointed out that some of the marginal setae of the fore wing crossed each other and that they did not do so in Caecilius but he retained Ptenolasia in the Caeciliidae which subsequent authors have also done. A perusal of the description (Enderlein, 1911, p. 321, fig. 45 and text fig. F) makes it clear Ptenolasia has many Pseudocaeciliid features. There are strongly developed alveolae to the setae, as in Cladioneura but not in Caeciliidae; marginal setae cross each other, as in Philotarsidae and Pseudocaeciliidae but not in Caeciliidae; the subgenital plate bears a rounded posterior median lobe, easily derived from the divided lobe in the Pseudocaeciliidae but not in the Caeciliidae.

The evidence suggests relationship to the Pseudocaeciliidae rather than the Caeciliidae. The male is not known.

The Trichopsocidae and the Pseudocaeciliidae form the most plesiomorphous group within the Psooomorph line with 2-segmented tarsi.

We turn now to those groups of the same line which together form the sister group of the Pseudocaeciliid-Trichopsocid line namely, the Caecilietae and Ectopsocinae.

The members of this group are shown to be a monophyletic group by modification of the female genitalia, the use of silk as a covering for the eggs and usually specializing in inhabiting dried or green leaves. The Caecilietae have all but lost the external valve of the gonapophyses; in the Ectopsocinae it has become well developed and elongated whilst the other valves have diminished in importance. At the same time the phallosome has become simple in the Caecilietae but retained complexity in the Ectopsocinae; in the Ectopsocinae dorsal structures at the end of the male abdomen also attain complexity. The loss of teeth on the claws and narrowing of the apex of the lacinia has also occurred in both Caecilietae and Ectopsocinae. The Caecilietae are also unique in having a broadly triangular, protruding labial palp.

The relationships between the Caecilietae, Ectopsocinae and other Psocomorpha are shown in figure 6.9.

RELATIONSHIPS WITHIN THE CAECILIETAE

This is a large group of genera and species in which, at present, three families are recognized. The form of the female genitalia, lacinia, labial palp, claw characters and egg laying habits, all strongly apomorphous, indicate without doubt that it is a monophyletic group as does the relatively simplified male phallosome. The families at present are not distinctly defined and some genera, e.g. Taeniostigma are included in groups from which, by definition, they should be excluded. It is in such a group of genera as are at present included in the Caeciliidae, where there appears to be a set of characters which assume various conditions and where these conditions appear in various combinations that the practice of attempting to use overall resemblances to determine relationships is most likely to lead the phylogenist astray. Only by tracing through the character conditions in other transformation series can superficial resemblances, which so often occur where there are many closely related groups, be seen through and a logical evolutionary sequence found. We shall, therefore, ignore here the current family groupings within the Caecilietae and consider all the genera within this homogeneous group in relation to each other.

At the outset it would be wise to deal with certain genera.

Ptenolasia has already been considered with the Pseudocaeciliidae.

Matsumuraiella is apparently an offshoot of the line which gave rise to the Caecilietae. Its genitalia are not as reduced as in the Caecilietae and the areola postica is variable, sometimes being tall enough to fuse with the media. It must have arisen after the line which gave rise to the Ectopsocinae as its genitalia are in the transformation series leading to the condition found in the Caecilietae. Its probable position is indicated in figure 6.9.

Tagalopsocus and Ptenopsila are still too poorly known to enable them to be discussed. It seems best to leave them in association with the other Caeciliid genera until further data is available.

Dasydemella is something of a problem as the illustrations given with the description do not agree with it. Until further material is available its position cannot be discussed. The description suggests that it is a Caeciliid; the illustrations suggest Elipsocid affinities. For the present it must be held with the other doubtful genera.

In the remaining twenty-five genera certain strongly apomorphous characters are present which unite them into a small number of monophyletic groups. We shall deal with these first and then consider intragroup relationships. The groups do not entirely coincide with currently accepted family groupings.

Important characters are the already apomorphous genitalia, the presence of a spur vein from the hind angle of the pterostigma and the nature of the relationship between the areola postica and the media.

One group of genera (largely the present Stenopsocidae) can be considered monophyletic on the basis of the strongly apomorphous connection between the areola postica and the media, either by a crossvein or by fusion, the latter being a more advanced condition than the former. These genera retain the relatively plesiomorphous character of a seta on the external valve remnant. The remaining genera can be arranged into two groups, one in which the seta is lost and one in which it is retained but in which the areola postica is free. The first group cannot be included in the third by virtue of the apomorphous condition of its areola postica. The third cannot be included in the second because the latter has apomorphously lost the external valve seta and for the same reason the first cannot be included in the second. The broad evolutionary sequence of events in this complex of genera seems, therefore, to have been a dichotomy in which one branch achieved connection between areola postica and media. The line without such fusion gave rise to one group in which the external valve seta was lost and another in which it was retained. These relationships are indicated in figure 6.14. The relationships of genera within each of these groups will now be discussed.

The first group (I) includes Graphopsocus, Stenopsocus, Taeniostigma, Kodamaius and Epikodamaius. The last two genera (if distinct from each other - Epikodamaius is possibly based on a venational aberration) are synapomorphous in having Rs and M joined by a crossvein. This is clearly a case in which this relationship between the two veins has arisen as an apomorphous condition although generally the condition would be considered as plesiomorphous. This reappearance of a plesiomorphous feature has already been discussed. Kodamaius and Epikodamaius form a sister group to the remaining genera. Of these Taeniostigma has carried the fusion of the apex of the areola postica with the media to a further stage than in Stenopsocus or Graphopsocus and the setation has also been further reduced in Taeniostigma. Stenopsocus and Graphopsocus are very closely related genera differing in colour pattern and the degree of setation of the hind wing margin. Thesuggested relationships of this group are indicated in figure 6.15.

The second group (II) includes those genera which have the external valve of the gonapophyses reduced to the point of losing even the seta. On the one hand within this group are Kolbea, Teliapsocus, Dasypsocus and Schizopechus in which there is no sign of a spurvein to the pterostigma and on the other Fulleborniella, Ypsiloneura, Amphipsocus, Xenopsocus, Harpezoneura, Pentathyrsus and Amphipsocopsis which have a spurvein.

Considering the group without a spurvein the next dichotomy has involved loss of wing membrane setae; Kolbea and Eocaecilius have glabrous membranes whereas the other genera have retained this plesiomorphous feature but have other apomorphous features of their own. Schizopechus has a many-branched Cu_{1a}; Teliapsocus and Dasypsocus do not. The latter two genera are very closely related, they both have a strong basal extension to the dorsal valve of the gonapophyses but in Teliapsocus the setae of the branches of the veins are in a simple row as opposed to the somewhat more plesiomorphous double row in Dasypsocus. Eocaecilius has somewhat membranous genitalia and a slightly acuminate fore wing (Lacroixiella and Eocaecilius are probably synonymous).

Considering the genera in which there is a spurvein to the pterostigma they are found to include a number of genera which clearly form a monophyletic group bearing the apomorphous feature of multiplicity of vein branches; amongst these some have tufts of setae on the veins. All these retain the plesiomorphous condition of having relatively hairy wing veins and margins. Pentathyrsus and Harpezoneura have apomorphous hair tufts on the veins and Pentathyrsus has expansions of the vertex peculiar to itself. Of the genera without hair tufts (Xenopsocus and Amphipsocopsis) Amphipsocopsis has an apomorphous form of lacinia. The genera which are not includable in the above, by virtue of their venation not involving an increase in vein branching, can be grouped into those in which setal reduction has taken place (Ypsiloneura and

Fulleborniella) and that in which it has not (Amphipsocus). Ypsiloneura is somewhat apomorphous relative to Fulleborniella in that M in the fore wing is 2-branched and Rs may not be branched. The relationships suggested above are indicated in figure 6.16.

The third group (III) is in some ways the most plesiomorphous in the Caecilietae. They exhibit the most plesiomorphous condition of the gonapophyses and venation. They do, however, show various apomorphous features which enable their relationships to be established.

The genera Dasydemella, Tagalopsocus and Ptenopsila are listed within this group but their relationships, as mentioned, cannot be established because of lack of information.

The genera Paracaecilius, Asiopsocus, Notiopsocus and Enderleinella all have the gonapophyses strongly reduced and somewhat membranous. They form a small group of closely related genera which stand as the sister group to the remaining genera of group III, which have thegenitalia typical of the Caecilietae. Their genitalic forms are strongly apomorphous and Asiopsocus is polymorphic and Enderleinella-Paracaecilius-Asiopsocus form a transformation series in which genitalic reduction is progressive.

The relationships of Notiopsocus are very difficult to determine; the male is unknown and the attachment of this genus to Peripsocidae on account of its lacking an areola postica is not warranted (discussed above). The genitalic reduction is similar to that which has taken place in the Caeciliidae and it is tentatively suggested that Notiopsocus arose from the stock which gave rise to Paracaecilius. This is indicated in figure 6.17.

Of the other five genera, Isophanes, Dypsocus and Coryphosmila are strongly synapomorphous in head shape; the vertex is sharp. They form a sister group to Mepleres and Caecilius. Within the Isophanes-Dypsocus-Coryphosmila line Isophanes and Dypsocus have the apical areas of the fore wing reduced with resultant distortion of vein arrangement. Coryphosmila has venation as in Caecilius. Of Mepleres and Caecilius the former shows apomorphous reduction of M to 2 branches in the fore wing. The relationship suggested for the genera of group III as indicated by the evidence of their apomorphous features is indicated in figure 6.17.

The overall result of this reassessment of the relationships within the Caecilietae, based on establishment of monophyletic groups exhibiting apomorphous features, leads to a somewhat different arrangement in the hierarchy of categories, which will be discussed later when considering the reclassification of the order.

RELATIONSHIPS WITHIN THE ECTOPSOCINAE

The separation of the Peripsocinae and Ectopsocinae and the exclusion of Notiopsocus from the Peripsocidae has been discussed. The Ectopsocinae comprises Ectopsocus, Ectopsocopsis and Interpsocus; Anomopsocus has been referred to this family but it is considered to be more closely related to the Lachesillidae and will be dealt with there.

The Ectopsocinae are united by the lack of an areola postica, the form of the pterostigma and the genitalia in which reduction of the dorsal and ventral valves has progressed and the external valve has become emphasised; also, they are inhabitants of dried leaves and cover their eggs with silk. The three genera are closely related.

Ectopsocus and Ectopsocopsis share several apomorphous features not found in Interpsocus, such as an Rs - M crossvein in the hind wing, complex but peculiar sclerifications of the penial bulb and the development of complex dorsal structures at the end of the male abdomen. These two genera form a sister group to the more plesiomorphous Interpsocus. Ectopsocus and Ectopsocopsis each exhibit features which are more advanced than in the other genus. Ectopsocopsis has a more specialized subgenital plate and dorsal plates to the end of the male abdomen; the female genitalia are more reduced than in Ectopsocus. These relationships suggested for the genera within the Ectopsocinae are indicated in figure 6.18.

It is interesting to note that in the otherwise most plesiomorphous genus of the line consisting of the Caecilietae and Ectopsocinae, namely Interpsocus, the plesiomorphous habit of encrusting the eggs with debris is retained with the apomorphous use of silk.

RELATIONSHIPS WITHIN THE "3-SEGMENTED TARSI" LINE

We turn now to another main line of psocopteran evolution, that is, the line which has been referred to here as the "3-segmented tarsi" line. As pointed out already, groups with 2-segmented tarsi are also included but it will be seen that these form the extremes of transformation series derivable from the main basic stock of the line, that is, that which gave rise also to the "2-segmented tarsi" line. In fact, the groups with which we shall deal first are plesiomorphous but generally "psocomorph" in most features and the main modifications from the basic forms are in genitalia and in reduction of various organs.

In searching for groups with apomorphous features peculiar to themselves within this line we find that three such groups can be distinguished.

One small group (I) has the female gonapophyses and wings usually considerably reduced or absent altogether in one or both sexes; in fact, they are extremely neotenic. At the same time where wings are retained theyhave setose membranes. Some species are viviparous and the male phallosome is very simple, often being reduced to a somewhat ring-like form. This group includes the Archipsocidae and <u>Lesneia</u>.

A second group (II) has developed a median posterior lobe to a varying extent and of varying form on the hind margin of the subgenital plate; at the same time some modification of the dorsal valve of the gonapophyses involving reduction of the pointed apical division has taken place. This group includes the Philotarsidae, Elipsocidae, Psoculidae and Mesopsocidae. In this group there are setae occupying relatively specialized positions on the subgenital plate e.g. the pre-apical band. These features are not shared with group I.

The third group (III) is one in which the dorsal valve of the gonapophyses has been modified so as to lose its obviously divided nature. The subgenital plate usually bears a posterior median lobe. This group includes the Lachesillidae (including Anomopsocus and Graphocaecilius) and the Psocetae.

In general all of these groups are bark dwellers or lichen feeders (a few inhabit dried leaves) and nearly all lay eggs in groups, encrusted with debris.

Group I stands in sister-group relationship to the other groups. The gonapophyses are extremely reduced; in many species they are lacking and in some species of Archipsocidae the loss appears to be correlated with viviparity, those species with a small remnant lay eggs whereas those without are viviparous. In all genera polymorphism occurs, with one or both sexes showing extreme neoteny (hence reduction in number of tarsal segments). In Lesneia, previously placed in the Elipsocidae, the male is winged and has setae on the wing membrane (an Archipsocid feature, possibly apomorphous in this case, considering the many other strongly apomorphous features in the group such as coalescence of tergites, polymorphy and loss of genitalia). Although there are sclerifications of the male penial bulb these are simple and not extensive. In the group as a whole, therefore, we find synapomorphous development in certain features and it stands in sister group relationship to the other five groups in the "3-segmented tarsi" line. Group I retains some features in plesiomorphous condition which appear in apomorphous conditions in groups II and III. Within the latter two groups, those genera in which the dorsal valve of the gonapophyses has lost its divided form (II) appear to represent a separate line of development from those in which the division is retained, although the division of the dorsal valve which represents the pointed apex may be quite small.

The genera of group II share an apomorphous condition having a posterior lobe to the subgenital plate; this may be divided and in more apomorphous forms, may bear specially placed setae on the margin. Also, the hind margin of the subgenital plate may have the median part membranous on either side of which the setae may be specially grouped into two groups with a few strong setae in each group. There is usually a preapical band of setae on the body of the plate. Some of these features are shared with group III but the latter has apomorphous characters in the gonapophyses. In group II the hypandrium may be apomorphous in having lateral lobes, sometimes these are large and conspicuous. The hypandrium in group III tends to become complex in the more apomorphous genera and the phallosome becomes simpler. The relationships between the three groups are indicated in figure 6.19.

RELATIONSHIPS WITHIN GROUP I

The main features of this small group have been given above. Reduction and apomorphous modifications have been carried to greater extremes in the Archipsocidae than in Lesneia. The latter has retained the third tarsal segment in the apterous female and a normal venation in the winged male although the female has lost the gonapophyses. The male has also retained some sclerification of the penial bulb. On the other hand, the Archipsocidae have lost a tarsal segment even in winged forms and have reduced venation and a very simplified phallosome. The Archipsocidae stand as a sister group to Lesneia and within the Archipsocidae, Archipsocus and Archipsocopsis represent two closely related genera differing in degree of reduction of genitalia. The relationships between the three genera are indicated in figure 6.19.

RELATIONSHIPS WITHIN GROUP II

Within this group, as in others, can be traced transformation series in which increasing glabrosity of wings is evident. Also, transformation series in other characters, such as genitalia, tarsal characters, and venational features can be worked out.

The families Philotarsidae, Elipsocidae, Psoculidae and Mesopsocidae between them include a large number of genera.

At the outset we may deal with certain genera. Lenkoella is a synonym of Notiopsocus and, as such, has already been discussed. Hemicaecilius is probably based on an aberrant specimen of Graphocaecilius, Graphocaecilius will be dealt with later when discussing the Lachesillidae. Lesneia has been discussed with the Archipsocidae.

In the remaining twenty-six genera in these families it is possible to make groupings based on apomorphous conditions of characters and relate these to one another.

The genera Mesopsocus, Labocoria and Hexacyrtoma have very similar genitalia to one another. Both sexes are winged in Labocoria and the eyes are on lateral extensions of the head. Mesopsocus is almost identical but lacks eye stalks and in some species the females are apterous, as in Hexacyrtoma. It is doubtful whether the latter genus should be retained at all. In both Labocoria and Mesopsocus the wings are glabrous. The median lobe of the subgenital plate is strongly developed and of characteristic shape, usually with a distinctive pattern. The male phallosome of Mesopsocus has only weak sclerifications of the penial bulb. In many respects, this group of three genera are the most apomorphous of those now under consideration and clearly belong to a small monophyletic line. The dorsal valve of the gonapophyses is usually broad, somewhat rectangular with a small pointed process representing the apical division of the valve.

A similar arrangement is found in the strongly nymphoid Psoculus, in which, in addition, the ventral valve is broadened and membranous and the tarsi 2-segmented. The subgenital plate has a median lobe but this is triangular and does not have the characteristic Mesopsocus-like pattern. It seems, however, that Psoculus is probably closely related to the other three genera and that it stems from the same stock. These relationships are indicated in figure 6.20.

The remaining genera are those at present included in the Philotarsidae and Elipsocidae. These two families are clearly closely related and the genera included in them exhibit a number of characters in which different stages in transformation series have been reached in different genera. Both families include brachypterous or polymorphic genera but it is possible to associate these with winged genera through genitalic similarities. It seems that the Elipsocidae as a whole is a more apomorphous group than the Philotarsidae as judged by setal and female genitalic characters; when considering the male phallosome it seems that in both groups there has been simplification of the sclerifications of the penial bulb.

In the Philotarsidae there is much heavier body pubescence than in the Elipsocidae. The fore wing has a setose margin, near the apex of which the setae cross each other. The hind wing bears setae all along the margin and these cross each other behind the apex. The subgenital plate bears a relatively strong posterior median lobe which is at least somewhat tapering and which bears evenly spaced marginal setae. The dorsal valve of the gonapophyses usually bears a relatively small pointed process which represents the apical division. A series can be found in the phallosomes in which some have strong sclerifications whilst others have virtually none. The eggs are encrusted with debris and covered with some silk.

The Elipsocidae have much sparser pubescence. The fore wing has marginal setae which may be obvious but never dense or may be hardly visible. The hind wing bears marginal setae at most between R_{2+3} and R_{4+5}. There is no crossing of marginal setae. The subgenital plate bears a pair of posterior lobes each of which carries a few apical setae or there may be a short, broad median lobe, the apical setae of which are grouped into two sets. In some cases there are virtually no posterior lobes but two groups of marginal setae are present. The dorsal valve of the gonapophyses varies considerably and the extent of the division is variable. The phallosome exhibits a series in which reduction of penial bulb sclerification is evident. The eggs are encrusted with debris.

Within the Philotarsidae, Philotarsus, Aaroniella and Haplophallus clearly belong together and fall well within the scope of the characters for the family. Zelandopsocus is less pubescent than the other genera and does not have crossing marginal setae; also, in the hind wing, although the whole margin is setose, the setae between R_{2+3} and R_{4+5} are stronger than the others. The hind wing veins are glabrous as opposed to other Philotarsids, which have some setae on at least some of the vein branches. The phallosome is strongly sclerified and the dorsal valve has a strong apical process. The subgenital plate has a small median lobe with a few evenly spaced marginal setae. Zelandopsocus is a leaf litter inhabitant whereas the other Philotarsids (except Austropsocus) are mainly bark dwellers. In many respects, Zelandopsocus is intermediate between the other Philotarsidae and the Elipsocidae. Unfortunately the eggs of Zelandopsocus are not known. Austropsocus is brachypterous in both sexes but is otherwise very like Zelandopsocus; it is also a leaf litter inhabitant and can be considered as a brachypterous island-dwelling form of Zelandopsocus

The mesopsocid genera, Mesopsocus, Labocoria, and

Hexacyrtoma, together with Psoculus, stand as a sister group to the remaining genera of group II by vertue of their strongly apomorphous wing and genitalic characters. The other genera, that is, the Philotarsidae and Elipsocidae are divisible into two groups of genera, one of which consists of the strongly setose genera and the other of the more glabrous genera. Initially, both groups had a subgenital plate with a median lobe; this was retained in the Philotarsid groups and in Zelandopsocus and Austropsocus but the line giving rise to Zelandopsocus became more strongly apomorphous in even greater loss of setae and in developing a divided posterior lobe. The relationships of the Philotarsidae (except Zelandopsocus and Austropsocus) the Elipsocidae and Zelandopsocus and Austropsocus are indicated in figure 6.21.

Relationships within the remaining Philotarsidae

The characters of the genera Philotarsus, Aaroniella and Haplophallus have been compared by Thornton (1959a). Aaroniella has some apomorphous features not shared with the other genera, such as dark areas around alveolae on the veins and white apices to antennal segments. In other characters it is plesiomorphous. Philotarsus and Haplophallus share some relatively apomorphous features, such as fewer setae on the hind wing veins and lack of sclerification of penial bulb. These two genera represent one line of development and Aaroniella another. Philotarsus has a few apomorphous features not shared with Haplophallus such as an elongate trichobothrial field. The relationships of these three genera are indicated in figure 6.21.

Relationships within the Elipsocidae

Smithers (1964e) grouped the genera of Elipsocidae on the basis of morphological similarity into five groups to which subfamily rank was given. The groupings were as follows:

1. Nepiomorphinae: Nepiomorpha and Paedomorpha.
2. Pseudopsocinae: Reuterella, Pseudopsocus and Palmicola.
3. Propsocinae: Propsocus, Pentacladus, Antarctopsocus and Spilopsocus.
4. Elipsocinae: Elipsocus, Hemineura, Kilauella, Cuneopalpus, Palistreptus and Drymopsocus.
5. Lesneiinae: Lesneia.

The opinions implied in this grouping need revision in the light of new data and as a result of the subsequent description of Nothopsocus and Roesleria and the placing of Lesneia near Archipsocus.

Within the Elipsocidae the plesiomorphous conditions are: relatively long, 13-segmented antennae; fore wing with Rs and M fused for a length; free areola postica; media 3-branched; margin and veins fairly strongly setose; hind wing with Rs and M fused for a length, and with strong marginal setae between R_{2+3} and R_{4+5}; tarsi 3-segmented; hypandrium simple; subgential plate with lobe bearing strong marginal setae; dorsal valve divided apically; both sexes macropterous; wings without pattern; maxillary palp with normal fourth segment. Within the Elipsocidae transformation series move away from these conditions.

All of the genera except Nothopsocus, Palmicola, Nepiomorpha, Paedomorpha and Roesleria have a modified subgenital plate and this character appears to indicate a primary dichotomy in the family. Within this group, Roesleria and Paedomorpha stand apart in having strongly reduced ventral valves and form a sister group to Nepiomorpha, Palmicola and Nothopsocus. The latter three genera are very similar to one another in fundamental features and can be considered as a unit for present purposes.

Of the remaining genera Spilopsocus shows indication of a division of the lobe of subgenital plate by virtue of setal grouping on the margin. The genitalia, however, are retained in a plesiomorphous condition. This condition is extended in Propsocus, Pentacladus and Antarctopsocus, which also have strongly patterned wings in common with Spilopsocus. The former three genera have a sister group relationship to Spilopsocus and the four together bear that same relationship to the remaining genera in which there are apomorphous modifications to the dorsal valve and where the subgenital plate bears grouped setae on the hind margin. The relationships within the Propsocus, Pentacladus and Antarctopsocus group are simple. All have an apomorphously lobed male hypandrium and strongly bilobed subgenital plate. Antarctopsocus is always brachypterous and stands apart from the other two very similar genera which have a closed areola postica. They differ mainly in the number of branches of M, there are more than three branches in Pentacladus. There remain those genera which have the marginal setae of the subgenital plate grouped so as to indicate incipient bilobing. Of these, Elipsocus, Cuneopalpus, Drymopsocus and Hemineura agree in having the pointed apical division of the dorsal valve reduced to a rudiment. These genera are very closely related. Cuneopalpus is set apart by the shortened form of the fourth maxillary palp segment; the other three genera differ in minor characters of venation and development of polymorphism and can here be considered as a unit.

Pseudopsocus and Reuterella together form the sister group to the Cuneopalpus - Elipsocus - Drymopsocus - Hemineura line of development and have retained a strong apical division to the dorsal valve. They differ in the degree of polymorphism; Reuterella has 2-segmented tarsi. The genera Kilauella and Palistreptus are too poorly known to be placed with certainty but they are probably related to Elipsocus. The relationships implied above are indicated in figure 6.22.

RELATIONSHIPS WITHIN GROUP III

Group III arose from the same stock that gave rise to Group II. At the base of this line of development, therefore, stood a somewhat plesiomorphous Philotarsid-like Psocomorph. Also, it lacked any division of the dorsal valve of the gonapophyses, had a median posterior lobe on the hind margin of the subgenital plate and had 3-segmented tarsi. From such stock can be derived the genera of group III by a number of transformation series which culminate in the most apomorphous genera of this line, namely, those of the Thyrsophoridae.

Before considering the main line of development it is necessary to deal with the Lachesillidae, Graphocaecilius, Hemicaecilius, and Anomopsocus. One of the most difficult problems of psocid phylogeny lies in the placing of Lachesilla and Graphocaecilius. The discovery of Eolachesilla, however, has made possible more logical thoughts on this group. Eolachesilla, with its 3-segmented tarsi, sparsely setose wings and gonapophyses in which the external valve is emphasized is a link between the other members of the "3-segmented tarsi" line and the strongly apomorphous Lachesilla. Within this small complex of genera Eolachesilla stands opposed to the other genera in which the tarsi are 2-segmented and the gonapophyses are reduced to the setose external valve only.

Initially, the wings were, as in Eolachesilla, setose on the veins and margin although even in that genus the hind wings are glabrous.

Graphocaecilius (and probably Hemicaecilius) retain complex sclerifications of the penial bulb, and some wing setae but only the external valve remains of the gonapophyses. Graphocaecilius, therefore, stands as sister group to Anomopsocus and Lachesilla, in both of which the phallosome sclerification includes or consists of a Y-shaped structure. In Anomopsocus the hypandrium bears inconspicuous projections which could well be forerunners of the complex apophyses and spines of Lachesilla. These two genera differ in that Lachesilla has glabrous wings and retains a free areola postica whereas Anomopsocus has the areola postica fused to the media and retains a few wing setae.

For the suggested placing of these genera to be accepted it must be assumed that the subgenital plate lost its median lobe prior to the period at which Eolachesilla evolved. Unfortunately, we have no evidence to suggest how this was achieved and for the time being there must remain an element of doubt so far as the placing of those genera is concerned. The suggested relationships are indicated in figure 6.23.

We turn now to the main evolutionary developments and relationships in group III. The families Psilopsocidae, Myopsocidae, Thyrsophoridae and Psocidae (the Psocetae) share a number of apomorphous features which indicates that this large assemblage of species represents a monophyletic line within which, to establish internal relationships, we should seek subordinate groups with synapomorphous features. The wings are nearly always glabrous; the paraprocts of the males bear stout processes; the external valve of the gonapophyses tends to be transverse and curved around the dorsal valve, there are complex sclerifications associated with the entrance to the spermatheca and the phallosome tends to be simplified.

Within this group of families the Psocidae, Thyrsophoridae and Myopsocidae have in common the apomorphous feature of an areola postica fused to the media. In this respect the

Psilopsocidae stand as a sister group to them but have apomorphous features not found in the other families, such as a peculiar sclerification of the apex of the abdomen in the nymph. Of the families with a closed discal cell the Psocidae and Thyrsophoridae are apomorphous in having 2-segmented tarsi whereas the Myopsocidae, with 3-segmented tarsi, have apomorphous colour patterns peculiar to them alone and also have the dorsal valve of the gonapophyses long and pointed. The hypandrium is also strongly sclerified in a way not found in the Psocidae or Thyrsophoridae. These latter families are very similar but in the Thyrsophoridae we have a peculiar apomorphous fusion of R_{4+5} and M and an elongation of the wings, in addition to other apomorphous features. The relationships of these families are easily established on the features indicated as well as others and are indicated in figure 6.24.

It remains now to discuss the relationships of the groups within each of these families.

Relationships within the Psilopsocidae

At present only one genus is included in the Psilopsocidae.

Relationships within the Myopsocidae

Myopsocus and Lophopterygella share the apomorphous (secondary) feature of an Rs-M crossvein in the hind wing and of a comparatively simple phallosome as opposed to Phlotodes in which Rs and M are fused in the hind wing. Phlotodes is a sister group to the other two genera; Lophopterygella is very similar to Myopsocus differing mainly in having apomorphous curving of the wing margin between the veins. The relationships between the three genera are indicated in fig. 6.25.

Relationships within the Thyrsophoridae

In this family Thyrsophorus has apomorphously expanded fore legs. The other two genera have normal fore legs but Dictypsocus has a complex anastomosis of veins in midwing. Each genus has some apomorphous features of its own, but Thyrsopsocus and Dictyopsocus do not share the features of broadened fore legs with Thyrsophorus.

Thyrsopsocus and Dictyopsocus appear to represent sister groups which together have Thyrsophorus as a sister group. These relationships are indicated in figure 6.26.

Relationships within the Psocidae

Of all families in the order, the Psocidae is perhaps the most difficult to deal with although so many species have been described. For many years it was customary to place in Psocus almost any species with 2-segmented tarsi and a closed discal cell. Pearman's redefinition of Psocus (1932a) excluded over a hundred species from the genus and as most of these were very poorly known it was necessary to place them in Psocidus, a "holding genus" from which they could be removed when better known. The species in Psocidus must, therefore, be virtually ignored in this discussion. Despite this, it is possible, because of the large number of better-known genera, to indulge in some discussion of relationships and evolutionary trends within the family and to construct a framework into which one might hope, with confidence, to insert the poorly known groups as they are restudied.

The genera of Psocidae can be placed initially in a small number of groups, the members of each of which carry at least a few apomorphous features not found in the other groups.

The Amphigerontiinae stand apart as a distinctive group in which the males are strongly apomorphous in having the sternites anterior to the hypandrium strongly ascerotized and fused with the hypandrium. Also, the phallosome is strongly apomorphous in consisting of two parameres only, these sometimes separated.

The genus Antipsocus, placed alone in the subfamily Antipsocinae by Roesler, cannot be discussed in relation to other genera of Psocidae as it is not well known. Steleops and Brachinodiscus are too poorly known for further comment.

The Metylophorini and Cerastipsocini have in common a rounded, fleshy, dorsal valve of the gonapophyses; the hypandrium is complex and may be asymmetrical and the antennae are much lengthened.

The Psocinae include the most plesiomorphous genera of the family although it is possible to recognize two trends in the apomorphous development of the male hypandrium, one in which there occurs a variety of spines, apophyses, hooks and processes, symmetrically arranged or not and a second in which there is a median longitudinal upcurving strap-like development on the hypandrium. The strap-like structure is of various forms and is usually flanked by laterally extending processes of some sort from near its base. The female genitalia of the Amphigerontiinae and Psocinae are relatively plesiomorphous for the family.

The genus Cycetes has been placed in a tribe of its own, the Cycetini. In only one feature does this genus appear not to come within the Cerastipsocini. It has R_{4+5} touching M in the fore wing. As the Cerastipsocini have R_{4+5} curving strongly towards M after separation from R_{2+3} a small exaggeration of this would lead to the condition found in Cycetes and that genus should be considered with the Cerastipsocini.

The Amphigerontiinae must have arisen before the stage at which the dorsal valve of the gonapophyses became broad and fleshy, that is, before the Metylophorini and Cerastipsocini arose, as theyhave the dorsal valve in the more plesiomorphous condition, which they share with the Psocinae. The Metylophorini and the Cerastipsocini have several apomorphous features in common, such as long antennae and the form of the dorsal valve. The Cerastipsocini have, however, a shortened fourth maxillary palp segment and strong divergence of the arms of the radial fork, features which, in the Metylophorini, are retained in the plesiomorphous condition. It would seem, therefore, that the Amphigerontiinae developed as a sister group to the remaining Psocidae and that the Metylophorini - Cerastipsocini line represent the sister group of the Psocinae. These relationships are indicated in figure 6.23.

Within the Amphigerontiinae the genera Blastopsocidus and Neoblaste are synapomorphous in the development of strong, asymmetrical apophyses on the hypandrium; Amphigerontia, Blaste and Neopsocopsis have a symmetrical hypandrium; Elaphopsocus is very plesiomorphous in this feature, having a simple hypandrium. It does have, however, an apomorphous crossvein between the areola postica and the media; a feature not shared with any other genus in the subfamily. It would seem, therefore, the Elaphopsocus represents the sister group to the remaining Amphigerontiinae and that the latter show two distinct lines of development in each of which the hypandrium has developed apomorphously in its own way. In that line which has developed asymmetrical apopophyses, there has also been a tendency for the first and second sections of Cu_{1a} to come to lie in the same straight line. Within each of the evolutionary lines thus established the genera are very closely related and can be treated as a unit. The relationships within the Amphigerontiinae are indicated in figure 6.28.

Mention has already been made of the two major lines ofdevelopment within the Psocinae as indicated by development of the hypandrium. The line in which the hypandrium has developed a strap-like median structure includes the Ptycta - Copostigma complex, Pearmania, Atlantopsocus, Ghesquierella, Hyalopsocus and Camelopsocus. The line in which the hypandrium bears various apophyses and spines includes Psocus, Neopsocus, Trichadenotecnum and Oreopsocus.

Within the former line, Hyalopsocus and Camelopsocus tend towards asymmetry in the hypandrium whereas the other genera do not. In the latter line, Trichadenotecnum and Oreopsocus have the first and second sections of Cu_{1a} nearly in a straight line whereas in Psocus and Neopsocus there is a distinct angle between these sections of the veins.

This implies a dichotomy in each line. The relationships of genera within the Psocinae as suggested above are indicated in figure 6.29.

Within the Cerastipsocini all the genera except Psococerastis have strongly diverging arms of the radial fork, this being an apomorphous feature which marks them off as a small monophyletic group of genera. Eremopsocus stands apart from Cerastipsocus, Scaphopsocus and Cycetes in having apomorphously thickened antennae. These three genera are closely related and differ in minor morphological features, they can be considered as a unit for present purposes. The sister group relationships implied above are indicated in figure 6.30.

The three genera of Metylophorini which are well enough known for serious consideration are Metylophorus, Diplacanthoda and Pilipsocus. Metylophorus and Diplacanthoda share the apomorphous feature of an elongate lobe to the subgenital plate; Pilipsocus retains this feature in plesiomorphous short, form. Diplacanthoda is remarkably apomorphous in that it carries large thoracic spines unique amongst Psocoptera. Metylophorus and Diplacanthoda appear to form a sister group to Pilipsocus although the two former genera are not close in overall morphology. With the discovery of more species of Pilipsocus generic limits in this tribe could well be altered and a better appraisal of relationships be possible. The tentative relationships suggested above are indicated in figure 6.31.

CHAPTER VII. PROPOSED CLASSIFICATION OF THE PSOCOPTERA

1. INTRODUCTORY COMMENTS

The phylogenetic system of reasoning put forward by Hennig (1966) makes it possible to establish the relationships of groups. This automatically results in the groups concerned being arranged in a hierarchy; some groups are equivalent to others and some are subordinate to others. This result of the system is discussed by Hennig (1966, p. 154 et seq.) and his discussion need not be repeated here. The most important fact which emerges, however, from a practical point of view is that all sister groups are of equivalent status in the hierarchy. Any expression of the hierarchy, whether verbal, pictorial, mathematical or physical must clearly show this equivalence. Whilst this is not too difficult to achieve when dealing only with a small section of the animal kingdom, as most specialist zoologists do, the problem is of a different calibre when the whole animal kingdom is involved. In that case the widely accepted categories in each group must, of necessity, be compared from group to group and it becomes immediately apparent that gross changes in status are required if the true equivalence of groups in different phyla are to be indicated.

Using one of Hennig's examples (Hennig, 1966, p. 187) we find that the "orders" of placental mammals become equivalent to the families of cyclorrhaphous Diptera and are not equivalent to the orders of insects. The mammals would be equivalent to an order of insects and the Marsupialia and Placentalia would become families. The logic of such a system is clear but one of the practical problems involved in making the sweeping changes in concept and nomenclature is well put by Hennig (1966, p. 191): "Presumably even the most convincingly presented objective reasons will not bring these specialists to the point of giving up life-long habits and speaking of classes and orders where they are accustomed to speaking of families and vice versa". As the equivalence of groups is based on the age of origin of the groups concerned, Hennig (1966) has suggested a compromise in which different time scales are designated for different groups so that the present absolute ranking in the hierarchy might be retained to a large extent within each group. For example, in mammals, groups arising from the Upper Cretaceous to the Oligocene would now represent orders and those arising from

Triassic to Lower Cretaceous would represent classes. This would result in little change in the present nomenclature of the hierarchy of mammals. If these same periods were applied to the hierarchy in insects, gross changes would need to be made in current classifications. On the other hand, if the period from Mississippian to Permian were considered as the period of origin at the ordinal level for insects and that from the Cambrian to Devonian for origin at the class level the changes required would be fewer. Conversion from one to another would be relatively simple and the equivalence of groups in the mammals and insects be readily ascertained when when necessary even though specialists in their respective groups could continue using more conventional levels for their groups.

For the present, for practical purposes, and until such time as adequate phylogenetic studies have been made in most of the phyla of the animal kingdom some such compromise seems reasonable. In any case, it is just not possible to say what are the phylogenetic relationships of many phyla and thus inter-phylum comparison is in most cases not possible.

The problem of the absolute ranking of categories is also discussed by Hennig (1966) and he concludes that the geological periods can give an indication of whether a given category in the hierarchy should be considered as a Class, Order, Family and so on. Groups arising during given geological periods would have equivalent status. For this present study this question does not concern us as we have adopted the category of "Order" for the insects usually referred to as the Psocoptera and have shown that this group is a monophyletic one. Our concern at this stage in our endeavours to arrive at a logical classification of these insects is with the grouping of the known genera into higher categories on the basis of the relationships arrived at by phylogenetic study. Study of the material available has given us an indication of what the major dichotomies have been in the evolution of the Psocoptera and we now must express this as a classification.

Where in the past genera have been grouped into families (and species into genera) on the basis of overall resemblance it was possible to combine certain groups of genera in more than one way with equal justification. By grouping the genera on the basis of synapomorphous features only, this is no longer possible as any genus which does not have the necessary apomorphous features cannot form part of the monophyletic line which has them. Thus, the relative positions of genera become determined, not by an arbitrary selection of combinations of characters, but by the possession of certain definite characters in relatively apomorphous condition. There is already in use a set of categories, namely, Genus, Family, Order and Class which, if there is need, can be extended by the use of the prefixes "sub" and "super". In a classification in which the grouping is determined by the classifier it is possible to limit the categories used to these traditional ones and extend or restrict the categories in the hierarchy. Doubtless the form which many current classifications assume are the result of the classifier of a large group attempting to force his hierarchy to fit into the traditional "straight-jacket" of categories or that of a small one loosely expanding his small group to fit into the many categories available.

The expression, in a classification based on phylogenetic relationships (especially of a large group), of all the dichotomies which the various monophyletic lines have undergone is obviously not possible, nor would this in any case be necessary, especially when a discussion of the phylogenetic relationships is given at the time the classification is proposed. Nevertheless, the more dichotomies which can be expressed, without loss of clarity, the better.

It has been pointed out above that expression of equivalence of groups is not at present possible between distantly related animals although this is clearly desirable (whatever this may do to our traditional classifications!) and should remain one of the ultimate goals of zoologists professing to be systematists. It is essential that strict attention be given to equivalent groups within limited monophyletic lines being assigned to equivalent categories in the hierarchy. Where the fossil history of a group is well known it is possible to assign category levels to given periods and within the framework so provided to assign equivalent rank to sister groups. This is not a possible line of approach in the Psocoptera as the fossil evidence gives no indication of the time of origin of any of the groups which we would, for instance, now term families. The true fossil Psocoptera are far removed from modern forms and by the Oligocene the forms were very similar to living forms; we know very little of what happened between the Upper Permian and the Oligocene.

In certain parasite insect groups it is possible to link the history of the parasites with that of their hosts; this is not possible with the Psocoptera.

Zoogeographic studies can give an indication of sister group relationship as sister groups frequently occupy different areas. This is referred to by Hennig (1966, p. 169) as "vicariance relations of higher order" meaning higher than the subspecific level, for which level the principles involved were originally enunciated. The zoogeography of the of the Psocoptera is discussed in Chapter VIII.

Morphology and biology can give an indication of the absolute ranking into which groups should be placed and, in the case of the Psocoptera, this must, at present, be the main source of data on which to erect a classification.

In Chapter VI the phylogeny and evolution within the order has been discussed and the main dichotomies and sister groups in the order have been determined so far as is possible with present data. It is possible to trace the major divisions and subdivisions in the order through the dichotomies and this provides the basis for the suggested classification which is given later in this work. It will be seen that seven categories above the Genus and below Order are used. These are Tribe, Subfamily, Family, Superfamily, Group, Division and Suborder. These categories have been used in order to ensure clarity and each corresponds to a major dichotomy in the evolutionary sequence. It would not, of course, always be necessary to include the categories of Group or Division, or indeed some of the other categories, provided that at each point equivalent groups were given the same category and it was ensured that sister groups retained equivalence.

The following suggested classification is based on what are believed to be the main evolutionary events in the history of the group, that is, the first dichotomy leads to the two suborders, the next dichotomy represents the rise of what is destined to be a Division and so on. The categories, therefore, bear a definite relation to the evolution of the order. It would be just as meaningful for general purposes if the categories of Division, Group, Superfamily and Tribe were omitted; their hidden existence, however, as indicative of real events in the evolutionary history of the order should not be forgotten.

The classification suggested later differs from those previously suggested in one important general way as well as in detail. The so called "higher" genera are grouped into a small number of families relative to the "lower" genera, in which the number of families is relatively greater than previously suggested. This is because the animals are, so to speak, classifying themselves according to their evolutionary history and are not being grouped by a classifier into groups whose members bear a general overall resemblance to one another. For example, the genera previously grouped into the three families Mesopsocidae, Philotarsidae and Elipsocidae are all included in a single tribe of the Psocidae. Roesler (1944) went some way towards this when he grouped those genera with 3-segmented tarsi from the above families into a single family, but this he did on the basis of general resemblances and so excluded some genera which are clearly members of the same line of evolution. Following through the evolutionary development of monophyletic lines and using this as a basis for classification has resulted in a somewhat "top-heavy" arrangement, in that some tribes contain many genera whilst, at the other extreme, there are superfamilies consisting of only one genus. This may appear inconvenient and difficult for some systematists to accept; the inconvenience cannot be helped, something happened in nature and the study of it leads to such a classification.

The classification arrived at is of quite practical use. It is often stated or suggested that a classification which reflects the phylogeny of a group is difficult to use for other purposes, for example, in the making of identification keys. When such a classification is based on the establishment of monophyletic lines characterized by synapomorphous features, the making of keys is no more difficult than usual and may, in fact, be easier because each dichotomy in the evolutionary history of the group is characterized by the development in one or other line of apomorphous features which can frequently be used as characters in keys.

It is not suggested that the classification put forward here is perfect; it is based on imperfect, currently known data and could at best only be as good as the data.

It is, however, an attempt at providing a more rational grouping of genera, using something more stable than opinion based on subjective conclusions regarding the general resemblances between genera, namely, the phylogeny of the insects themselves.

Figure 7.1 is a combination of the dendrograms given in Chapter VI showing the relationships of the genera. Figure 7.2 is a diagram indicating how the major groupings of genera have been related to the dichotomies thought to have taken place during the evolution of the order.

2. PROPOSED CLASSIFICATION OF THE PSOCOPTERA

Order PSOCOPTERA

Suborder TROGIOMORPHA

Division TROGIOFORMIA

Group PERIENTOMETAE

Superfamily THYLACELLOIDEA

Family THYLACELLIDAE

Thylacella Enderlein,* Thylax Hagen.

Superfamily PERIENTOMOIDEA

Family LEPIDOPSOCIDAE

Cyptophania Banks, Echinopsocus Enderlein,* Echmepteryx Aaron, Lepidopsocus Enderlein, Pteroxanium Enderlein, Scolopama Enderlein.

Family PERIENTOMIDAE

Subfamily LEPOLEPIDINAE

Lepolepis Enderlein.

Subfamily PERIENTOMINAE

Lepium Enderlein,* Nepticulomima Enderlein, Notolepium Enderlein, Parasoa Thornton,* Perientomum Hagen, Proentomum Badonnel, Soa Enderlein.

Group TROGIETAE

Superfamily TROGIOIDEA

Family ANOMOCOPIIDAE

Anomocopeus Badonnel.

Family TROGIIDAE

Trogium Illiger, Lepinotus Heyden, Cerobasis Kolbe, Myrmecodipnella Enderlein.

Superfamily PSOQUILLOIDEA

Family PSOQUILLIDAE

Subfamily PSOQUILLINAE

Psoquilla Hagen.

Subfamily RHYOPSOCINAE

Balliella Badonnel, Rhyopsocus Hagen, Eosilla Ribaga.

Family EMPHERIIDAE

* Empheria Hagen, *Trichempheria Enderlein.

Division PSYLLIPSOCIFORMIA

Group PRIONOGLARETAE

Superfamily PRIONOGLAROIDEA

Family PRIONOGLARIDAE

Prionoglaris Enderlein.

Group PSYLLIPSOCETAE

Superfamily SPELEKETOROIDEA

Family SPELEKETORIDAE

Speleketor Gurney.

Superfamily PSYLLIPSOCOIDEA

Family PSYLLIPSOCIDAE

* Psyllipsocus Selys-Longchamps.

Family PSOCATROPIDAE

Psocatropos Ribaga, Dolopteryx Smithers, Dorypteryx Aaron.

Suborder PSOCOMORPHA

Division AMPHIENTOMIFORMIA

Group LIPOSCELETAE

Superfamily LIPOSCELOIDEA

Family LIPOSCELIDAE

Subfamily LIPOSCELINAE

* Liposcelis Motschulsky.

Subfamily EMBIDOPSOCINAE

Embidopsocus Hagen, Belapha Enderlein, Belaphotroctes Roesler, Belaphopsocus Badonnel, Troctulus Badonnel.

Family SPHAEROPSOCIDAE

* Sphaeropsocus Hagen, Badonnelia Pearman, Sphaeropsocopsis Badonnel.

Superfamily PACHYTROCTOIDEA

Family PACHYTROCTIDAE

Subfamily TAPINELLINAE

* _Psylloneura_ Enderlein, _Tapinella_ Enderlein.

Subfamily PACHYTROCTINAE

Antilopsocus Gurney, _Pachytroctes_ Enderlein.

Group AMPHIENTOMETAE

Superfamily MUSAPSOCOIDEA

Family MUSAPSOCIDAE

Musapsocus Mockford

Superfamily AMPHIENTOMOIDEA

Family TROCTOPSOCIDAE

Subfamily TROCTOPSOCINAE

Troctopsocus Mockford, _Troctopsocopsis_ Mockford, _Troctopsoculus_ Mockford.

Subfamily PROTROCTOPSOCINAE

Protroctopsocus Mockford.

Family AMPHIENTOMIDAE

Subfamily ELECTRENTOMINAE

Manicapsocus Smithers, _Epitroctes_ Mockford, _Phallopsocus_ Badonnel, * _Electrentomum_ Enderlein, * _Parelectrentomum_ Roesler.

Subfamily AMPHIENTOMINAE

Tribe COMPSOCINI

Electrentomopsis Mockford, _Compsocus_ Banks.

Tribe AMPHIENTOMINI

Cymatopsocus Enderlein, _Tineomorpha_ Enderlein, * _Amphientomum_ Pictet, _Hemiseopsis_ Enderlein, _Marcenendius_ Navas, _Nephax_

Pearman, *Paramphientomum* Enderlein, *Pseudoseopsis* Badonnel, *Seopsis* Enderlein,*Seopsocus* Roesler, *Stigmatopathus* Enderlein, *Stimulopalpus* Enderlein, *Syllysis* Hagen.

Division PSOCIFORMIA

Group EPIPSOCETAE

Superfamily EPIPSOCOIDEA

Family CALLISTOPTERIDAE

Callistoptera Enderlein.

Family EPIPSOCIDAE

Subfamily GOJINAE

Goja Navas.

Subfamily EPIPSOCINAE

Neurostigma Enderlein, * *Epipsocus* Hagen, *Epipsocopsis* Badonnel.

Superfamily PTILONEUROIDEA

Family CLADIOPSOCIDAE

Subfamily CLADIOPSOCINAE

Cladiopsocus Roesler.

Subfamily EUPLOCANIINAE

Triplocania Roesler, *Euplocania* Enderlein.

Family PTILONEURIDAE

Ptiloneuropsis Roesler, *Ptiloneura* Enderlein.

Group PSOCETAE

Superfamily CALOPSOCOIDEA

Family POLYPSOCIDAE

Polypsocus Hagen, Monocladellus Enderlein.

Family CALOPSOCIDAE

Calopsocus Hagen, Neurosema McLachlan, Dirla Navas.

Superfamily PSOCOIDEA

Family CAECILIIDAE

Subfamily PSEUDOCAECILIINAE

Tribe TRICHOPSOCINI

Trichopsocus Kolbe, * Palaeopsocus Kolbe.

Tribe PSEUDOCAECILIINI

Pseudocaecilius Enderlein, Trichocaecilius Badonnel, Scottiella Enderlein, Pseudoscottiella Badonnel, Scytopsocus Roesler, Heterocaecilius Lee and Thornton, Cladioneura Enderlein, Ophiodopelma Enderlein, Mesocaecilius Okamoto, Ptenolasia Enderlein.

Subfamily CAECILIINAE

Tribe ECTOPSOCINI

Ectopsocus McLachlan, Ectopsocopsis Badonnel, Interpsocus Edwards.

Tribe CAECILIINI

Matsumuraiella Enderlein, Stenopsocus Hagen, Graphopsocus Kolbe, Taeniostigma Enderlein, Kodamaius Okamoto, Epikodamaius Kuwayama, Eocaecilius Badonnel, * Kolbea Enderlein, Teliapsocus Chapman, Dasypsocus Enderlein, Schizopechus Pearman, Harpezoneura Enderlein, Pentathyrsus Enderlein, Xenopsocus Kolbe, Amphipsocopsis Smithers, Fulleborniella Enderlein, Ypsiloneura Pearman, Amphipsocus McLachlan, Isophanes Banks, Dypsocus Hagen, Coryphosmila Enderlein, * Caecilius Curtis, Mepleres Enderlein, Paracaecilius

Badonnel, Notiopsocus Banks, Asiopsocus Gunther, Enderleinella Badonnel, Tagalopsocus Banks, Dasydemella Enderlein, Ptenopsila Enderlein.

Family PSOCIDAE

Subfamily ARCHIPSOCINAE

Tribe ARCHIPSOCINI

* Archipsocus Hagen, Archipsocopsis Badonnel.

Tribe LESNEIINI

Lesneia Badonnel.

Subfamily PSOCINAE

Tribe ELIPSOCINI

Labocoria Enderlein, Hexacyrtoma Enderlein, Mesopsocus Enderlein, Psoculus Roesler, Aaroniella Mockford, *Philotarsus Kolbe, Haplophallus Thornton, Zelandopsocus Tillyard, Austropsocus Smithers, Pseudopsocus Kolbe, Reuterella Enderlein, Cuneopalpus Badonnel, * Elipsocus Hagen, Drymopsocus Smithers, Hemineura Tetens, Kilauella Enderlein, Palistreptus Enderlein, * Propsocus McLachlan, Pentacladus Enderlein, Antarctopsocus Smithers, Spilopsocus Smithers, Roesleria Badonnel, Paedomorpha Smithers, Palmicola Mockford, Nothopsocus Badonnel, Nepiomorpha Pearman.

Tribe PSOCINI

Graphocaecilius Enderlein, Hemicaecilius Enderlein, Eolachesilla Badonnel, Lachesilla Westwood, Anomopsocus Roesler, Kaestneriella Roesler, Peripsocus Hagen, Psilopsocus Enderlein, Lophopterygella Enderlein, Myopsocus Hagen, Phlotodes Enderlein, Thyrsopsocus Enderlein, Dictyopsocus Enderlein, Thyrsophorus Burmeister, Elaphopsocus Roesler, Amphigerontia Kolbe, Blaste Kolbe, Neopsocopsis Badonnel, Blastopsocidus Badonnel, Neoblaste Thornton, Hyalopsocus Roesler, Camelopsocus Mockford, Ptycta Enderlein, Copostigma Enderlein, Pearmania Badonnel, Ghesquierella Badonnel, Atlantopsocus Badonnel, * Trichadenotecnum Enderlein, Oreopsocus Roesler, Psocus Latreille, Neopsocus Kolbe, Psococerastis Pearman, Eremopsocus McLachlan, Cycetes Enderlein, Cerastipsocus Kolbe, Scaphopsocus Smithers, Diplacanthoda Enderlein, Metylophorus Pearman, Pilipsocus Badonnel.

PSOCIDA AGNOTA

Allopsocus Banks, Valenzuela Navas.

Note: The genera Hemipsocus and Anopistoscena have not been placed in the above scheme but are probably includable in the Caeciliidae. Electropsocus should probably be placed near Mesopsocus. Species at present in Psocidus will be distributed through the Psocini in due course.

CHAPTER VIII. ZOOGEOGRAPHY OF THE PSOCOPTERA

1. INTRODUCTORY COMMENTS

The object of this brief chapter is to ascertain to what extent it is possible to obtain confirmation of the proposed classification by zoogeographical data. The most important requirement in the zoogeographic study of any group is a sound phylogenetic classification and adequate collecting over the range of the group. The classification and relationships of the genera of Psocoptera suggested in this work are, within the limits of the reservations already indicated, considered to be an advance on any previously suggested, and whilst not the final word, provide a background against which to consider zoogeographical data.

The recorded distribution of each genus has been given in broad terms with the definition of the genus in Chapter IV and need not be repeated here. There are several important points to remember when considering the zoogeography of the Psocoptera. There will be a proportion of species which are wrongly referred to the genera in which they are now placed and the distribution of the genera will accordingly be inaccurately recorded. This is a source of error which only monographic treatment at the species level can eliminate. Several genera consist wholly, or in large part, of species which are closely associated with Man and are, therefore, widespread; it is usually not possible to suggest the area to which such species might be indigenous. Several genera contain species which are rapid colonizers, not necessarily man-assisted. These include such groups as those inhabiting dried leaves, a widespread temporary habitat in which such "opportunist" species can readily survive for short periods. There are many areas of the world where collecting has been too inadequate for assessment of the fauna to be made. There will be many groups where the recorded distribution is that of collections rather than of the insects.

With present knowledge, discussion of the distribution of groups of Psocoptera can be in very general terms only and considerable care must be exercised in drawing detailed conclusions. It should be noted that the categories referred to in the following discussion are those in the newly proposed classification of Chapter VII and not those at present in general use.

2. ZOOGEOGRAPHICAL COMMENTS

The Order, if the fossil forms are included, was well established by the Lower Permian. Many modern genera, in both suborders, have been found in Oligocene amber. Archipsylla, from the Jurassic, had wing venation which suggests that it was well on the way to being very similar to present-day species. The stock from which the two suborders,Trogiomorpha and Psocomorpha, arose was probably in existence at some time between Jurassic and Oligocene. As so many modern genera had already made their appearance by the Oligocene, some with strongly apomorphous features, we must conclude that the two suborders had probably become established as separate lines during the Cretaceous.

Apart from domestic species and a few restricted to tropical Queensland, the Trogiomorpha are absent from Australia and poorly represented in South America. They are most strongly represented in tropical Africa and through the Indo-Malayan and Oriental regions. The Psocomorpha are represented in all regions. Some such broad geographical relationship would be expected of sister groups at higher category levels.

Distribution of the Suborder Trogiomorpha

The Trogiomorpha are essentially warm climate insects. Comparatively few species occur naturally in cooler climates. Penetration of temperate zones has been largely in association with Man.

The Division Psyllipsociformia are almost entirely cave dwellers or occur in human habitations in the Palaearctic and Nearctic regions and, like the Division Trogioformia, do not appear to have been able to move into temperate areas without man's assistance or the presence of protective cave environments. They probably originated in tropical areas.

The Trogioformia are well represented in tropical Africa, the Indian and Oriental regions; as in the Psyllipsociformia several species are established in domestic association with Man in temperate areas. The Trogiomorpha give the impression of being a tropical group which has spread as far as possible within the limits of its ability to adapt to cool climatic conditions.

Distribution of the Suborder Psocomorpha

The Division Amphientomiformia are, apart from domestic and apparently other introduced species, very poorly represented in the Holarctic region and Australia. In the Liposceletae the large genus Liposcelis has many species common in stored products which are easily transported by man and in Embidopsocus (of 23 species) very few are Holarctic. The group is strongly represented in South America, Africa and the Oriental region.

The Division Psociformia are found in all regions. The Liposcelidae and Sphaeropsocidae are considered to be sister groups. The former family, if one ignores the domestic and easily transported species, has a wide distribution but is not common in Australia; the latter is found in amber and has an otherwise South American and Australian distribution, indicating a strong degree of mutual exclusion with modern Sphaeropsocids showing a classic "southern continent" distribution. The Pachytroctidae are mainly tropical and they would appear to be a branch of a stock which gave rise to the other members of the Liposceletae. The distribution of these groups seem to well defined and sufficiently mutually exclusive to support the arrangement of the groups suggested on morphological grounds.

The Amphientometae are composed of those groups which are South and Central American and those which are African and Indo-Oriental. The Amphientometae are virtually absent from the Holarctic. The distribution pattern supports the setting aside of the Amphientomini as opposed to the several South American genera. In the suggested classification the Electrentominae are shown as being more closely related to the Amphientomini than to the Musapsocidae and Troctopsocidae. The distributions of these groups do not support this conclusion; further collecting in South America might enable us to explain this contradiction. In general, however, the distribution of the Amphientomiformia supports the suggested classification.

The Psociformia is the largest of the four Divisions of the order and includes the most apomorphous genera. As a whole the group is widespread but there are certain sections of the group which have restricted distributions. Included are some genera, especially in the Psocini and the Caecilini, which are rapidly evolving and the detailed study of which would probably yield interesting zoogeographic information relating to the very recent history of the groups. The Epipsocetae are mainly South American with Epipsocus being more widespread(but not in Australia) and with a specialized African offshoot (Epipsocopsis). Callistoptera is a New Guinea genus but its relationships need investigation. It is known only from poorly preserved dry material not available for dissection. The Epipsocetae stand apart from the rest of the Psociformia onmorphological as well as geographical grounds. Amongst the remaining genera of Psociformia there are few restricted to South America but many have South American species. In some cases the generic placing is in doubt, e.g. Kolbea in which only one of ten species is South American. The superfamily Calopsocoidea contains a small South American family (Polypsocidae) and an Indo-Australian family (Calopsocidae), the two being sister groups and mutually exclusive. Within the Caeciliidae, the Trichopsocini and the Pseudocaeciliini are mutually exclusive although very different in number of species. The former is European, the latter covers the African and Indo-Australian regions. The work of Lee and Thornton (1967) suggests that Pseudocaecilius and its allies are now actively spreading and speciating in the Pacific Islands. The Pseudocaeciliinae are virtually absent from the New World. Some of the Ectopsocini are very vagile. Ectopsocus is worldwide, Ectopsocopsis is African (except for one widespread species which has not yet been found in Africa!) and Interpsocus is Australian. This distribution supports the suggested relationships for the many species included in these three genera. The Caeciliini includes a large number of genera. The position of Matsumuraiella is doubtful on morphological grounds and new material is necessary. Stenopsocus, Graphopsocus and Taeniostigma form a group which is mainly Palaearctic and Indo-Malayan. They form a sister group to the genera listed (page) from Eocaecilius to Amphipsocus which are African, including the specialized offshoot formed by Xenopsocus and Amphipsocopsis in Madagascar. The genera Dypsocus, Isophanes, Coryphosmila and Mepleres are in need of revision after which it may be possible to establish their relationships with the large and apparently rapidly evolving Caecilius (235 species) on more satisfactory zoogeographic grounds. On the available morphological data these genera seem to represent specialized offshoots of the Caecilius line.

In the Psocidae the tropical Archipsocus and Archipsocopsis form a sister group to the South African Lesneia. The Elipsocini offer some fascinating zoogeographic problems at the generic and specific level; these need much further collecting in areas such as South America and Australia for their solution. Within the Elipsocini there is a group of genera (Propsocus, Pentacladus, Antarctopsocus, Spilopsocus, Roesleria, Paedomorpha, Palmicola, Nothopsocus, Nepiomorpha) which, on analysis, all show southern affinities and seem to represent a complex of genera supporting the theory of the past existence of a southern continent. The other Elipsocini are virtually absent from the area occupied by these genera. More than this cannot be said with confidence at this stage. Within the Psocini we find that Australia is poor in species other than in Peripsocus and the Myopsocus-Phlotodes complex. South America has a group of genera not found elsewhere (Thyrsophorus, Thyrsopsocus and Dictyopsocus) whilst the sister group to these genera (those listed from Amphigerontia to Pilipsocus page 361) are absent or very poorly represented in South America. Little can be said of the genera Lachesilla, Eolachesilla, Kaestneriella and Anomopsocus.

The above comments on the distribution of the Psocoptera are inevitably sketchy; the group is very poorly known for many areas. The classification proposed in Chapter VII seems, in broad outline, to be supported by the study of distribution patterns as at present recorded. This gives added confidencethat the proposed classification is, in the main, reflecting the phylogeny of the order.

CHAPTER IX. GENERAL DISCUSSION

In this work an attempt has been made to apply the principles of phylogenetic systematics enunciated by Hennig (1966) to an order of insects, the Psocoptera.

It has been usual in phylogenetic studies to assemble data on the chosen taxonomic units and to seek out those having attributes in common. These units have been grouped together and been regarded as being closely related. Each set of closely related units has been given equivalence in the hierarchy of the classification and the sets of units have then been scrutinized to assess the relative closeness of affinity amongst them in order to decide upon the next rank in the hierarchy. Objections have been raised to this method of arriving at a classification. The characters chosen varied, often according to the whim of the student. Some characters were considered, sometimes on quite arbitrary grounds, to be more important as indicators of affinity, than others. It is often possible to arrange a given set of units in more than one way with equal justification using this method and many of the differences of opinion expressed in classifications have arisen because of this. In many cases there is no logical way of deciding between the merits of two classifications. Numerical taxonomy was developed essentially in an attempt to remove the bias of the student and replace it by an impartial mathematical process which would express in clear terms the degree of similarity and difference between the entities under consideration. To this extent it is a valuable taxonomic tool and provides a far superior measure of resemblance than any taxonomist could ever hope to achieve by visual study of data. It will be noted that the method involved the comparison of the units as a whole; their degree of overall resemblance was the criterion by which closeness of affinity was judged, hence the need for precision in assessing this and the claim by numerical taxonomists that they had found the correct way of setting about classifying organisms. Their claim that they could handle a vast number of characters and hence remove the need for chosing characters and, with it, bias is irrefutable.

Hennig (loc. cit.) however, has indicated, by extensive argument, that overall resemblance is not necessarily indicative of closeness of affinity and that similarity between taxonomic units in a few characters only, provided they are apomorphous, indicates community of origin and hence affinity.

He also shows that a relatively large array of plesiomorphous characters in common does not necessarily indicate closeness of affinity. Because of this many groups in classifications at present in use are not monophyletic. The numerical taxonomists, therefore, have set about perfecting a technique of measuring overall resemblance when overall resemblance is not the criterion on which affinity should be judged. This is not the fault of the numerical taxonomists (most of whom are mathematicians and not biologists) but of the traditional taxonomists who were attempting phylogenetic classification of organisms using criteria which could not satisfactorily be used for this purpose. The numerical taxonomists have been chasing a "red herring" set in motion by non-mathematical taxonomists.

There have been comparatively few attempts to apply Hennig's system in detail to groups of insects at present of high category in the hierarchy, e.g. at the ordinal level. This is understandable in view of the great size of most orders. Most of the smaller orders have suffered from the drawback that they are obviously poorly worked. This applies to some extent to the Psocoptera but the work carried out now in assembling data at the generic level has made possible this preliminary attempt at phylogenetic classification of the whole order. It is unfortunately difficult to asses the degree of success of such an attempt immediately. It must be tested. If the suggested classification and the phylogeny as described here are a reflection of what has happened in the evolutionary history of the order then newly discovered forms will fit into the scheme with relative ease and, with additional data, those which are poorly known and now misplaced should be moved to a satisfactory position without any major reconstruction of the framework of the classification. It is hoped that this classification will be used as a testing ground by students of the Psocoptera. If little change is needed in the light of new information, it will indicate that the system by which it has been arrived at, Hennig's system, is an adequate and useful one. If it breaks down, Hennig's approach will need re-evaluating. The fact that it has been possible to apply Hennig's principles consistently throughout the work and that major difficulties have nearly always been due to lack of data, suggests that the approach is a fruitful one to adopt for attempting to establish the phylogeny and classification of the Psocoptera.

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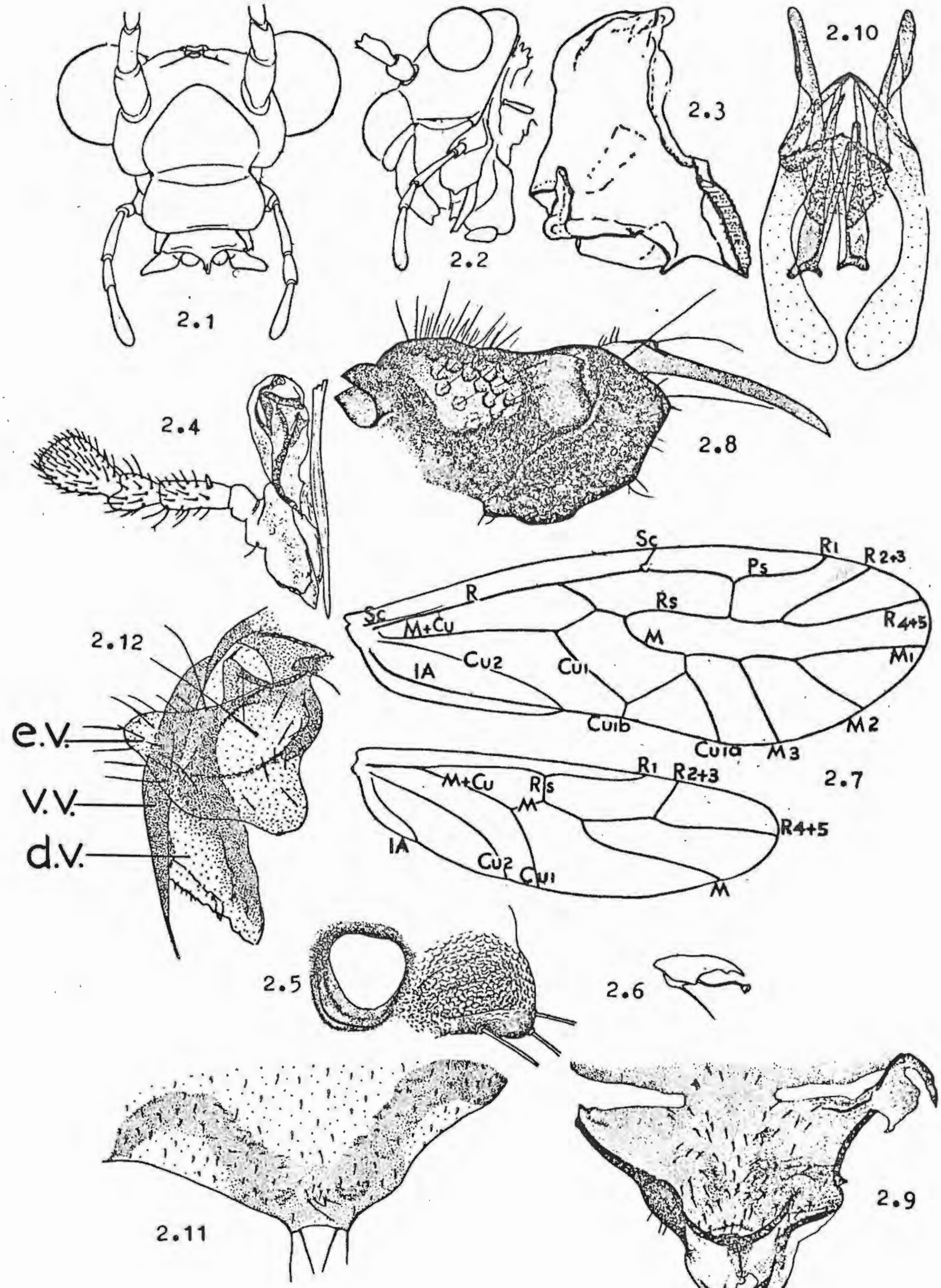
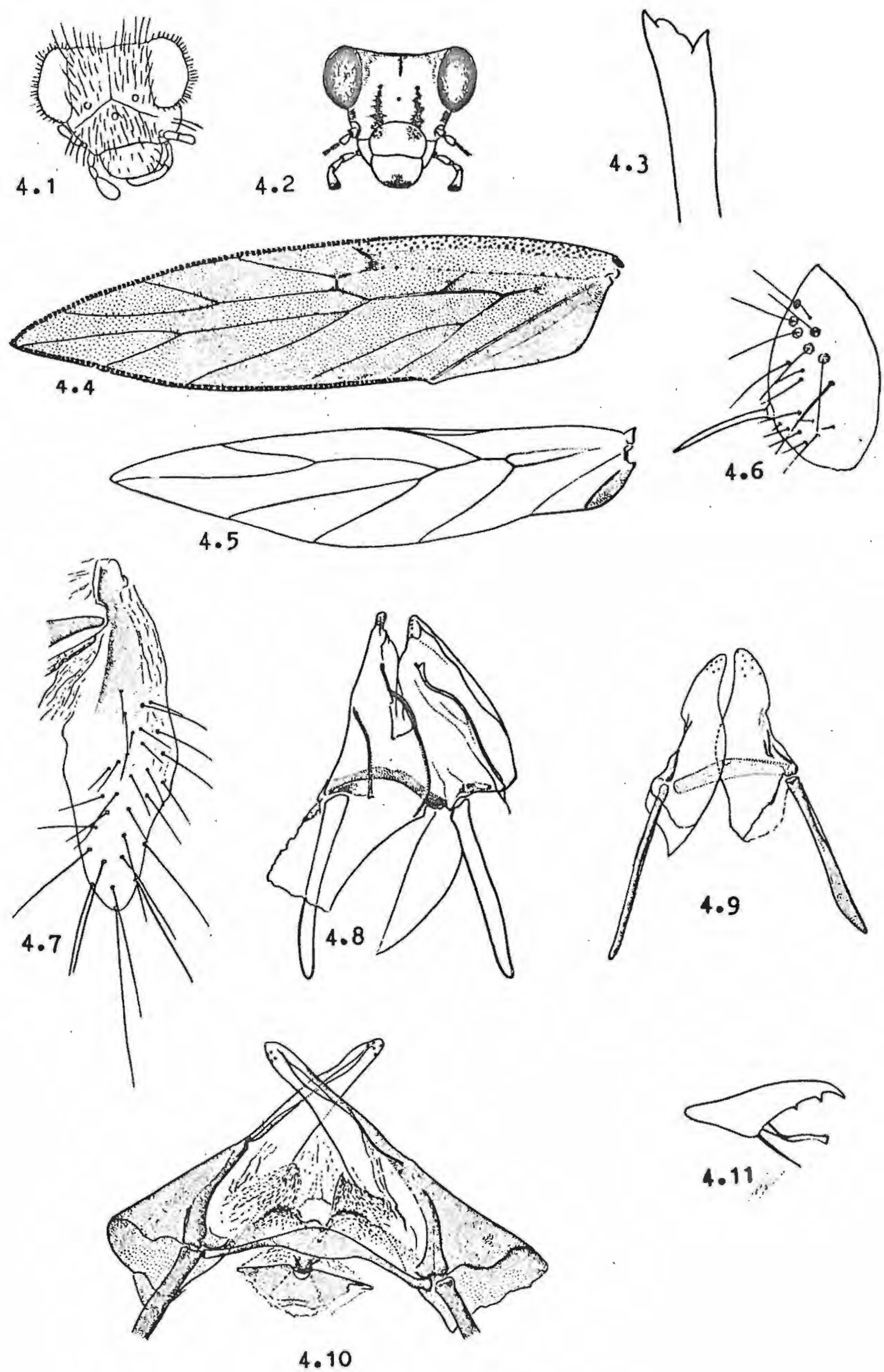
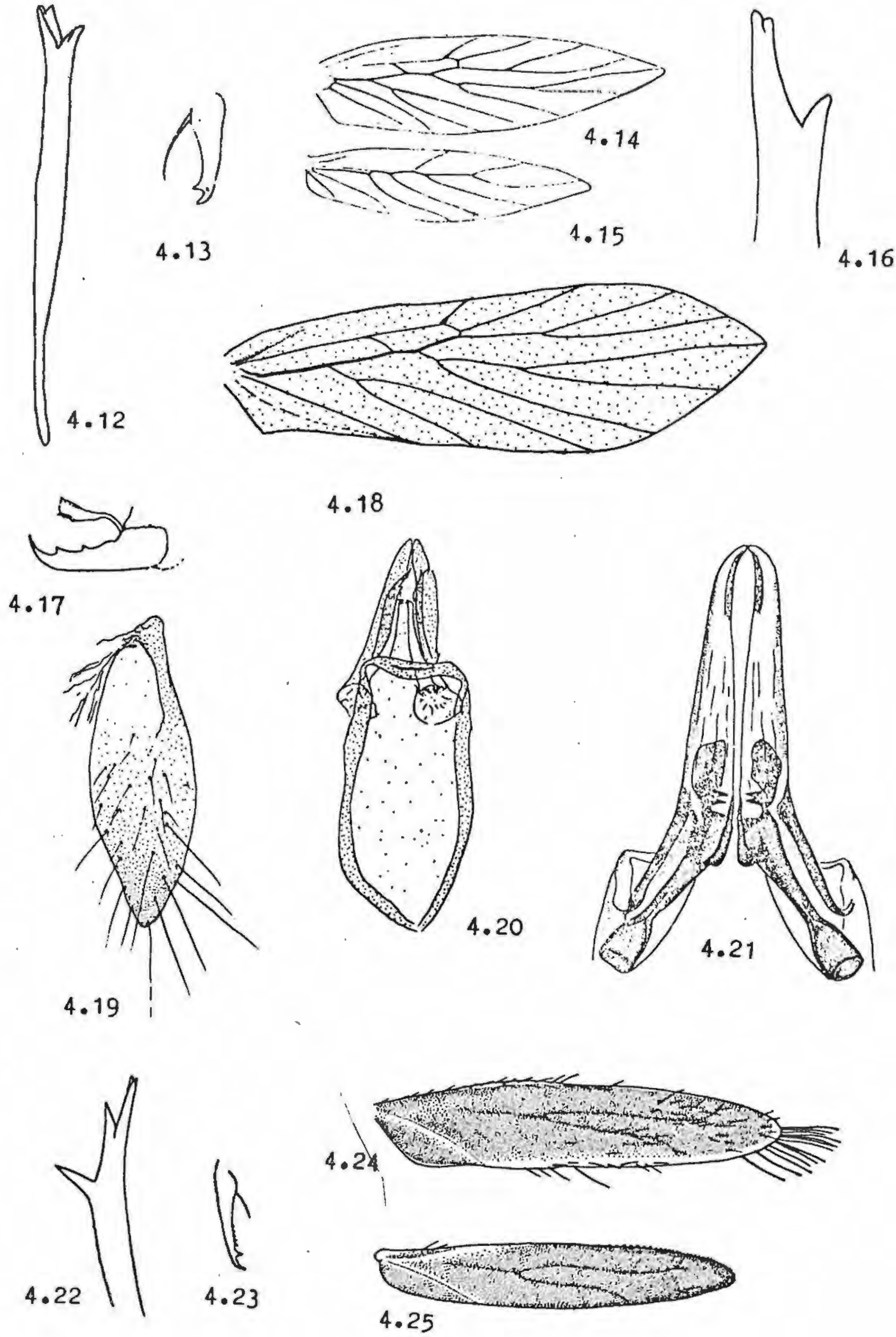


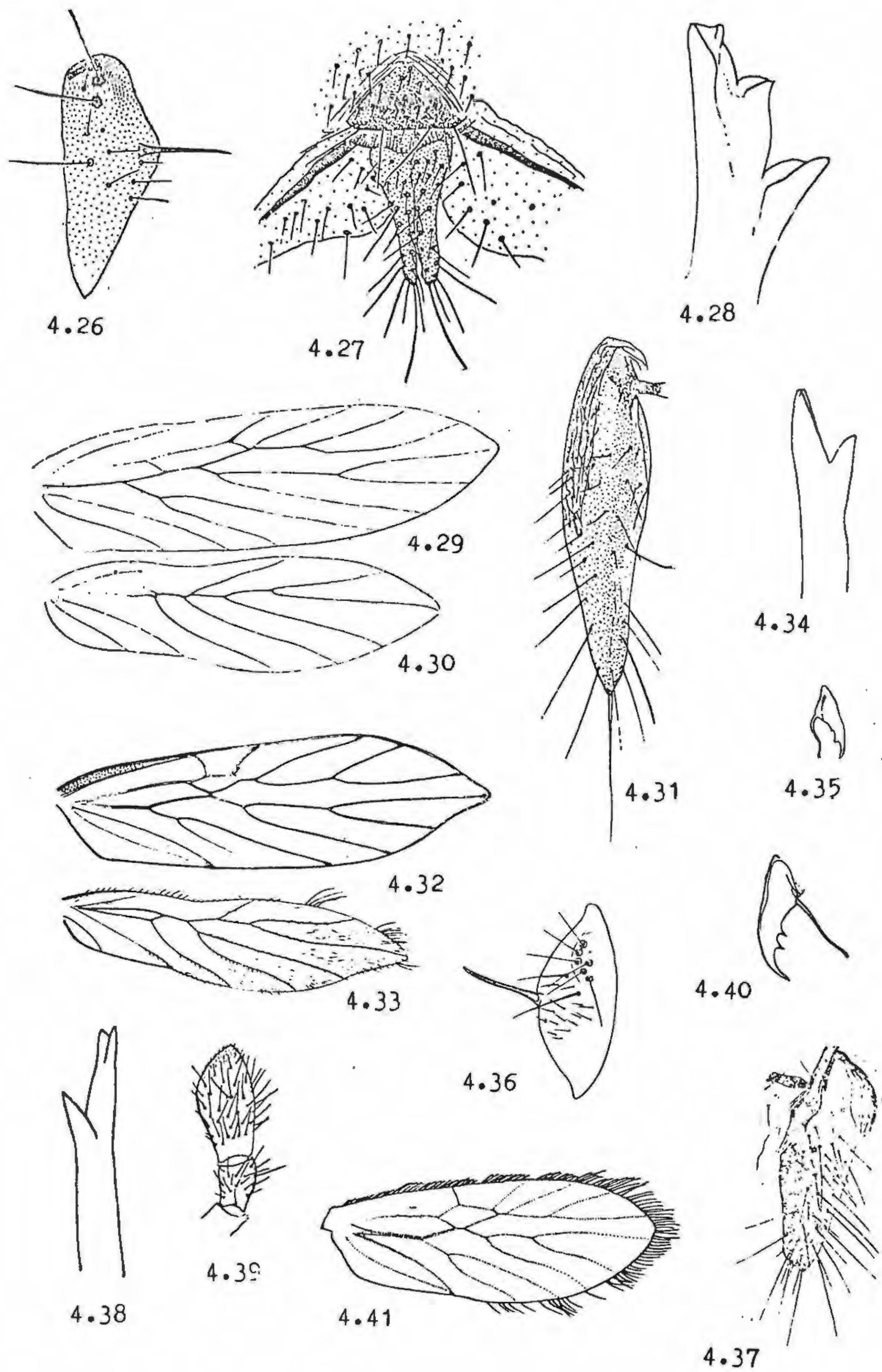
2.1 Stenopsocus stigmaticus (Imhoff and Labrum). Head, front view
2.2 Stenopsocus stigmaticus (Imhoff and Labrum). Head, lateral view
2.3 Isophanes capeneri Smithers. Mandible
2.4 Cerobasis guestfalica (Kolbe). Lacinia
2.5 Psococerastis gibbosa (Sulzer). Pearman's organ
2.6 Cuneopalpus cyanops Rostock. Claw
2.7 Stenopsocus immaculatus (Stephens). Fore and hind wings
2.8 Maheella longispinosa (Smithers). Paraproct
2.9 Blaste bicuspis Smithers. Hypandrium
2.10 Calopsocus guttatus Smithers. Phallosome
2.11 Spilopsocus ruidus Smithers. Subgenital plate
2.12 Elipsocus alettae Smithers. Gonapophyses



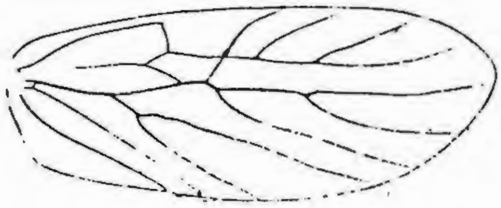
4.1 Thylacella eversiana Enderlein. Head
4.2 Thylacella fasciifrons Badonnel. Head
4.3 Thylacella madagascariensis Smithers. Lacinia
4.4 Thylacella madagascariensis Smithers. Fore wing
4.5 Thylacella madagascariensis Smithers. Hind wing
4.6 Thylacella madagascariensis Smithers. Paraproct
4.7 Thylacella montana Badonnel. Gonapophyses
4.8 Thylacella fasciifrons Badonnel. Phallosome
4.9 Thylacella montana Badonnel. Phallosome
4.10 Thylacella madagascariensis Smithers. Phallosome
4.11 Thylacella madagascariensis Smithers. Claw



4.12 *Lepium chrysochlorum* Enderlein. Lacinia
4.13 *Lepium luridum* Enderlein. Claw
4.14 *Lepium luridum* Enderlein. Fore wing
4.15 *Lepium luridum* Enderlein. Hind wing
4.16 *Nepticulomima saltuaria* Smithers. Lacinia
4.17 *Nepticulomima saltuaria* Smithers. Claw
4.18 *Nepticulomima saltuaria* Smithers. Fore wing
4.19 *Nepticulomima saltuaria* Smithers. Gonapophyses
4.20 *Nepticulomima saltuaria* Smithers. Phallosome
4.21 *Nepticulomima hosemanni* Enderlein. Apex of phallosome
4.22 *Parasoa haploneura* Thornton. Lacinia
4.23 *Parasoa haploneura* Thornton. Claw
4.24 *Parasoa haploneura* Thornton. Fore wing
4.25 *Parasoa haploneura* Thornton. Hind wing



4.26 *Parasoa haploneura* Thornton. Paraproct
4.27 *Parasoa haploneura* Thornton. Subgenital plate, Gonapophyses
4.28 *Perientomum fucatum* Smithers. Lacinia
4.29 *Perientomum ceylonicum* Enderlein. Fore wing
4.30 *Perientomum ceylonicum* Enderlein. Hind wing
4.31 *Perientomum fucatum* Smithers. Gonapophyses
4.32 *Proentomum personatum* Badonnel. Fore wing
4.33 *Proentomum personatum* Badonnel. Hind wing
4.34 *Proentomum personatum* Badonnel. Lacinia
4.35 *Proentomum personatum* Badonnel. Claw
4.36 *Proentomum personatum* Badonnel. Paraproct
4.37 *Proentomum personatum* Badonnel. Gonapophyses
4.38 *Soa angolana* Badonnel. Lacinia
4.39 *Soa angolana* Badonnel. Maxillary palp
4.40 *Soa angolana* Badonnel. Claw
4.41 *Soa angolana* Badonnel. Fore wing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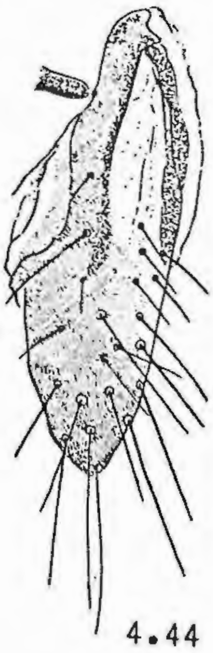
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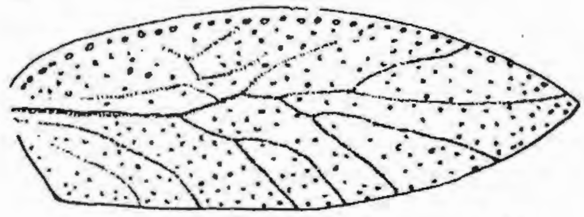
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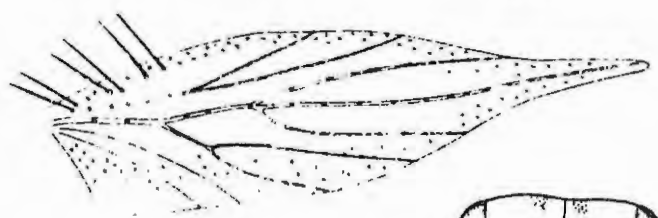
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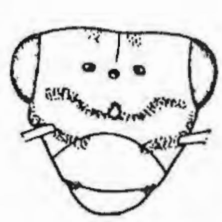
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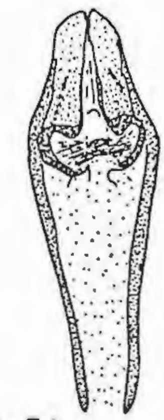
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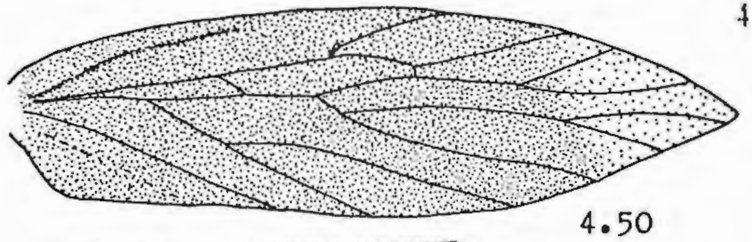
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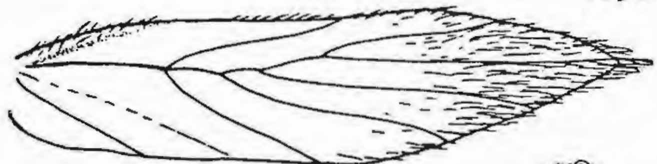
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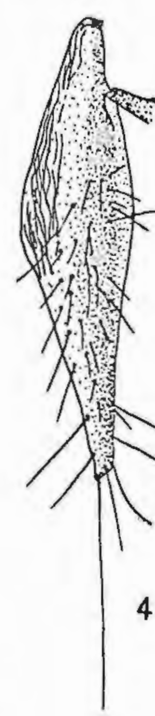
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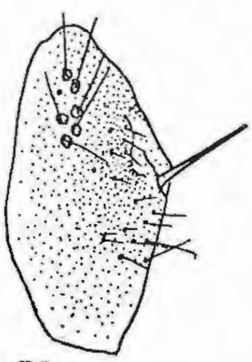
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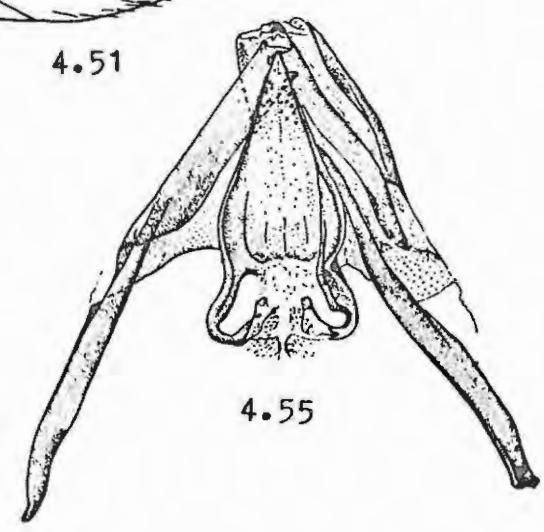
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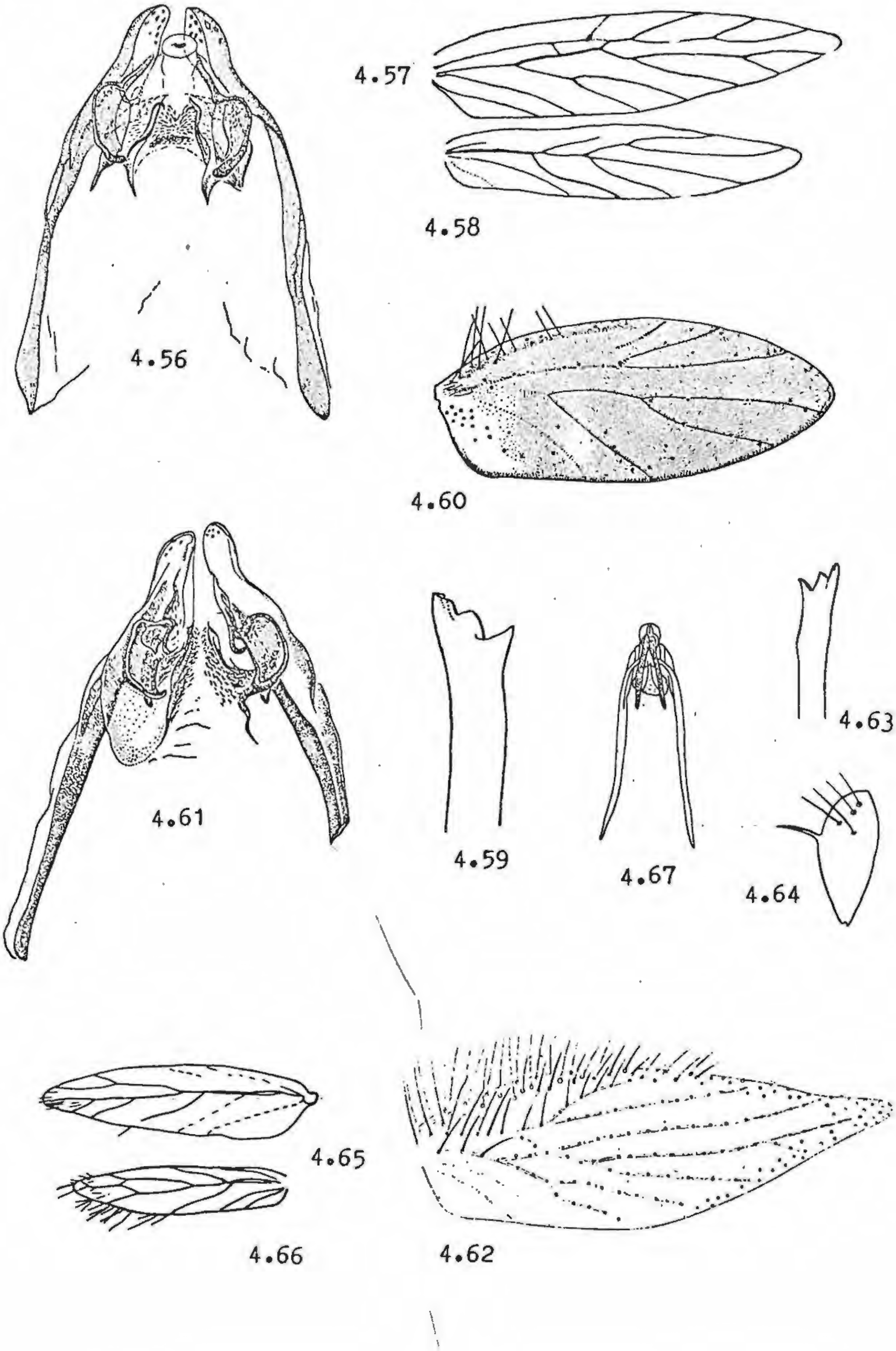
4.42 Soa flaviterminata Enderlein. Fore wing
4.43 Soa angolana Badonnel. Hind wing
4.44 Soa angolana Badonnel. Gonapophyses
4.45 Cytophania alutaceum (Enderlein). Fore wing
4.46 Echinopsocus erinaceus Enderlein. Fore wing
4.47 Echmepteryx quadrilineata Smithers. Lacinia
4.48 Echmepteryx similis Badonnel. Claw
4.49 Echmepteryx pallida Smithers. Head
4.50 Echmepteryx brunnea Smithers. Fore wing
4.51 Echmepteryx brunnea Smithers. Hind wing
4.52 Echmepteryx brunnea Smithers. Paraproct
4.53 Echmepteryx quadrilineata Smithers. Gonapophyses
4.54 Echmepteryx brunnea Smithers. Phallosome
4.55 Echmepteryx pauliani Badonnel. Phallosome



4.56 Echmepteryx terricolis Badonnel. Phallosome
4.57 Lepidopsocus ochreus Enderlein. Fore wing
4.58 Lepidopsocus ochreus Enderlein. Hind wing
4.59 Pteroxanium funebris Badonnel. Lacinia
4.60 Pteroxanium funebris Badonnel. Fore wing
4.61 Pteroxanium funebris Badonnel. Phallosome
4.62 Scolopama halterata Enderlein. Fore wing
4.63 Lepolepis bicolor Broadhead. Lacinia
4.64 Lepolepis bicolor Broadhead. Paraproct
4.65 Lepolepis occidentalis Mockford. Fore wing
4.66 Lepolepis occidentalis Mockford. Hind wing
4.67 Lepolepis occidentalis Mockford. Phallosome

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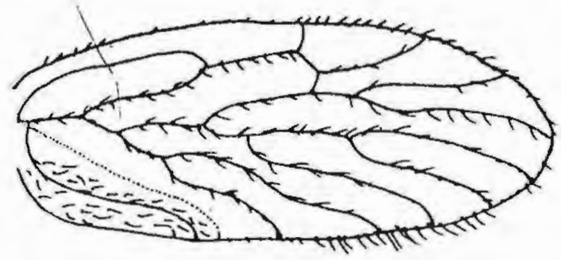

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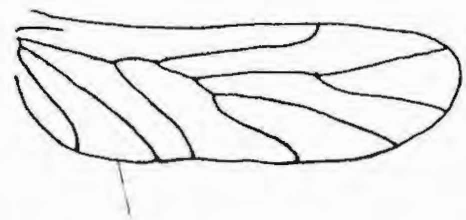

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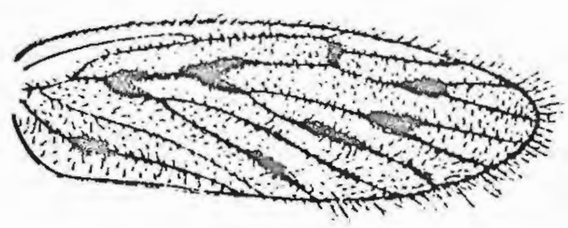

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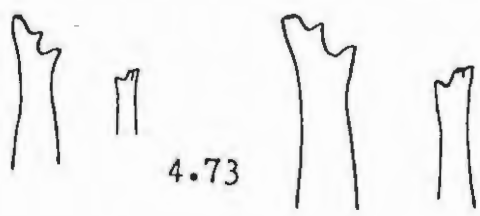

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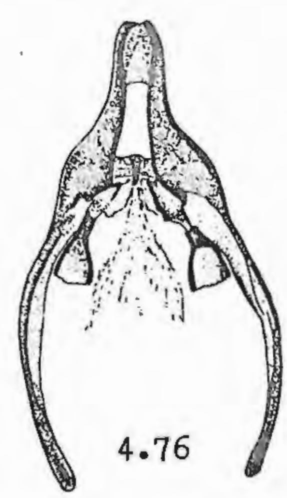
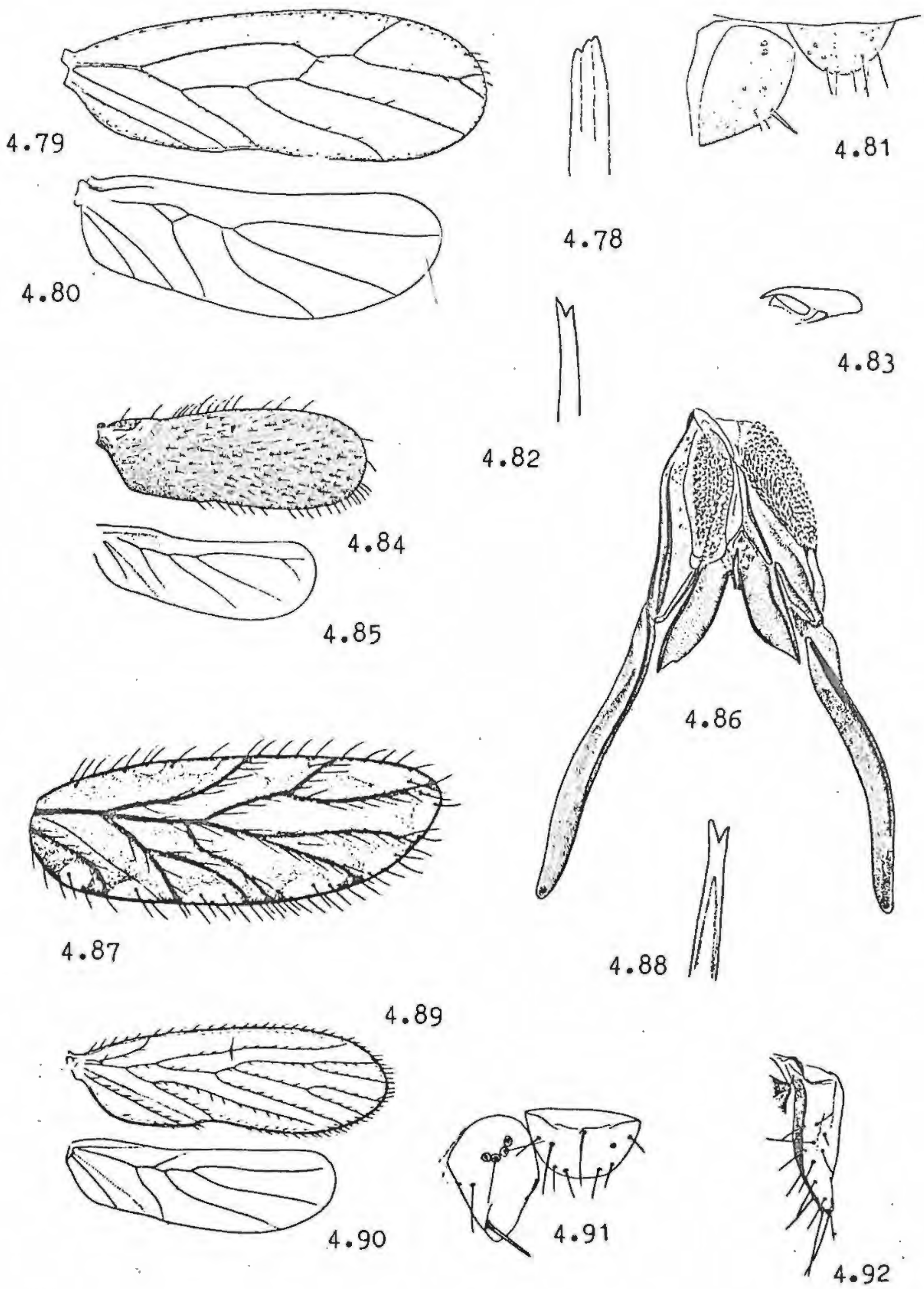
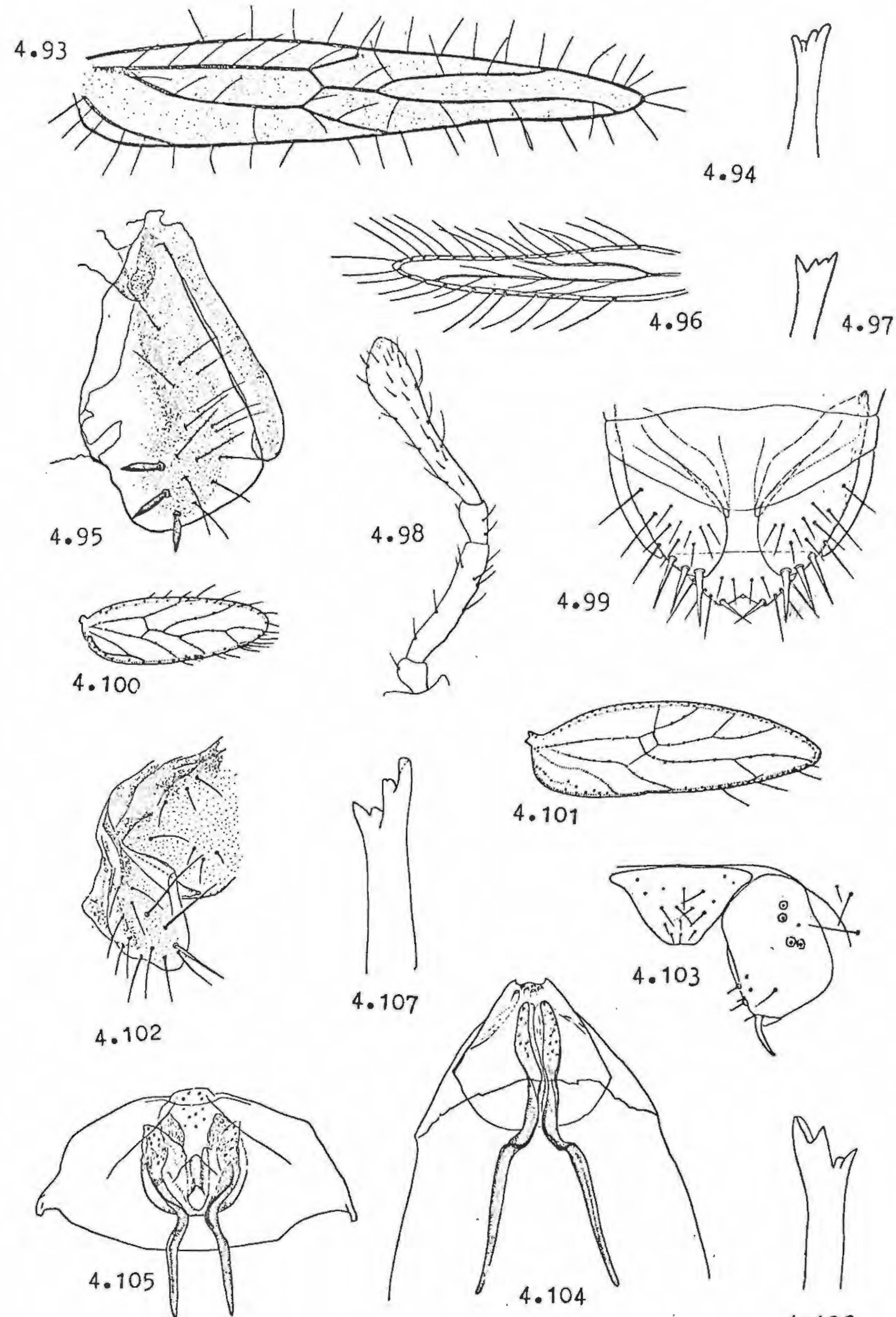


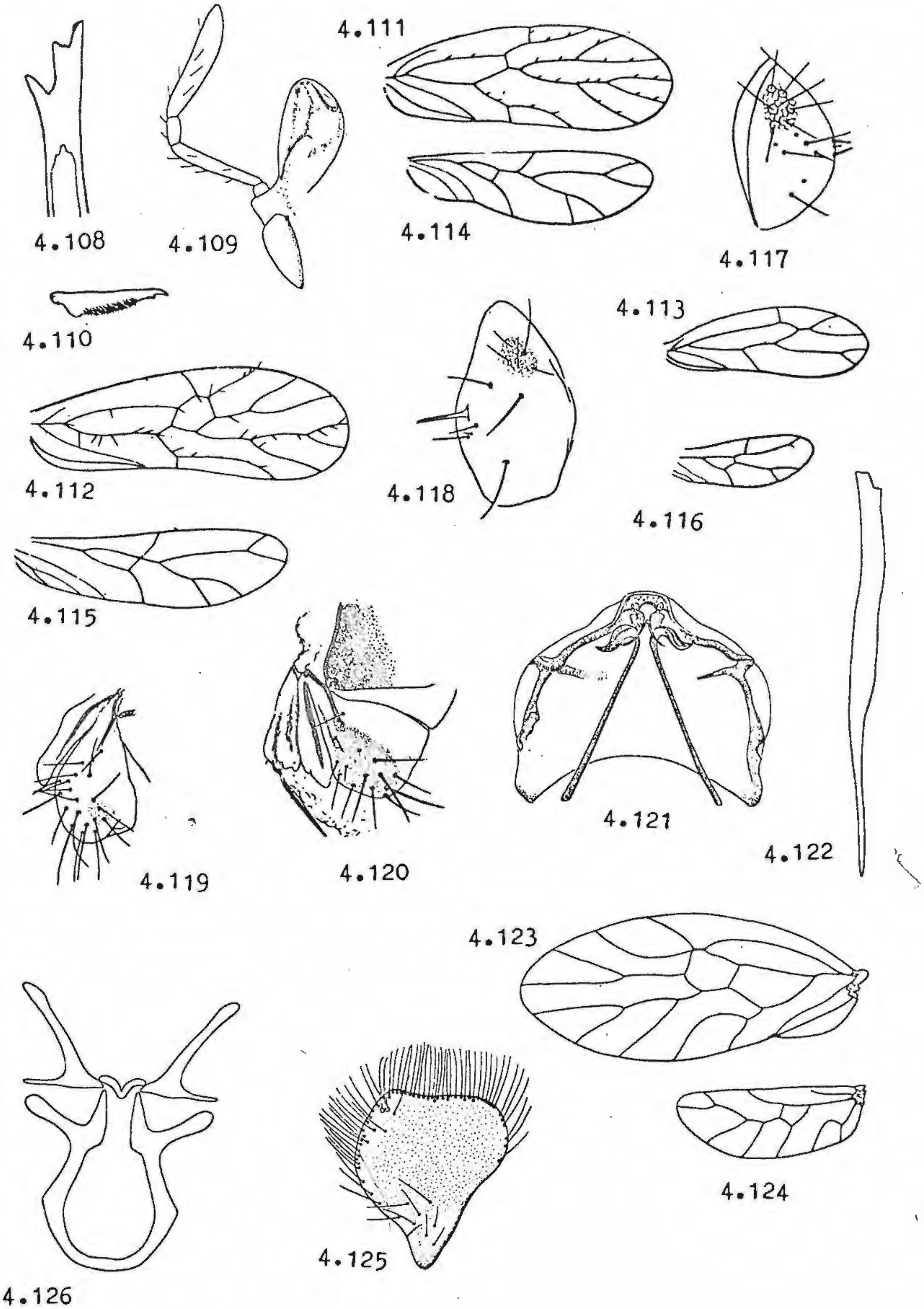
4.68 Empheria reticulata Hagen. Maxillary palp
4.69 Empheria reticulata Hagen. Fore wing
4.70 Empheria reticulata Hagen. Hind wing
4.71 Trichempheria villosa (Hagen). Fore wing
4.72 Trichempheria villosa (Hagen). Maxillary palp
4.73 Anomocopeus nasutus Badonnel. Lacinia
4.74 Anomocopeus nasutus Badonnel. Hypandrium
4.75 Cerobasis maculiceps Badonnel. Lacinia
4.76 Cerobasis maculiceps Badonnel. Phallosome
4.77 Myrmicodipnella aptera Enderlein. Gonapophyses



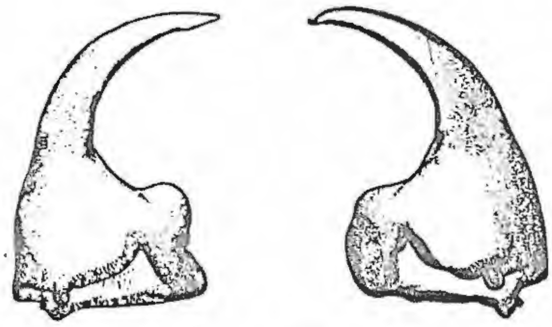
4.78 Balliella ealensis Badonnel. Lacinia
4.79 Balliella ealensis Badonnel. Fore wing
4.80 Balliella ealensis Badonnel. Hind wing
4.81 Balliella ealensis Badonnel. Paraproct
4.82 Eosilla denervosa (Enderlein). Lacinia
4.83 Eosilla denervosa (Enderlein). Claw
4.84 Eosilla denervosa (Enderlein). Fore wing
4.85 Eosilla denervosa (Enderlein). Hind wing
4.86 Eosilla denervosa (Enderlein). Phallosome
4.87 Psoquilla marginepunctata Hagen. Fore wing
4.88 Rhyopsocus afer (Badonnel). Lacinia
4.89 Rhyopsocus afer (Badonnel). Fore wing
4.90 Rhyopsocus afer (Badonnel). Hind wing
4.91 Rhyopsocus afer (Badonnel). Epiproct, paraproct
4.92 Rhyopsocus afer (Badonnel). Gonapophyses



4.93 Dolopteryx domestica Smithers. Fore wing
4.94 Dolopteryx domestica Smithers. Lacinia
4.95 Dolopteryx domestica Smithers. Gonapophyses
4.96 Dorypteryx pallida Aaron. Fore wing
4.97 Dorypteryx pallida Aaron. Lacinia
4.98 Dorypteryx pallida Aaron. Palp
4.99 Dorypteryx pallida Aaron. Gonapophyses
4.100 Psocatropos microps (Enderlein).Fore wing
4.101 Psocatropos pilipennis (Enderlein). Fore wing
4.102 Psocatropos microps (Enderlein). Gonapophyses
4.103 Psocatropos pilipennis (Enderlein). Paraproct
4.104 Psocatropos pilipennis (Enderlein). Phallosome
4.105 Psocatropos microps (Enderlein). Phallosome
4.106 Psocatropos microps (Enderlein). Lacinia
4.107 Psocatropos pilipennis (Enderlein). Lacinia



4.108 *Psyllipsocus ramburi* Selys-Longchamps. Lacinia
4.109 *Psyllipsocus ramburi* Selys-Longchamps. Maxillary palp
4.110 *Psyllipsocus ramburi* Selys-Longchamps. Claw
4.111 *Psyllipsocus ramburi* Selys-Longchamps. Fore wing macropt.
4.112 *Psyllipsocus collarti* Badonnel. Fore wing macropterous
4.113 *Psyllipsocus ramburi* Selys-Longchamps. Fore wing brachypt.
4.114 *Psyllipsocus ramburi* Selys-Longchamps. Hind wing macropt.
4.115 *Psyllipsocus collarti* Badonnel. Hind wing macropterous
4.116 *Psyllipsocus ramburi* Selys-Longchamps. Hind wing brachypt.
4.117 *Psyllipsocus collarti* Badonnel. Paraproct
4.118 *Psyllipsocus ramburi* Selys-Longchamps. Paraproct
4.119 *Psyllipsocus ramburi* Selys-Longchamps. Gonapophyses
4.120 *Psyllipsocus collarti* Badonnel. Gonapophyses
4.121 *Psyllipsocus collarti* Badonnel. Hypandrium and phallosome
4.122 *Speleketor flocki* Gurney. Lacinia
4.123 *Speleketor flocki* Gurney. Fore wing
4.124 *Speleketor flocki* Gurney. Hind wing
4.125 *Speleketor flöcki* Gurney. Gonapophyses
4.126 *Speleketor flocki* Gurney. Phallosome



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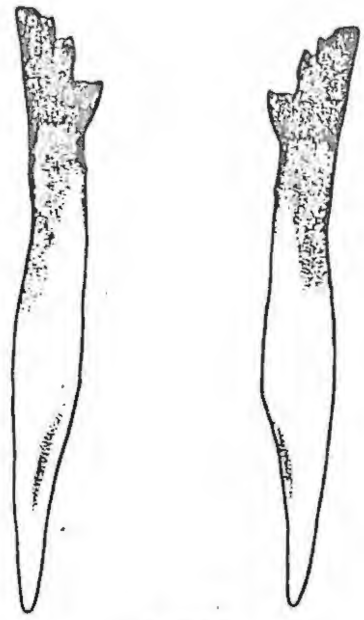

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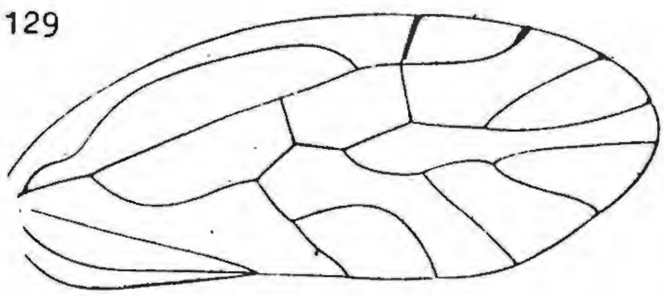

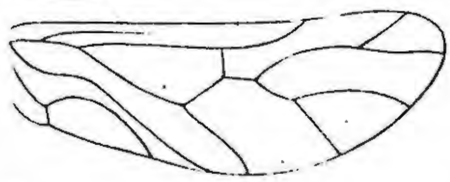

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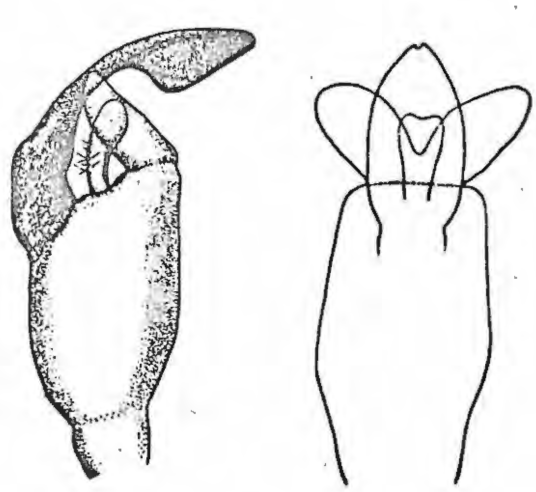
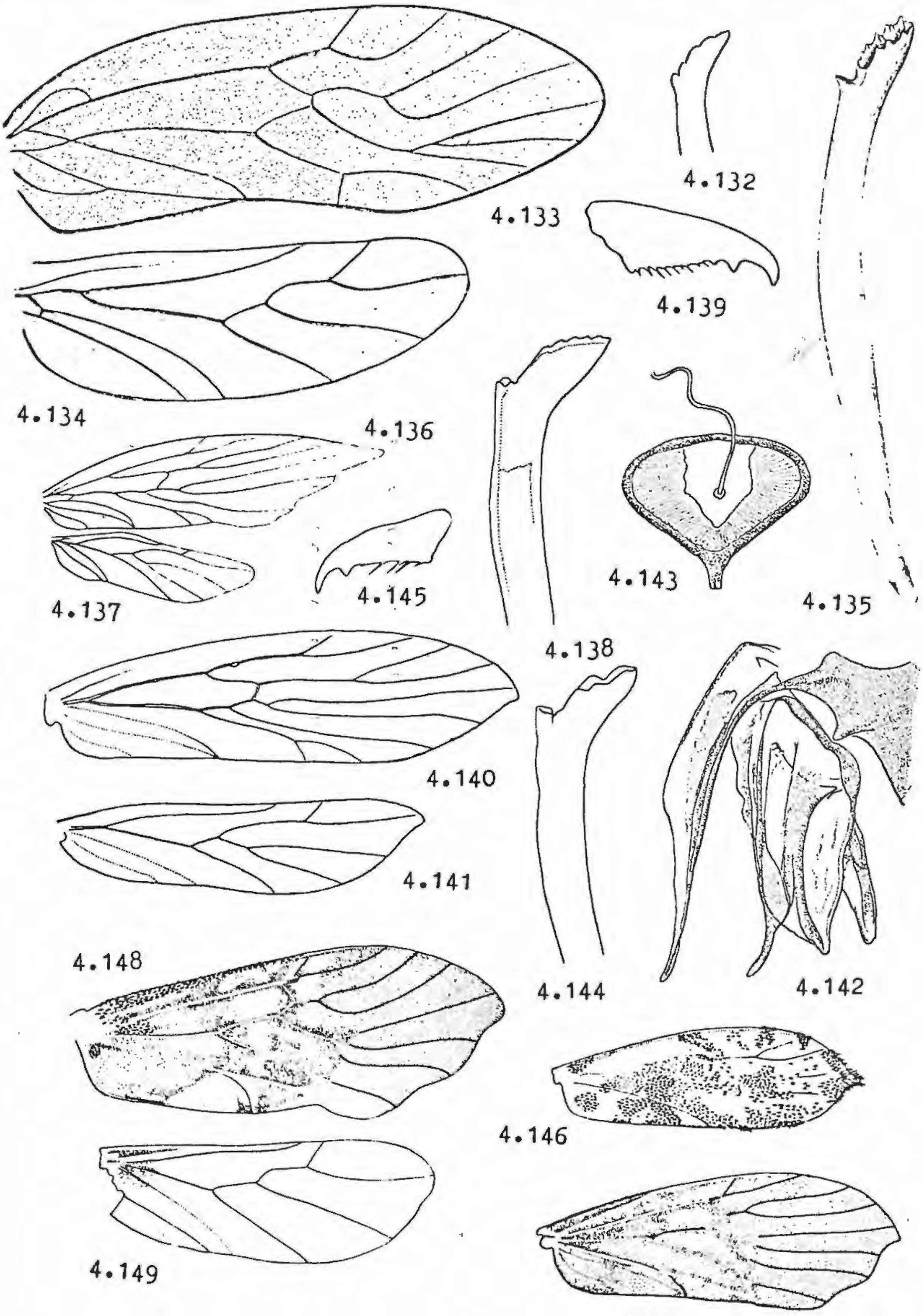
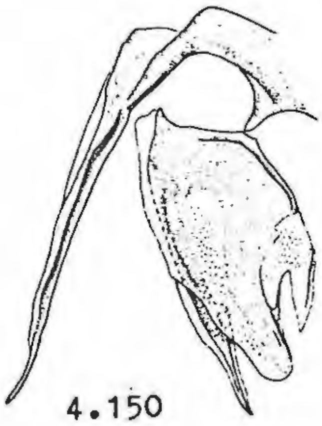


4.131

4.127 *Prionoglaris stygia* Enderlein. Mandible
4.128 *Prionoglaris stygia* Enderlein. Lacinia
4.129 *Prionoglaris stygia* Enderlein. Fore wing
4.130 *Prionoglaris stygia* Enderlein. Hind wing
4.131 *Prionoglaris stygia* Enderlein. Phallosome



4.132 *Electrentomum klebsianum* Enderlein. Lacinia
4.133 *Electrentomum klebsianum* Enderlein. Fore wing
4.134 *Electrentomum klebsianum* Enderlein. Hind wing
4.135 *Cymatopsocus opalinus* Enderlein. Lacinia
4.136 *Cymatopsocus opalinus* Enderlein. Fore wing
4.137 *Cymatopsocus opalinus* Enderlein. Hind wing
4.138 *Tineomorpha angolana* Badonnel. Lacinia
4.139 *Tineomorpha angolana* Badonnel. Claw
4.140 *Tineomorpha angolana* Badonnel. Fore wing
4.141 *Tineomorpha angolana* Badonnel. Hind wing
4.142 *Tineomorpha angolana* Badonnel. Gonapophyses
4.143 *Tineomorpha angolana* Badonnel. Spermathecal opening
4.144 *Amphientomum acuminatum* Smithers. Lacinia
4.145 *Amphientomum acuminatum* Smithers. Claw
4.146 *Amphientomum acuminatum* Smithers. Fore wing
4.147 *Amphientomum punctatum* Badonnel. Fore wing
4.148 *Amphientomum annulicornis* Badonnel. Fore wing
4.149 *Amphientomum annulicornis* Badonnel. Hind wing



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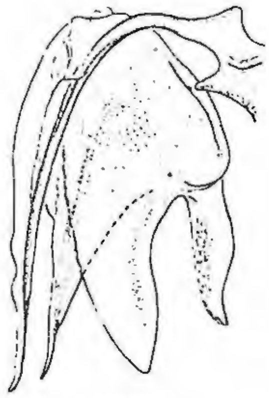

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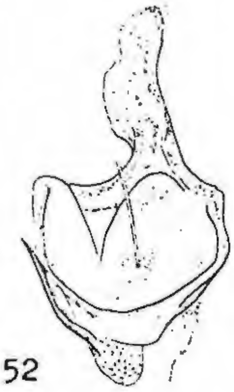

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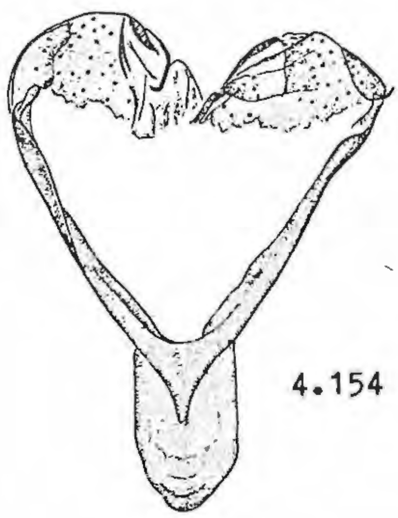

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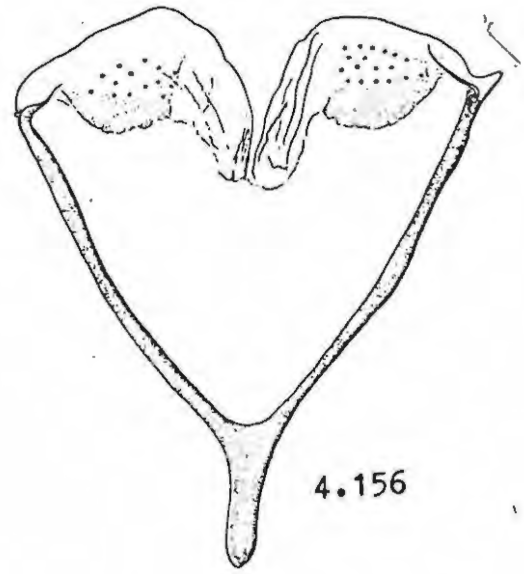

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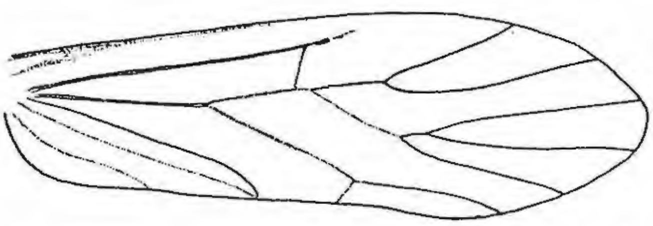

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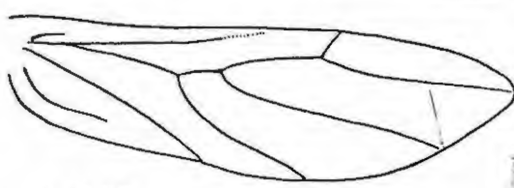

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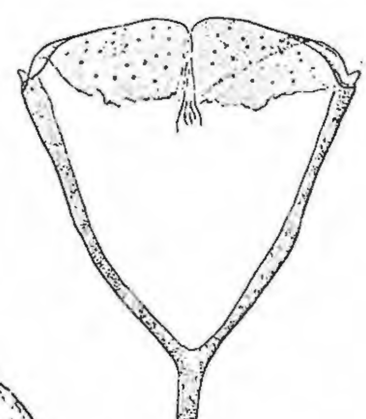

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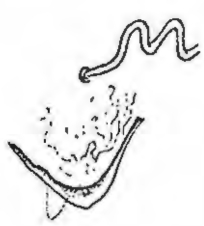
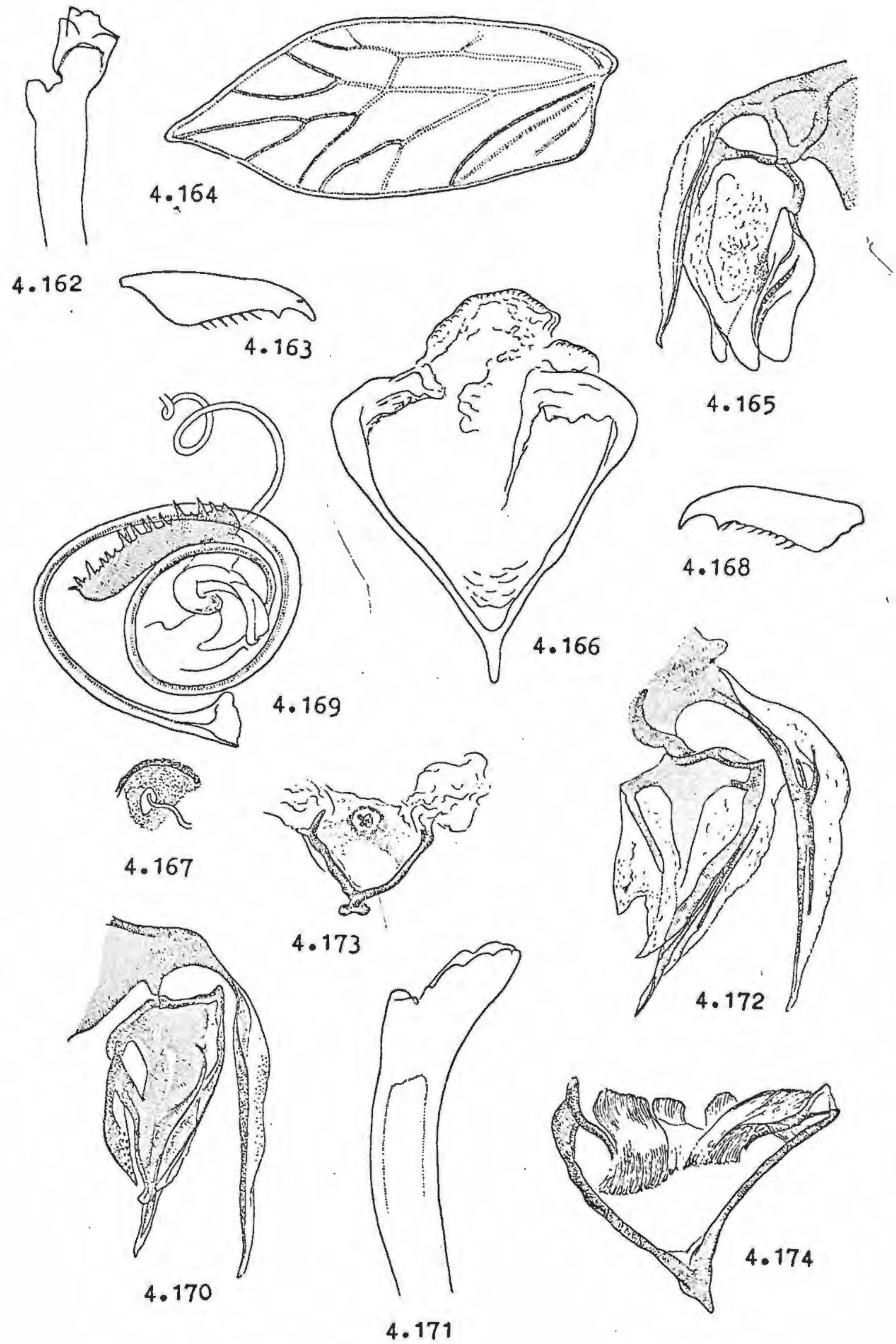


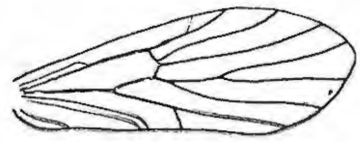
4.161

4.150 Amphientomum punctatum Badonnel. Gonapophyses
4.151 Amphientomum striaticeps Badonnel. Gonapophyses
4.152 Amphientomum striaticeps Badonnel. Spermathecal opening
4.153 Amphientomum punctatum Badonnel. Spermathecal opening
4.154 Amphientomum acuminatum Smithers. Phallosome
4.155 Amphientomum mimulum Badonnel. Phallosome
4.156 Amphientomum punctatum Badonnel. Phallosome
4.157 Hemiseopsis machadoi Badonnel. Claw
4.158 Hemiseopsis machadoi Badonnel. Fore wing
4.159 Hemiseopsis machadoi Badonnel. Hind wing
4.160 Hemiseopsis machadoi Badonnel. Gonapophyses
4.161 Hemiseopsis machadoi Badonnel. Spermathecal opening



4.162 *Nephax angolensis* Badonnel. Lacinia
4.163 *Nephax angolensis* Badonnel. Claw
4.164 *Nephax angolensis* Badonnel. Fore wing
4.165 *Nephax angolensis* Badonnel. Gonapophyses
4.166 *Nephax angolensis* Badonnel. Phallosome
4.167 *Nephax angolensis* Badonnel. Spermathecal opening
4.168 *Pseudoseopsis vilhenai* Badonnel. Claw
4.169 *Pseudoseopsis vilhenai* Badonnel. Spermatheca
4.170 *Pseudoseopsis vilhenai* Badonnel. Gonapophyses
4.171 *Seopsis pavonius* Badonnel. Lacinia
4.172 *Seopsis pavonius* Badonnel. Gonapophyses
4.173 *Seopsis pavonius* Badonnel. Spermathecal o
4.174 *Seopsis pavonius* Badonnel. Phallosome

4.175



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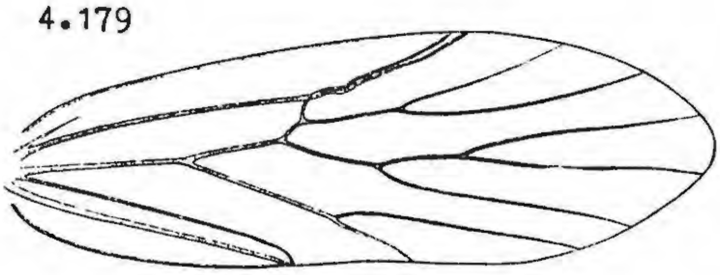

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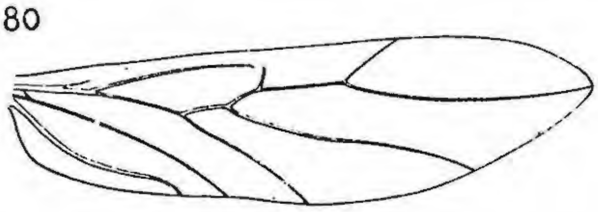

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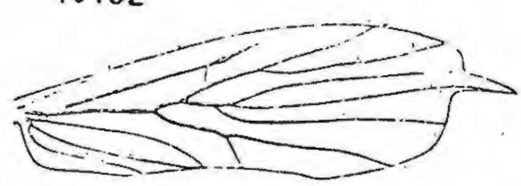

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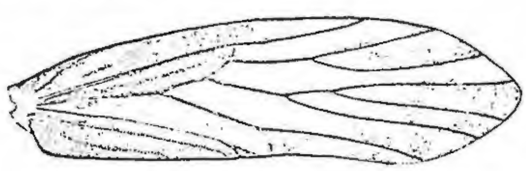
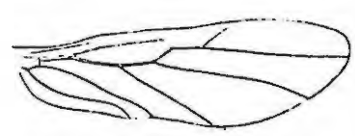
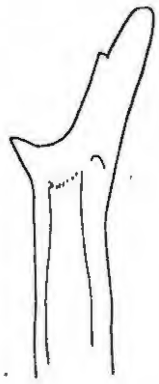




4.183

4.175 Seopsocus acuminatus Roesler. Fore wing ♂
4.176 Seopsocus rotundatus Roesler. Fore wing ♂
4.177 Seopsocus acuminatus Roesler. Hind wing ♂
4.178 Seopsocus acuminatus Roesler. Fore wing ♀
4.179 Stigmatopathus horvarthi Enderlein. Fore wing
4.180 Stigmatopathus horvarthi Enderlein. Hind wing
4.181 Stimulopalpus biocellatus Badonnel. Fore wing
4.182 Syllysis erato Enderlein. Fore wing
4.183 Syllysis erato Enderlein. Hind wing



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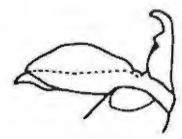

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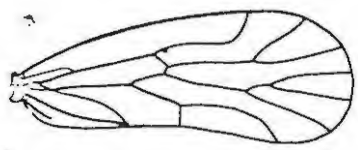

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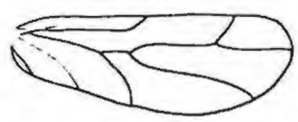

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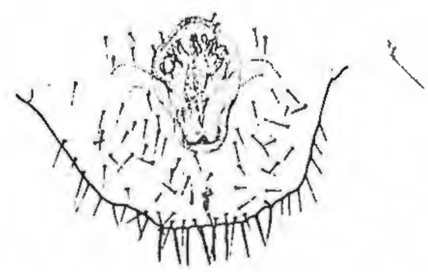

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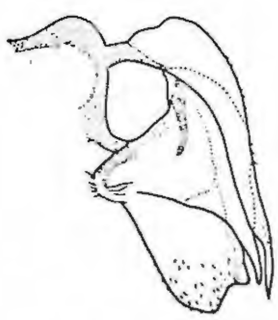

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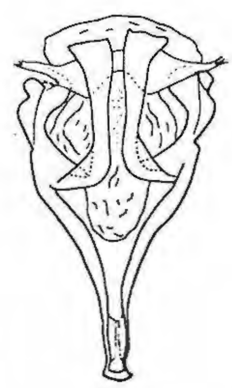

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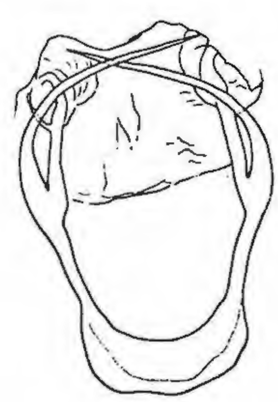
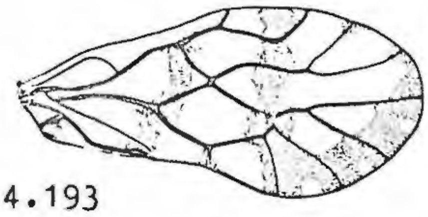


4.192

4.184 *Musapsocus creole* Mockford. Lacinia
4.185 *Musapsocus tabascensis* Mockford. Lacinia
4.186 *Musapsocus creole* Mockford. Claw
4.187 *Musapsocus creole* Mockford. Fore wing
4.188 *Musapsocus creole* Mockford. Hind wing
4.189 *Musapsocus creole* Mockford. Subgenital plate
4.190 *Musapsocus creole* Mockford. Gonapophyses
4.191 *Musapsocus creole* Mockford. Phallosome
4.192 *Musapsocus tabascensis* Mockford. Phallosome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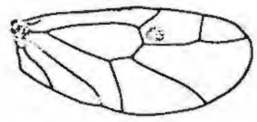
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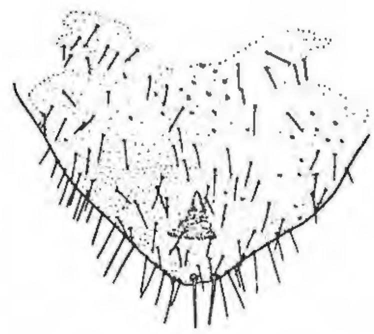
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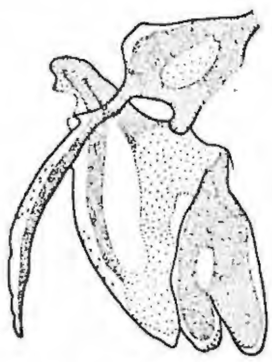
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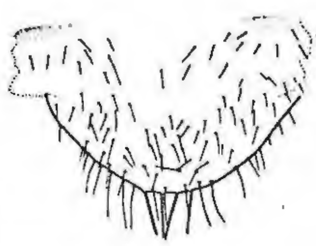
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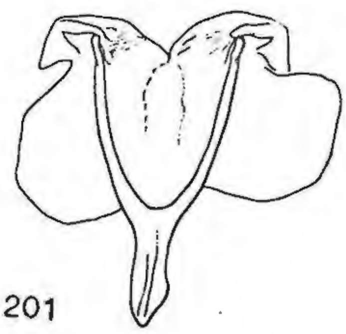
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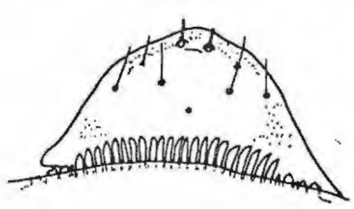
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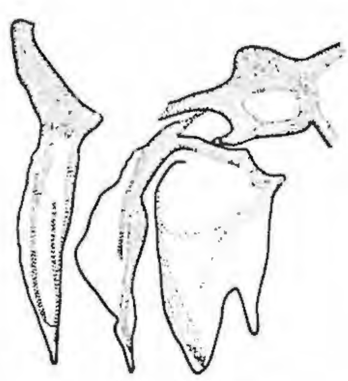
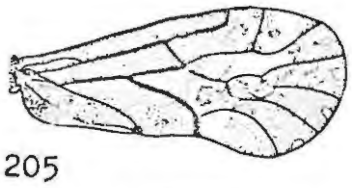

4.204


4.203

4.193 *Protroctopsocus enigmaticus* Mockford. Fore wing
4.194 *Protroctopsocus enigmaticus* Mockford. Hind wing
4.195 *Protroctopsocus enigmaticus* Mockford. Lacinia
4.196 *Protroctopsocus enigmaticus* Mockford. Subgenital plate
4.197 *Protroctopsocus enigmaticus* Mockford. Gonapophyses
4.198 *Troctopsocopsis martinicus* Mockford. Fore wing
4.199 *Troctopsocopsis martinicus* Mockford. Hind wing
4.200 *Troctopsocopsis martinicus* Mockford. Subgenital plate
4.201 *Troctopsocopsis luciensis* Mockford. Phallosome
4.202 *Troctopsocopsis martinicus* Mockford. Epiproct and clunial comb
4.203 *Troctopsocopsis martinicus* Mockford. Lacinia
4.204 *Troctopsocopsis martinicus* Mockford. Gonapophyses



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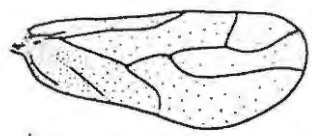

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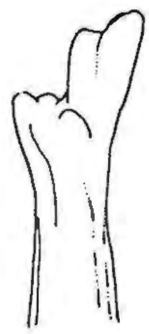

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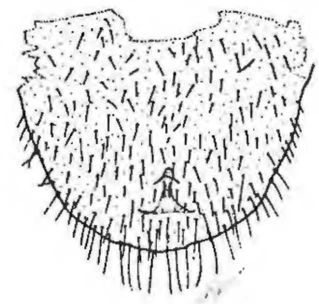

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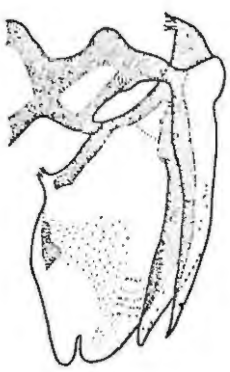

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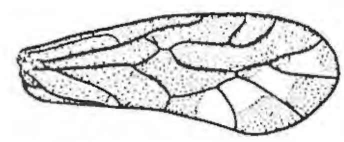

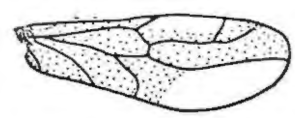

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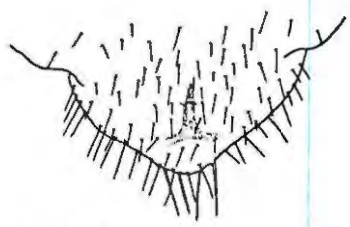

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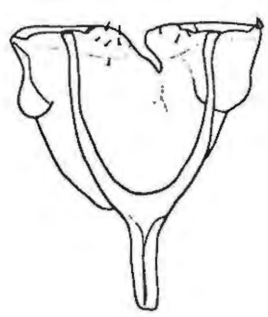

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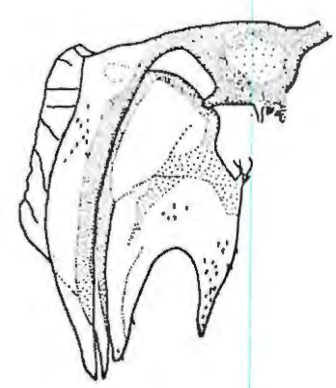

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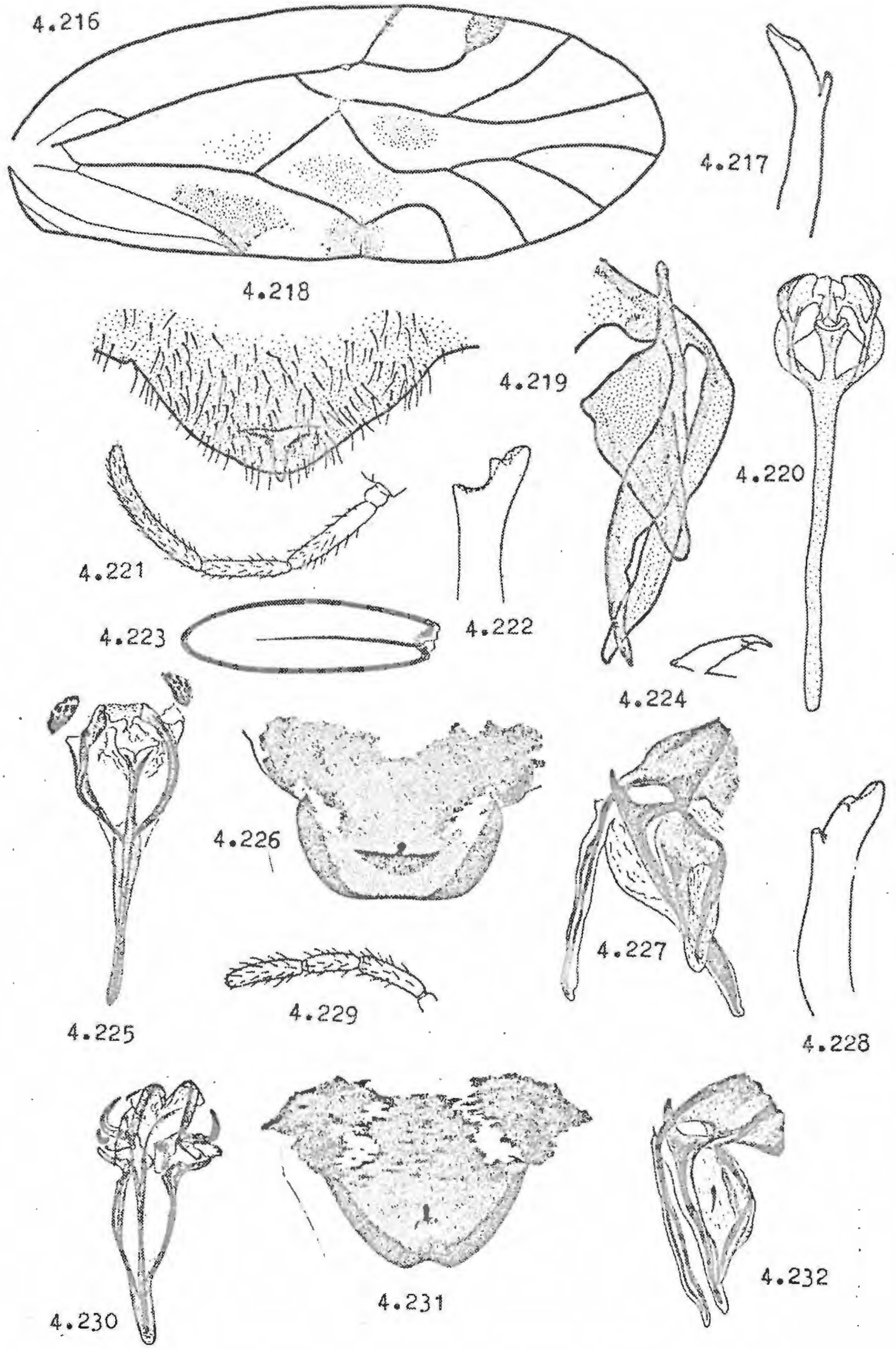
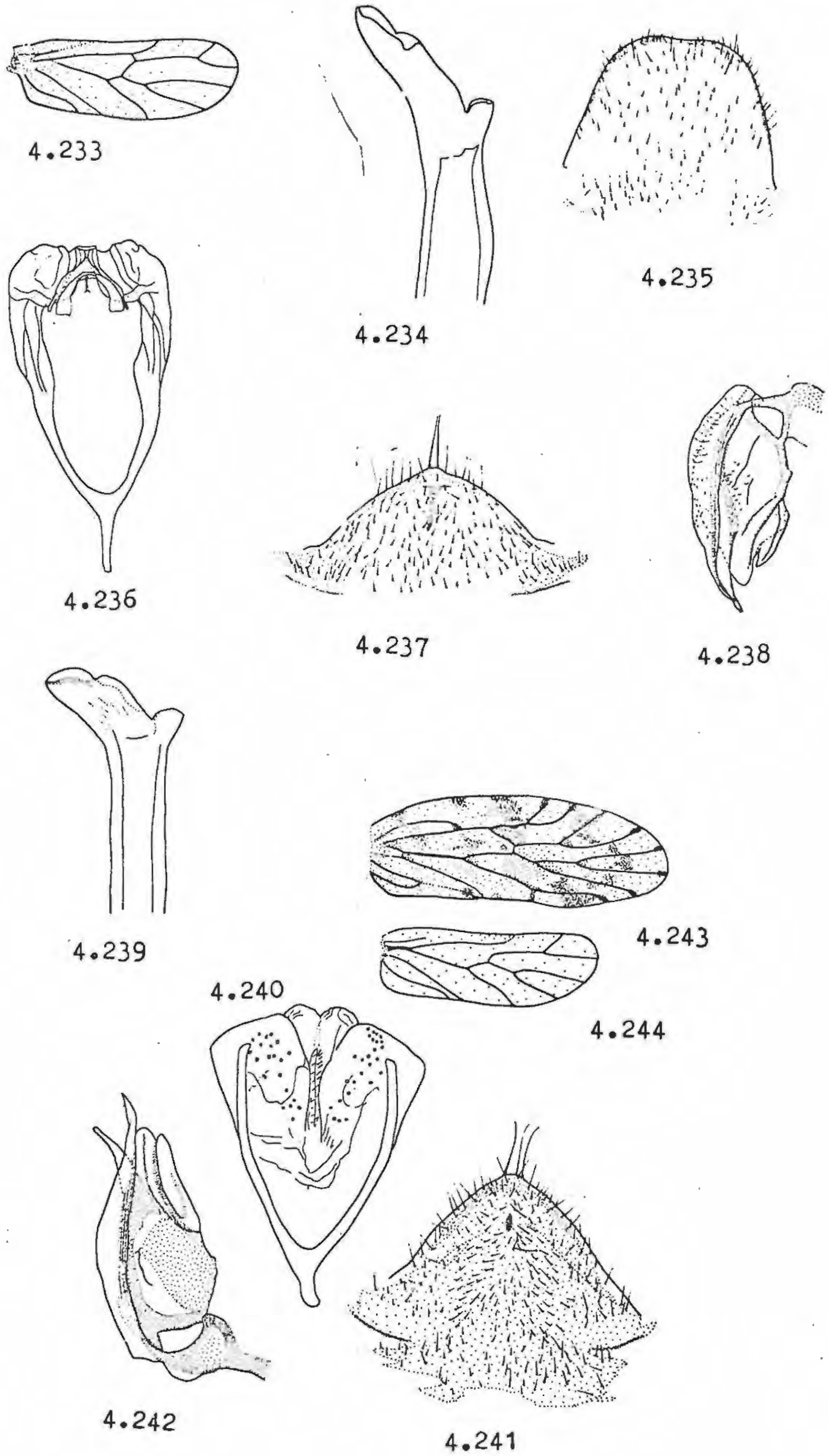
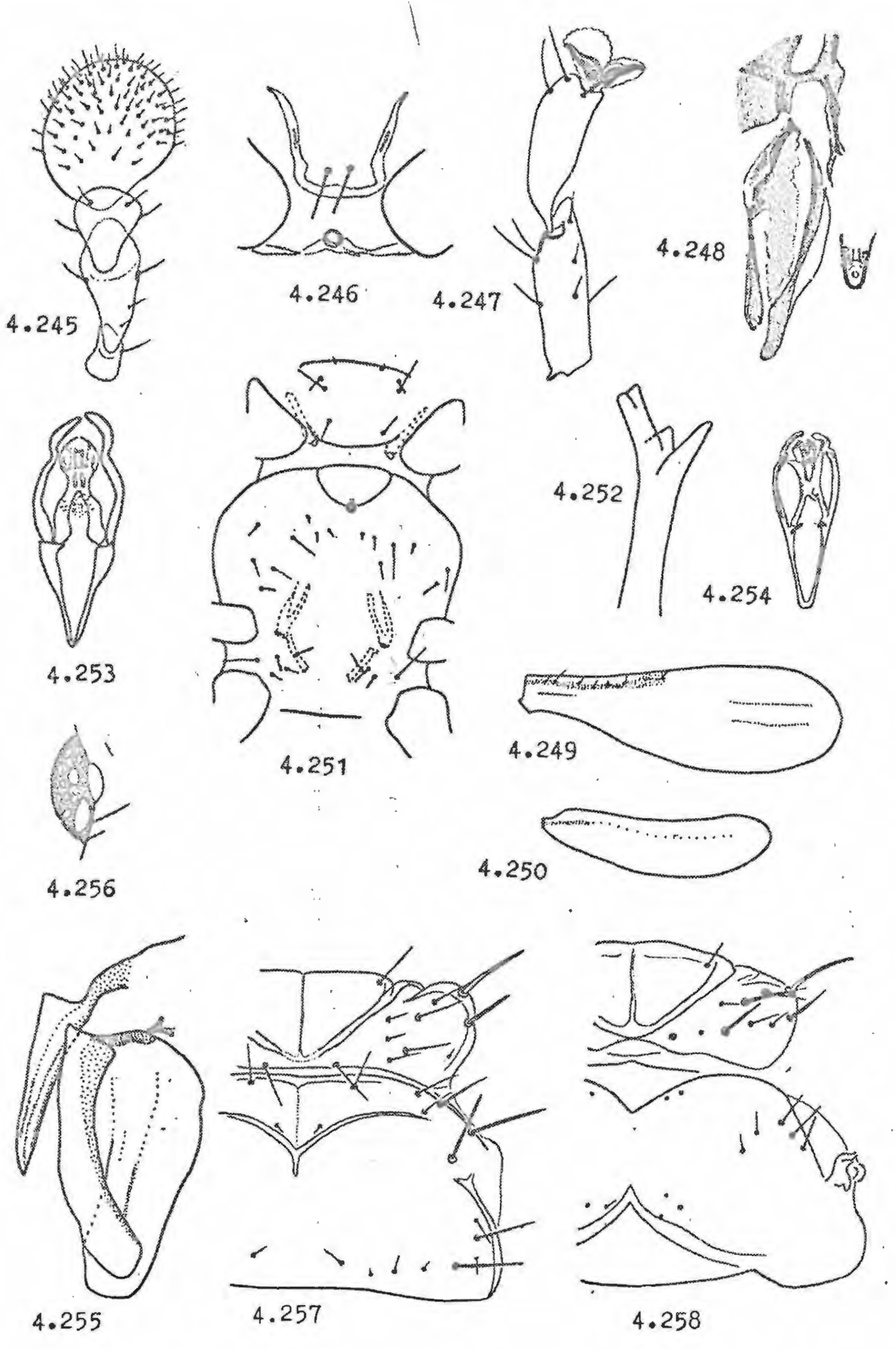
4.205 *Troctopsoculus morenus* Mockford. Fore wing
4.206 *Troctopsoculus morenus* Mockford. Hind wing
4.207 *Troctopsoculus morenus* Mockford. Lacinia
4.208 *Troctopsoculus morenus* Mockford. Subgenital plate
4.209 *Troctopsoculus morenus* Mockford. Gonapophyses
4.210 *Troctopsocus bicolor* Mockford. Fore wing
4.211 *Troctopsocus bicolor* Mockford. Hind wing
4.212 *Troctopsocus bicolor* Mockford. Subgenital plate
4.213 *Troctopsocus bicolor* Mockford. Phallosome
4.214 *Troctopsocus bicolor* Mockford. Gonapophyses
4.215 *Troctopsocus bicolor* Mockford. Lacinia



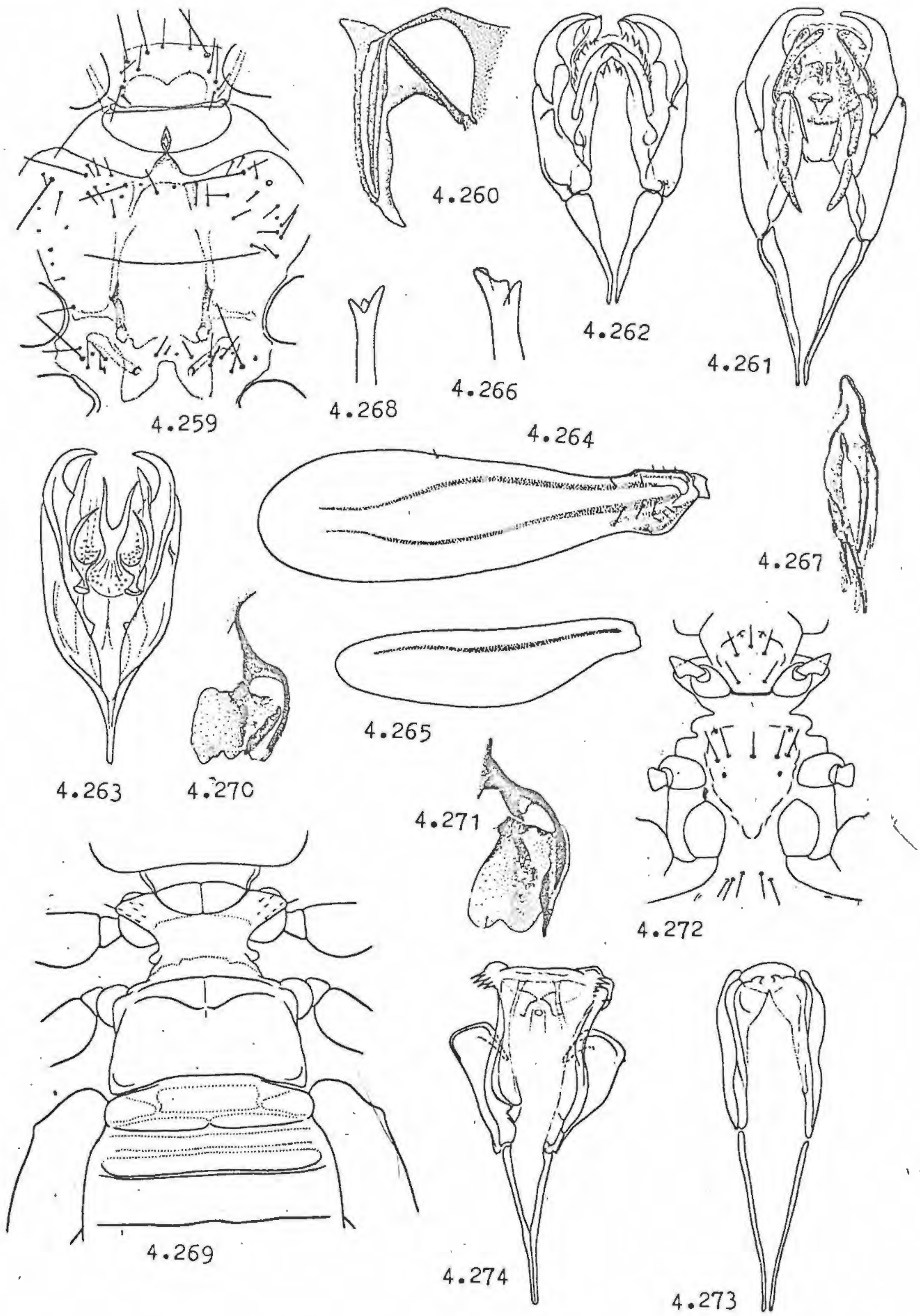
4.216 Manicapsocus alettae Smithers. Fore wing
4.217 Manicapsocus alettae Smithers. Lacinia
4.218 Manicapsocus alettae Smithers. Subgenital plate
4.219 Manicapsocus alettae Smithers. Gonapophyses
4.220 Nothoentomum tuxtlarum (Mockford). Phallosome
4.221 Nothoentomum palpalis Badonnel. Maxillary palp
4.222 Nothoentomum palpalis Badonnel. Lacinia
4.223 Nothoentomum palpalis Badonnel. Fore wing ♂
4.224 Nothoentomum palpalis Badonnel. Claw
4.225 Nothoentomum palpalis Badonnel. Phallosome
4.226 Nothoentomum palpalis Badonnel. Subgenital plate
4.227 Nothoentomum palpalis Badonnel. Gonapophyses
4.228 Phallopsocus carminatus Badonnel. Lacinia
4.229 Phallopsocus carminatus Badonnel. Maxillary palp
4.230 Phallopsocus carminatus Badonnel. Phallosome
4.231 Phallopsocus carminatus Badonnel. Subgenital plate
4.232 Phallopsocus carminatus Badonnel. Gonapophyses



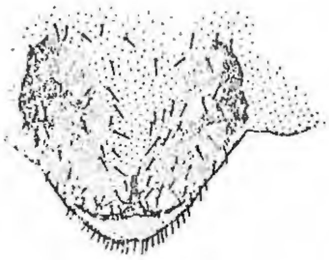
4.233 Compsocus elegans Banks. Hind wing
4.234 Compsocus elegans Banks. Lacinia
4.235 Compsocus elegans Banks. Hypandrium
4.236 Compsocus elegans Banks. Phallosome
4.237 Compsocus elegans Banks. Subgenital plate
4.238 Compsocus elegans Banks. Gonapophyses
4.239 Electrentomopsis variegatus Mockford. Lacinia
4.240 Electrentomopsis variegatus Mockford. Phallosome
4.241 Electrentomopsis variegatus Mockford. Subgenital plate
4.242 Electrentomopsis variegatus Mockford. Gonapophyses
4.243 Electrentomopsis variegatus Mockford. Fore wing
4.244 Electrentomopsis variegatus Mockford. Hind wing



4.245 Belaphopsocus vilhenai Badonnel. Maxillary palp
4.246 Belaphopsocus vilhenai Badonnel. Thoracic sternites
4.247 Belaphopsocus vilhenai Badonnel. Claws
4.248 Belaphopsocus vilhenai Badonnel. Gonapophyses
4.249 Belaphotroctes okalensis Mockford. Fore wing macropterous ♀
4.250 Belaphotroctes okalensis Mockford. Hind wing macropterous ♀
4.251 Belaphotroctes okalensis Mockford. Thoracic sternites macropterous ♀
4.252 Belaphotroctes okalensis Mockford. Lacinia
4.253 Belaphotroctes okalensis Mockford. Phallosome
4.254 Belaphotroctes ghesquierei Badonnel. Phallosome
4.255 Belaphotroctes hermosus Mockford. Gonapophyses
4.256 Embidopsocus angolensis Badonnel. Eye apterous
4.257 Embidopsocus leucomelas Enderlein. Thoracic nota apterous ♀
4.258 Embidopsocus leucomelas Enderlein. Thoracic nota alate ♀



4.259 Embidopsocus angolensis Badonnel. Thoracic sternites alate ♀
4.260 Embidopsocus femoralis Badonnel. Gonapophyses
4.261 Embidopsocus virgatus Enderlein. Phallosome
4.262 Embidopsocus congolensis Badonnel. Phallosome
4.263 Embidopsocus leucomelas Enderlein. Phallosome
4.264 Embidopsocus leucomelas Enderlein. Fore wing
4.265 Embidopsocus leucomelas Enderlein. Hind wing
4.266 Troctulus machadoi Badonnel. Lacinia
4.267 Troctulus machadoi Badonnel. Gonapophyses
4.268 Liposcelis discalis Badonnel. Lacinia
4.269 Liposcelis subfuscus Broadhead. Thoracic dorsa
4.270 Liposcelis paetus Pearman. Gonapophyses
4.271 Liposcelis pubescens Broadhead. Gonapophyses
4.272 Liposcelis paetus Pearman. Thoracic sternites
4.273 Liposcelis nigrocinctus Pearman. Phallosome
4.274 Liposcelis reticulatus Badonnel. Phallosome



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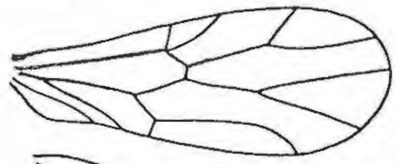

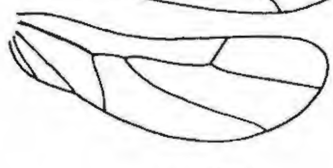

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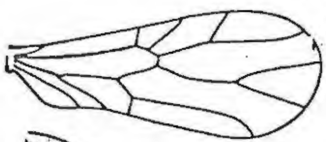

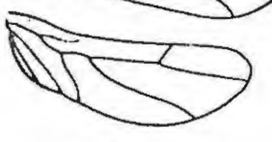

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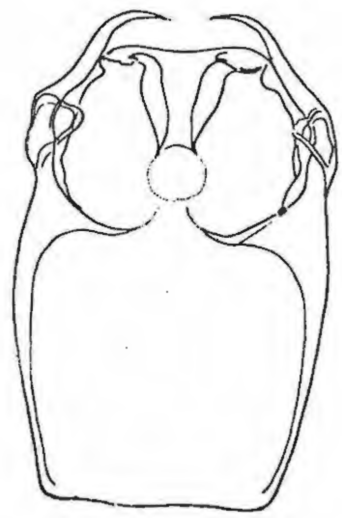

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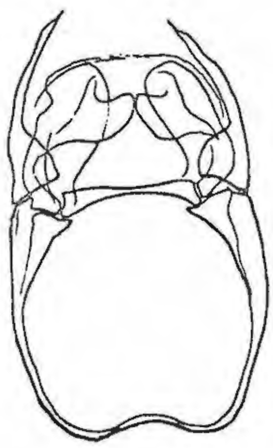

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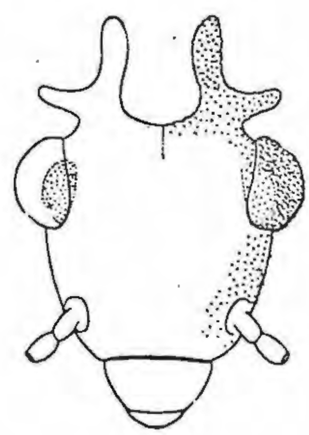

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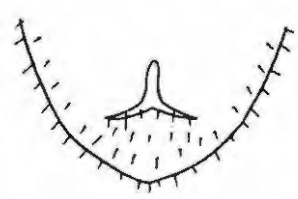

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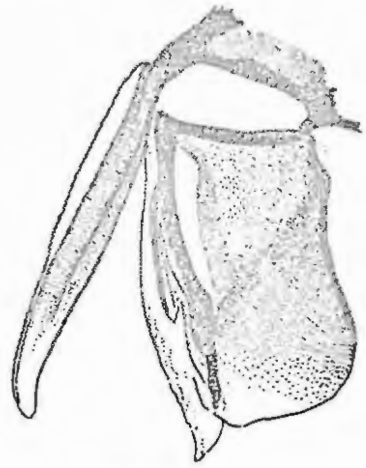
4.275 Tapinella fasciata Thornton and Wong. Subgenital plate
4.276 Tapinella fasciata Thornton and Wong. Gonapophyses
4.277 Tapinella maculata Mockford and Gurney. Lacinia
4.278 Tapinella africana Badonnel. Fore wing
4.279 Tapinella africana Badonnel. Fore wing
4.280 Tapinella africana Badonnel. Hind wing
4.281 Tapinella africana Badonnel. Hind wing
4.282 Tapinella curvata Badonnel. Phallosome
4.283 Tapinella madagascariensis Badonnel. Phallosome
4.284 Antilopsocus nadleri Gurney. Head
4.285 Antilopsocus nadleri Gurney. Lacinia
4.286 Antilopsocus nadleri Gurney. Subgenital plate

4.288



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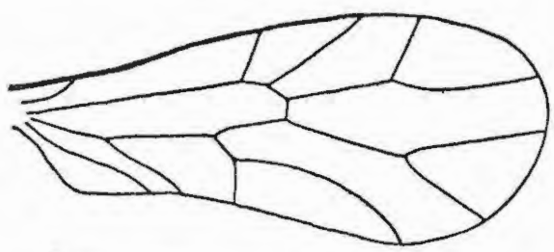

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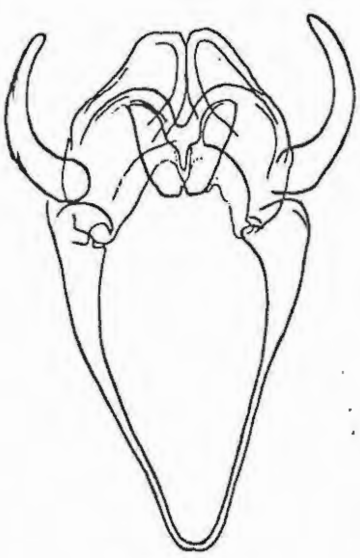

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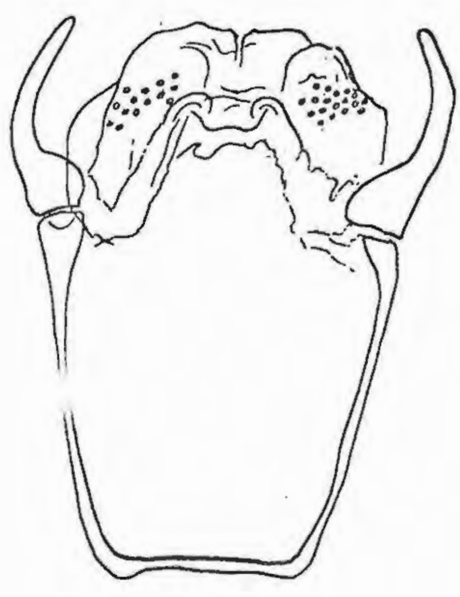

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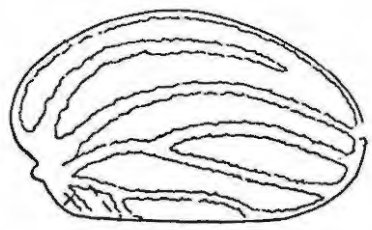
4.287 *Antilopsocus nadleri* Gurney. Claw
4.288 *Pachytroctes ealensis* Badonnel. Gonapophyses
4.289 *Pachytroctes nivecinctus* Badonnel. Gonapophyses
4.290 *Pachytroctes ealensis* Badonnel. Fore wing
4.291 *Pachytroctes ealensis* Badonnel. Hind wing
4.292 *Pachytroctes velutinus* Badonnel. Lacinia
4.293 *Pachytroctes nivecinctus* Badonnel. Phallosome
4.294 *Pachytroctes ambiguus* Badonnel. Phallosome



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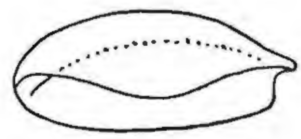

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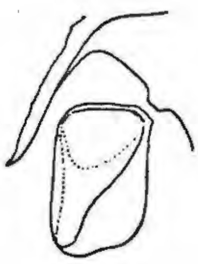

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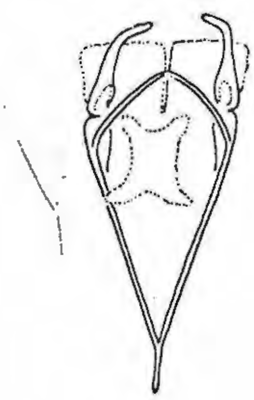

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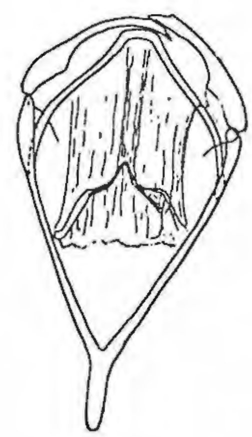

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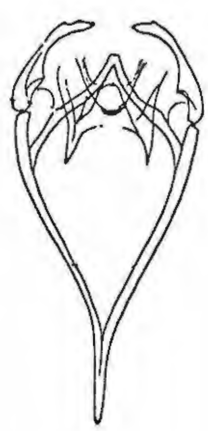

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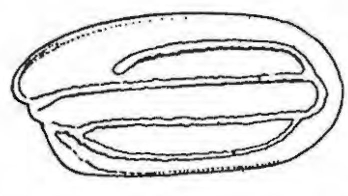

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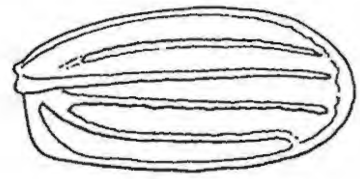

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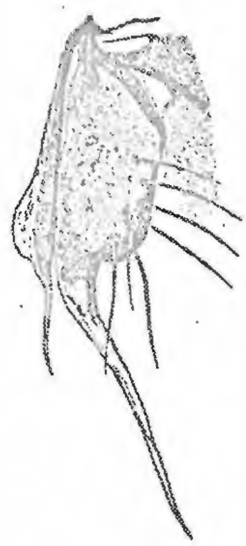
4.295 Sphaeropsocus kunowi Hagen. Fore wing ♀
4.296 Badonnelia titei Pearman. Fore wing ♀
4.297 Badonnelia titei Pearman. Subgenital plate
4.298 Badonnelia titei Pearman. Gonapophyses
4.299 Badonnelia titei Pearman. Phallosome
4.300 Badonnelia castrii Badonnel. Phallosome
4.301 Badonnelia similis Badonnel. Phallosome
4.302 Sphaeropsocopsis chilensis Badonnel. Fore wing ♀
4.303 Sphaeropsocopsis microps Badonnel. Fore wing ♀



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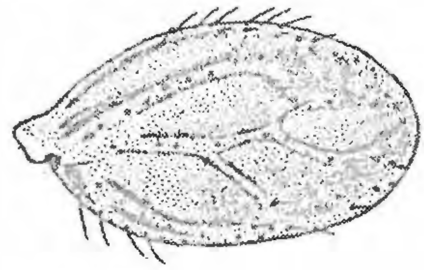

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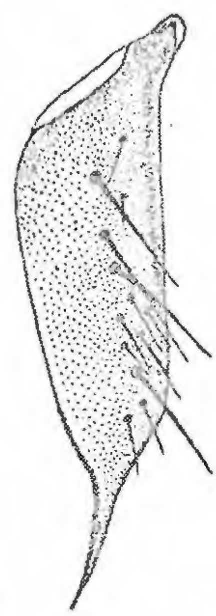

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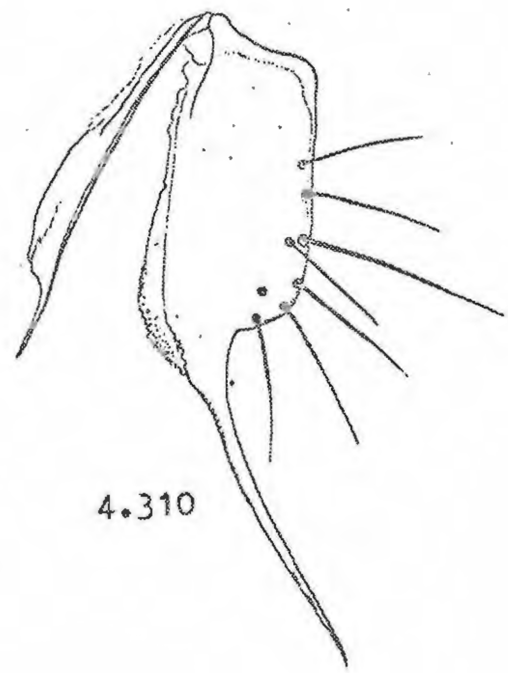

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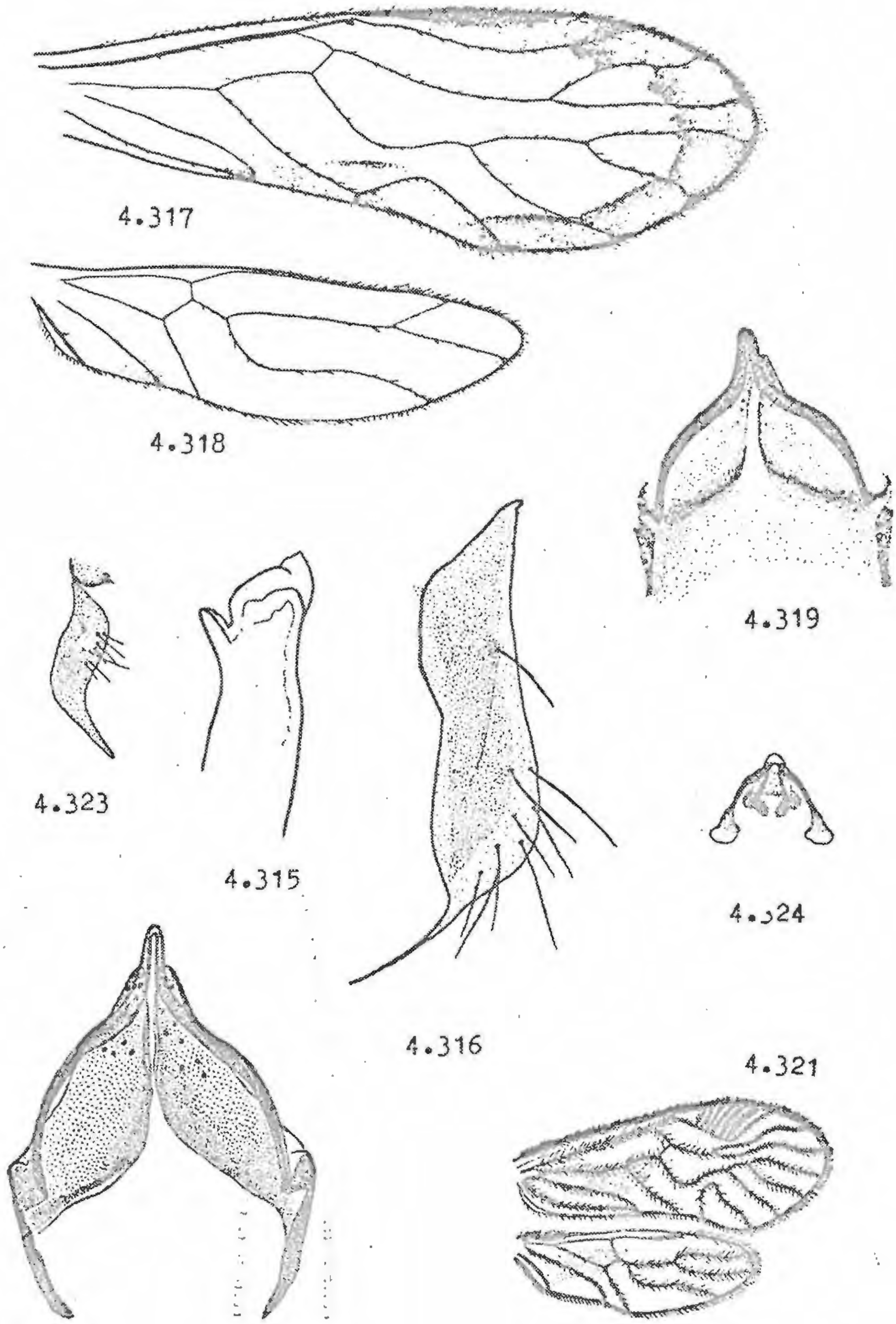
4.304 Epipsocus lucifugus (Rambur). Gonapophyses
4.305 Epipsocus lucifugus (Rambur). Lacinia
4.306 Epipsocus lucifugus (Rambur). Fore wing
4.307 Epipsocus angolensis Badonnel. Fore wing
4.308 Epipsocus lucifugus (Rambur). Hind wing
4.309 Epipsocus angolensis Badonnel. Gonapophyses
4.310 Epipsocus remyi Badonnel. Gonapophyses
4.311 Epipsocus remyi Badonnel. Lacinia
4.312 Epipsocus angolensis Badonnel. Lacinia
4.313 Epipsocus latistigma Roesler. Phallosome
4.314 Epipsocus plaumanni Roesler. Phallosome



4.315 Epipsocopsis stuckenbergi Smithers. Lacinia
4.316 Epipsocopsis spatulatus Smithers. Gonapophyses
4.317 Epipsocopsis stuckenbergi Smithers. Fore wing
4.318 Epipsocopsis stuckenbergi Smithers. Hind wing
4.319 Epipsocopsis stuckenbergi Smithers. Phallosome
4.320 Epipsocopsis machadoi Badonnel. Phallosome
4.321 Neurostigma dispositum Roesler. Fore wing
4.322 Neurostigma dispositum Roesler. Hind wing
4.323 Neurostigma dispositum Roesler. Gonapophyses
4.324 Neurostigma dispositum Roesler. Phallosome

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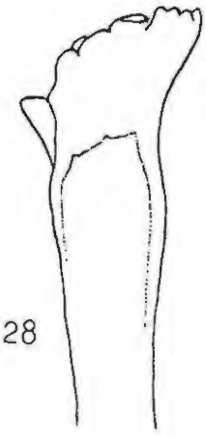

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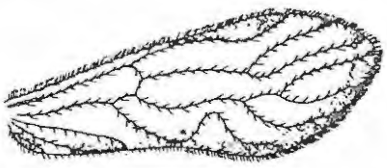

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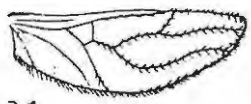

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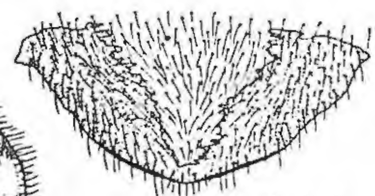

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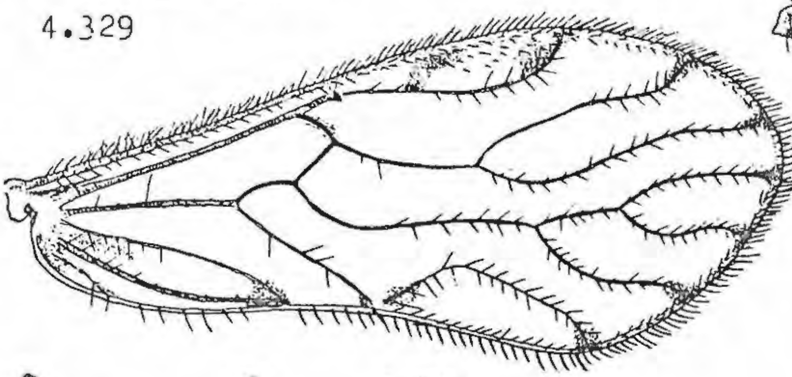

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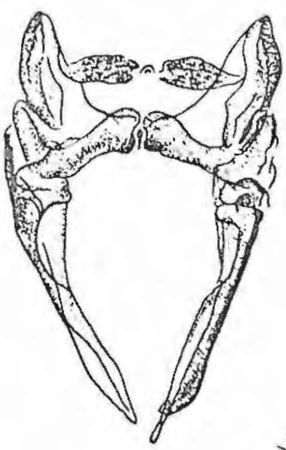

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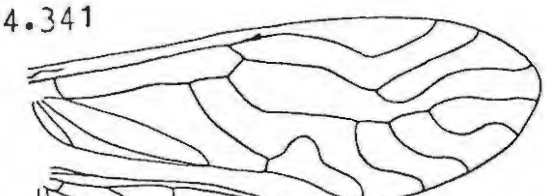

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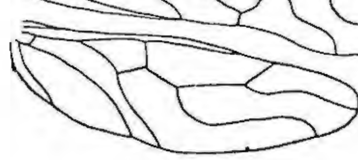

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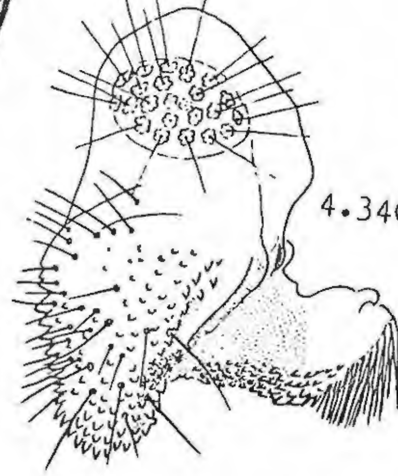

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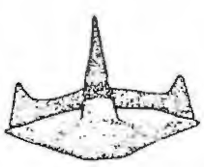

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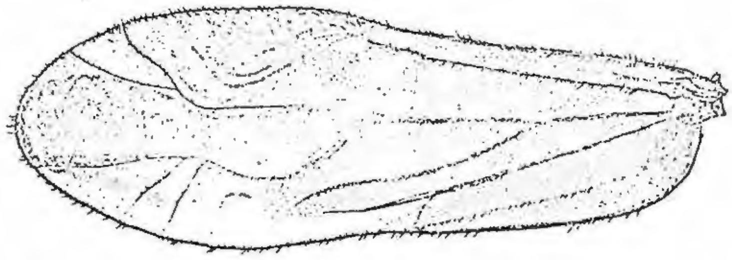
4.325 *Ptiloneura brasiliensis* (Roesler). Fore wing
4.326 *Ptiloneura brasiliensis* (Roesler). Hind wing
4.327 *Ptiloneura brasiliensis* (Roesler). Gonapophyses
4.328 *Triplocania africana* Badonnel. Lacinia
4.329 *Triplocania reflexa* Roesler. Fore wing
4.330 *Triplocania africana* Badonnel. Fore wing
4.331 *Triplocania magnifica* Roesler. Hind wing
4.332 *Triplocania magnifica* Roesler. Subgenital plate
4.333 *Triplocania magnifica* Roesler. Gonapophyses
4.334 *Triplocania magnifica* Roesler. Spermathecal opening
4.335 *Triplocania magnifica* Roesler. Hypandrium
4.336 *Triplocania reflexa* Roesler. Hypandrium
4.337 *Triplocania africana* Badonnel. Phallosome
4.338 *Triplocania magnifica* Roesler. Phallosome
4.339 *Triplocania reflexa* Roesler. Phallosome
4.340 *Triplocania africana* Badonnel. Paraproct
4.341 *Euplocania amabilis* Enderlein. Fore wing
4.342 *Euplocania amabilis* Enderlein. Hind wing



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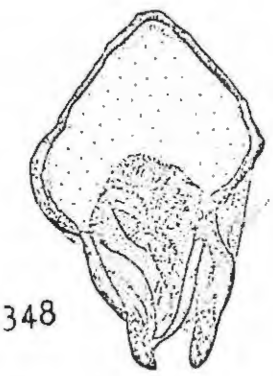

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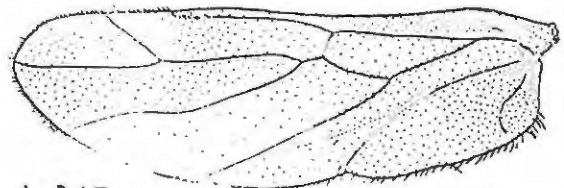

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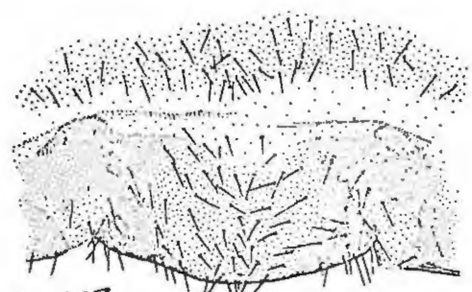

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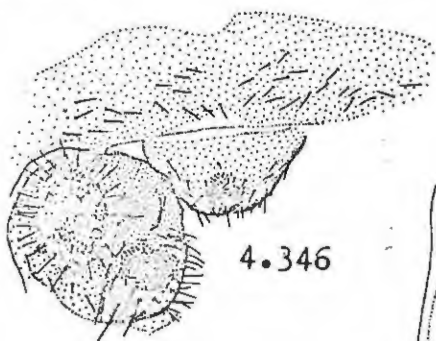

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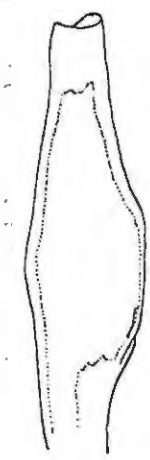

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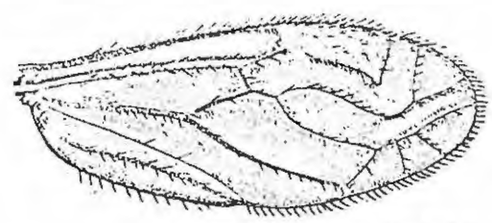

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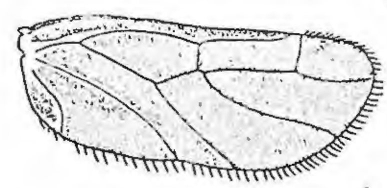

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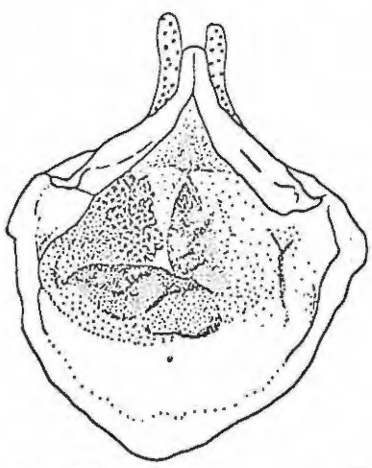

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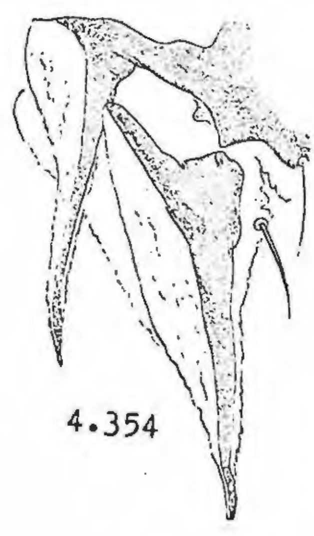

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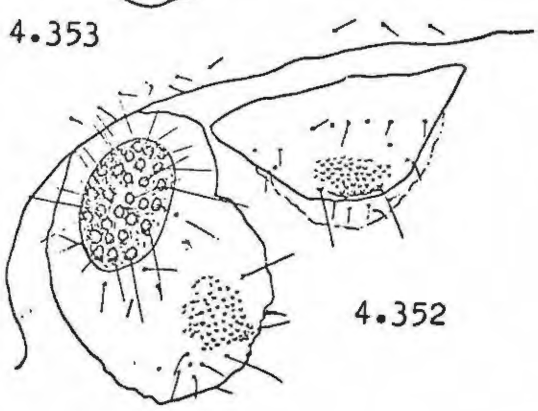
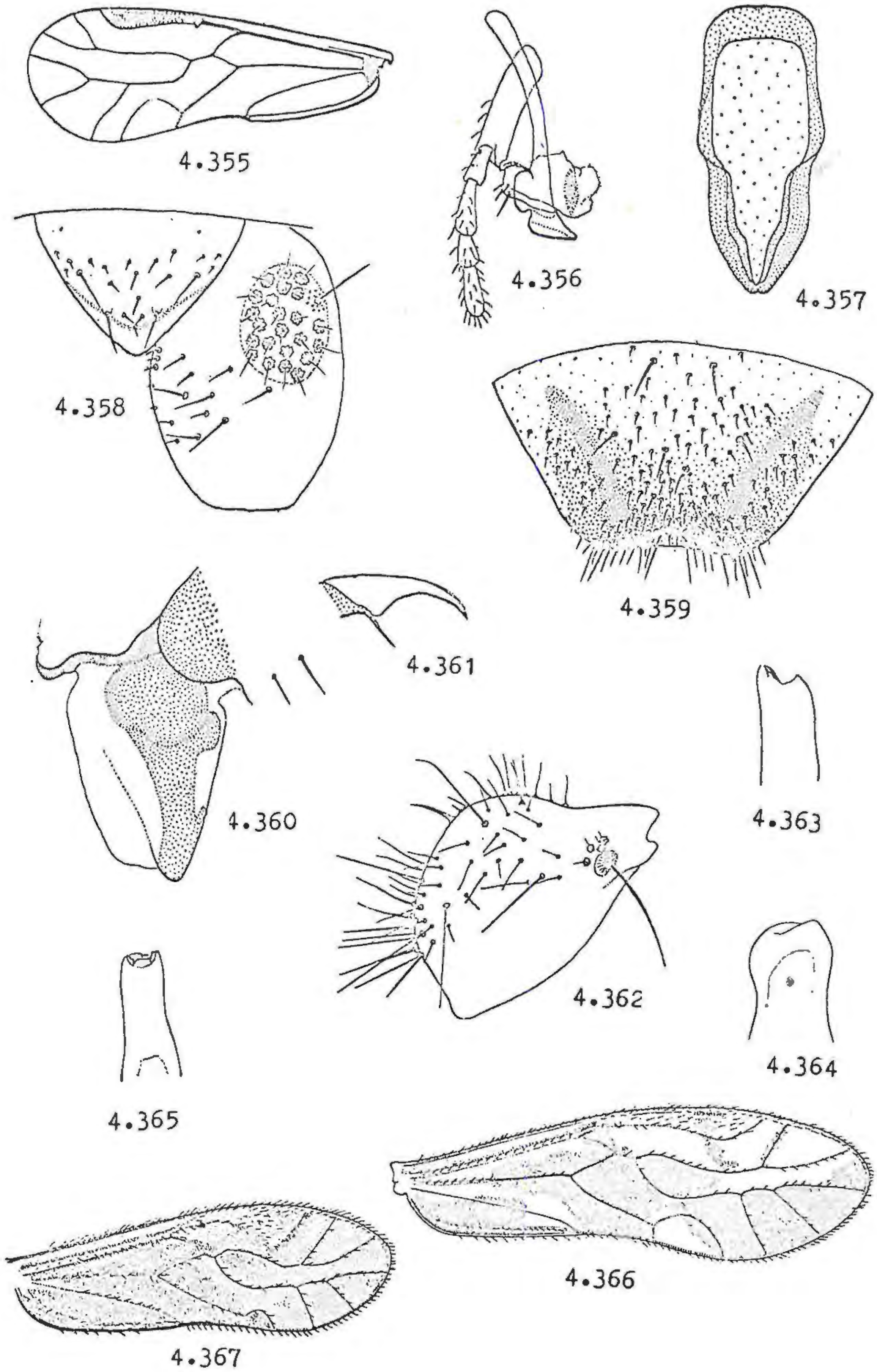
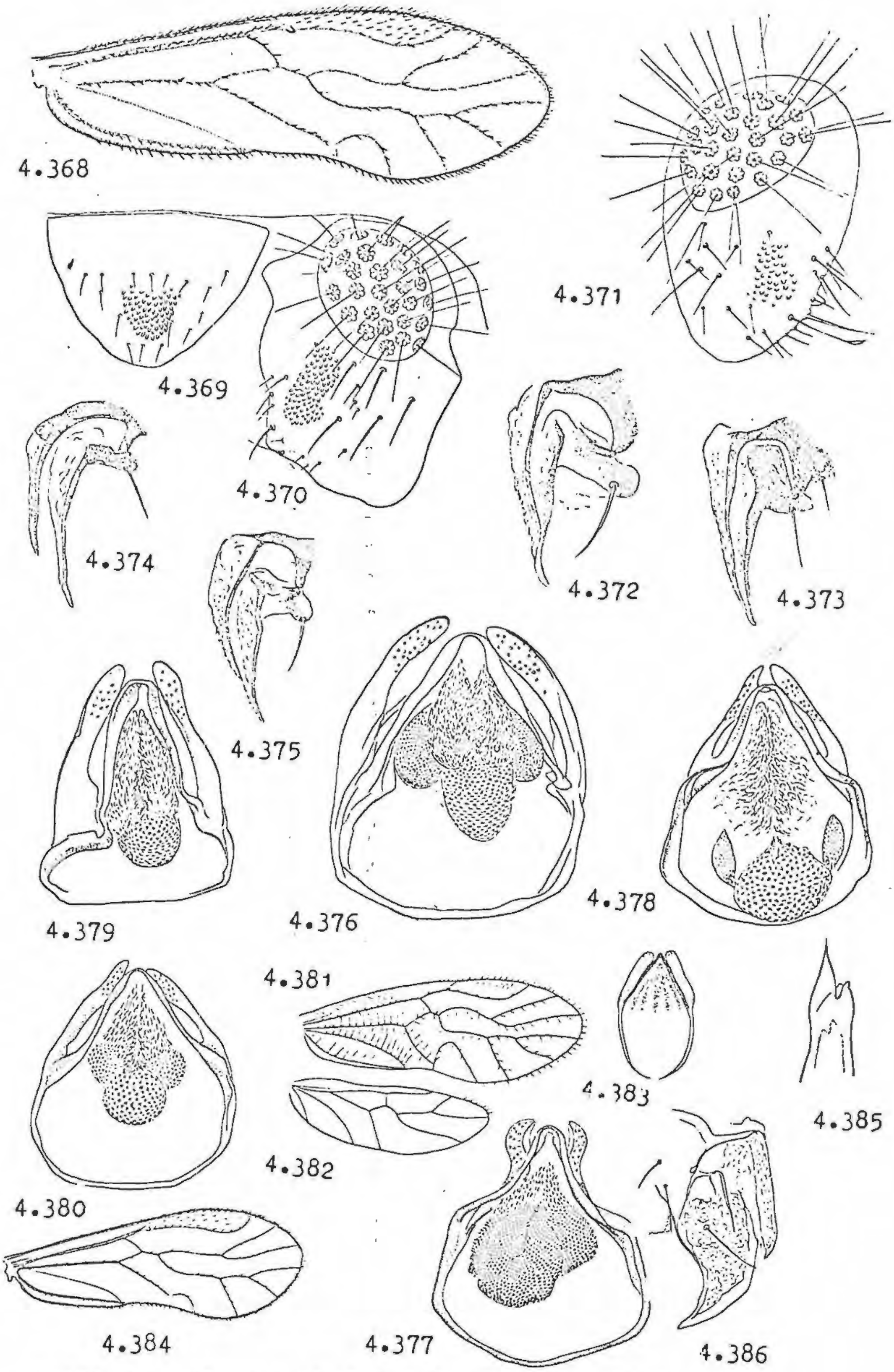


4.352

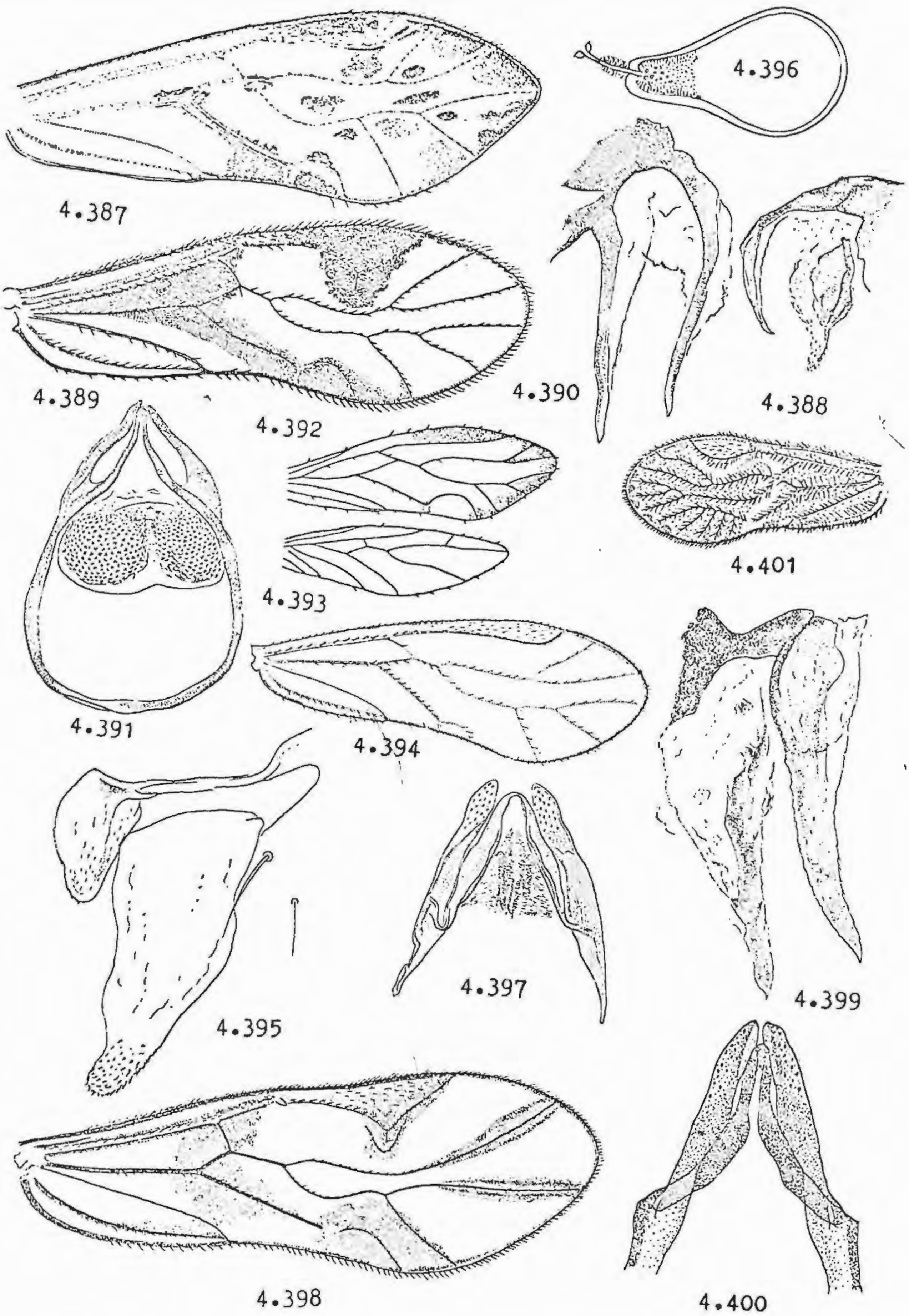
4.344 *Dypsocus fucosus* Thornton and Wong. Fore wing
4.345 *Dypsocus fucosus* Thornton and Wong. Hind wing
4.346 *Dypsocus fucosus* Thornton and Wong. Epiproct & Paraproct
4.347 *Dypsocus fucosus* Thornton and Wong. Hypandrium
4.348 *Dypsocus fucosus* Thornton and Wong. Phallosome
4.349 *Isophanes angolensis* Badonnel. Lacinia
4.350 *Isophanes angolensis* Badonnel. Fore wing
4.351 *Isophanes angolensis* Badonnel. Hind wing
4.352 *Isophanes capeneri* Smithers. Epiproct and Paraproct
4.353 *Isophanes capeneri* Smithers. Phallosome
4.354 *Isophanes angolensis* Badonnel. Gonapophyses



4.355 Asiopsocus mongolicus Gunther. Fore wing
4.356 Asiopsocus mongolicus Gunther. Lacinia
4.357 Asiopsocus mongolicus Gunther. Phallosome
4.358 Asiopsocus mongolicus Gunther. Epiproct and Paraproct ♂
4.359 Asiopsocus mongolicus Gunther. Subgenital plate ♀
4.360 Asiopsocus mongolicus Gunther. Gonapophyses
4.361 Asiopsocus mongolicus Gunther. Claw
4.362 Asiopsocus mongolicus Gunther. Paraproct ♀
4.363 Caecilius fuscopterus (Latreille). Lacinia
4.364 Caecilius flavidus (Stephens). Lacinia
4.365 Caecilius piceus Kolbe. Lacinia
4.366 Caecilius signatipennis Enderlein. Fore wing
4.367 Caecilius p'sicensis Badonnel. Fore wing

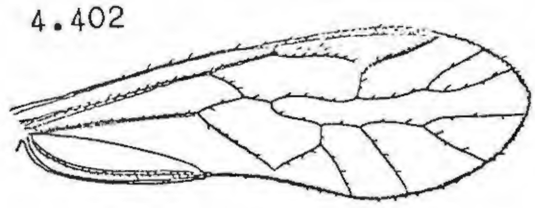


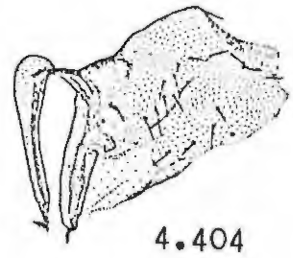
4.368 Caecilius machadoi Badonnel. Fore wing
4.369 Caecilius fuscopterus (Latreille). Epiproct
4.370 Caecilius fuscopterus (Latreille). Paraproct
4.371 Caecilius tsaratananensis Badonnel. Paraproct
4.372 Caecilius congolensis Badonnel. Gonapophyses
4.373 Caecilius dubius Badonnel. Gonapophyses
4.374 Caecilius soleili Badonnel. Gonapophyses
4.375 Caecilius collarti Badonnel. Gonapophyses
4.376 Caecilius machadoi Badonnel. Phallosome
4.377 Caecilius tsaratananensis Badonnel. Phallosome
4.378 Caecilius marginalis Badonnel. Phallosome
4.379 Caecilius lundensis Badonnel. Phallosome
4.380 Caecilius stuckenbergi Badonnel. Phallosome
4.381 Dasydemella silvestrii Enderlein. Fore wing
4.382 Dasydemella silvestrii Enderlein. Hind wing
4.383 Dasydemella gynopeza Roesler.Phallosome
4.384 Enderleinella obsoleta (Stephens). Fore wing
4.385 Enderleinella obsoleta (Stephens). Lacinia
4.386 Enderleinella obsoleta (Stephens). Gonapophyses



4.387 Eocaecilius wittei Badonnel. Fore wing
4.388 Eocaecilius wittei Badonnel. Gonapophyses
4.389 Fulleborniella nyassica Enderlein. Fore wing
4.390 Fulleborniella nyassica Enderlein. Gonapophyses
4.391 Fulleborniella nyassica Enderlein. Phallosome
4.392 Lacroixiella martini (Lacroix). Fore wing
4.393 Lacroixiella martini (Lacroix). Hind wing
4.394 Paracaecilius megops Badonnel. Fore wing
4.395 Paracaecilius oxystigma (Badonnel). Gonapophyses
4.396 Paracaecilius oxystigma (Badonnel). Spermatheca
4.397 Paracaecilius megops Badonnel. Phallosome
4.398 Ypsiloneura monostyla Badonnel. Fore wing
4.399 Ypsiloneura monostyla Badonnel. Gonapophyses
4.400 Ypsiloneura kirkpatricki Pearman. Phallosome apex
4.401 Schizopechus marshalli Pearman. Fore wing

4.402





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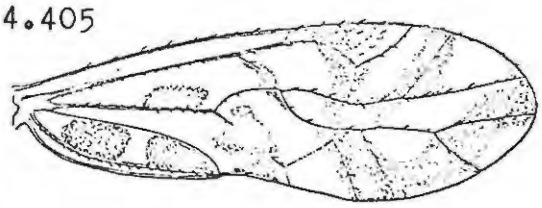

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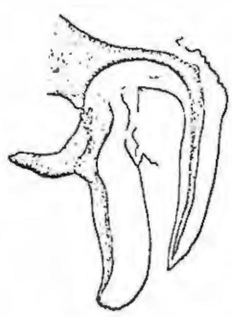

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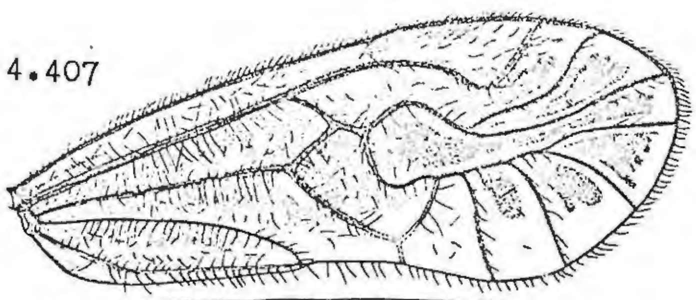

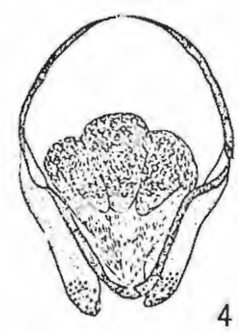

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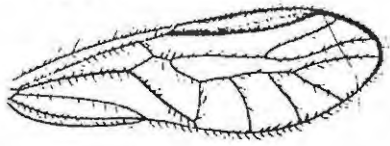

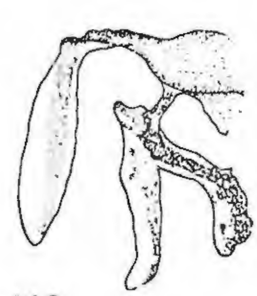

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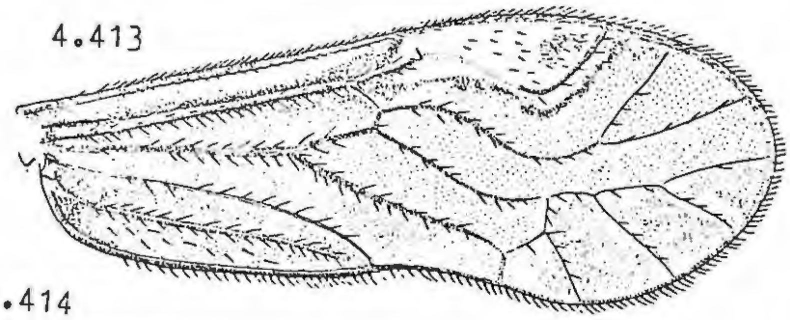
4.402 *Stenopsocus stigmaticus* (Imhoff & Labrum). Fore wing
4.403 *Stenopsocus stigmaticus* (Imhoff & Labrum). Gonapophyses
4.404 *Stenopsocus pallidus* Thornton & Wong. Gonapophyses
4.405 *Graphopsocus cruciatus* (L.). Fore wing
4.406 *Graphopsocus cruciatus* (L.). Gonapophyses
4.407 *Matsumuraiella radiopicta* Enderlein. Fore wing
4.408 *Matsumuraiella radiopicta* Enderlein. Hind wing
4.409 *Matsumuraiella radiopicta* Enderlein. Phallosome
4.410 *Matsumuraiella radiopicta* Enderlein. Gonapophyses
4.411 *Taeniostigma ingens* Enderlein. Fore wing
4.412 *Taeniostigma elongatum* (Hagen). Gonapophyses

4.413



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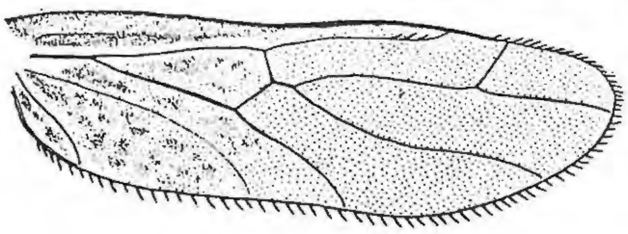

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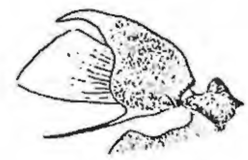

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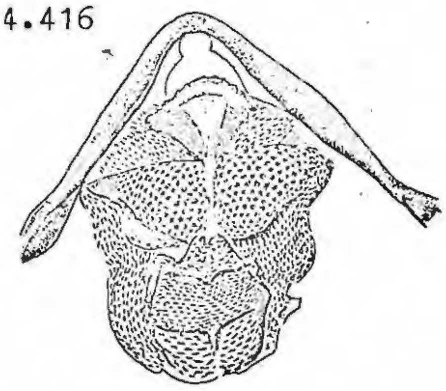

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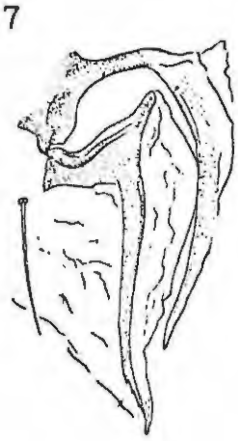

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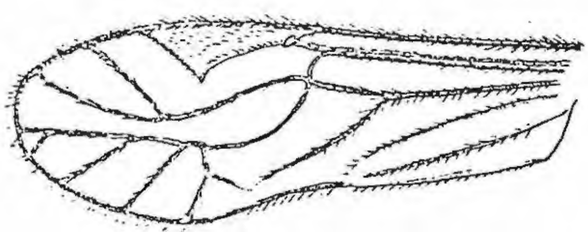

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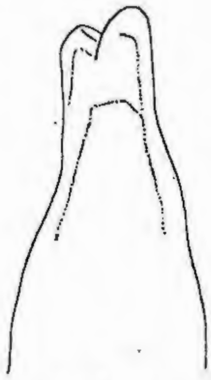
4.413 *Kodamaius angolensis* (Badonnel). Fore wing
4.414 *Kodamaius angolensis* (Badonnel). Hind wing
4.415 *Kodamaius collarti* (Badonnel). Claw
4.416 *Kodamaius angolensis* (Badonnel). Phallosome
4.417 *Kodamaius lamottei* (Badonnel). Gonapophyses
4.418 *Kodamaius lamottei* (Badonnel). Lacinia
4.419 *Epikodamaius ikomai* Kuwayama. Fore wing



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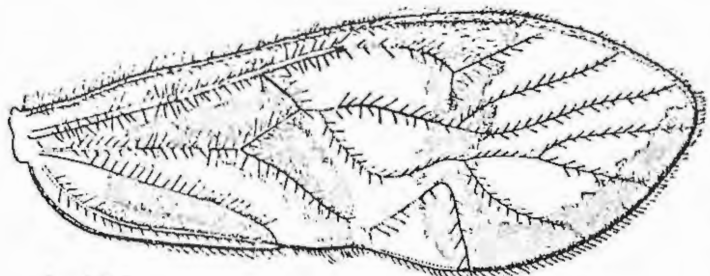

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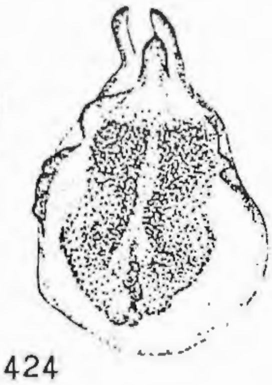

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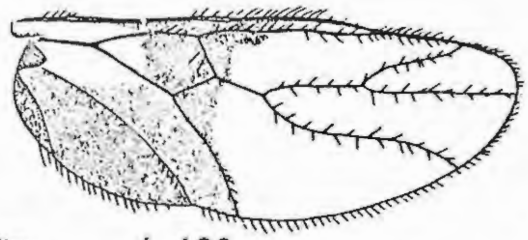

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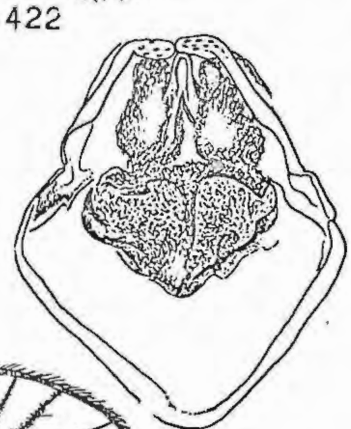

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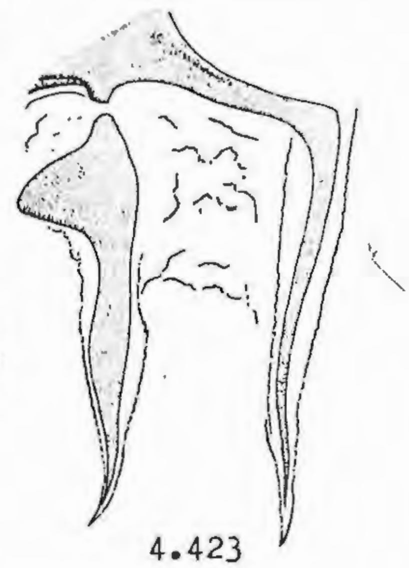

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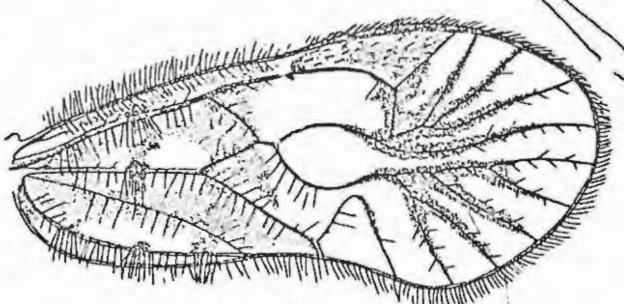

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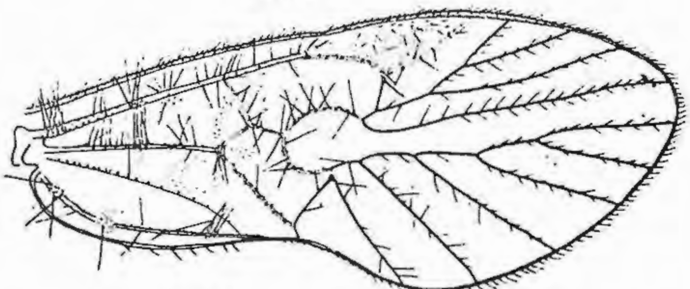

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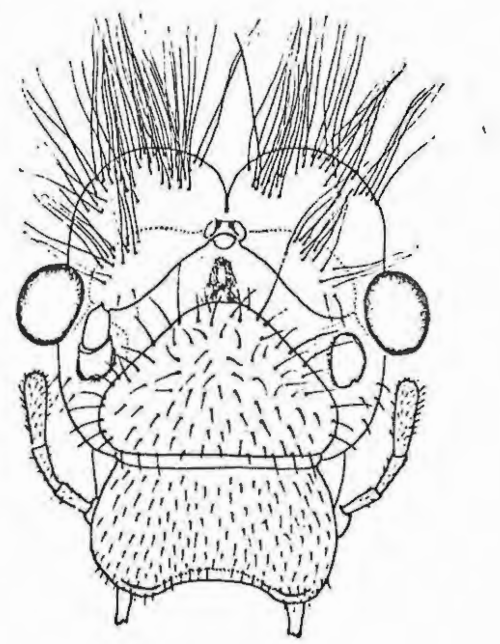

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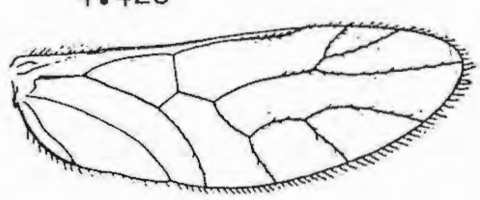
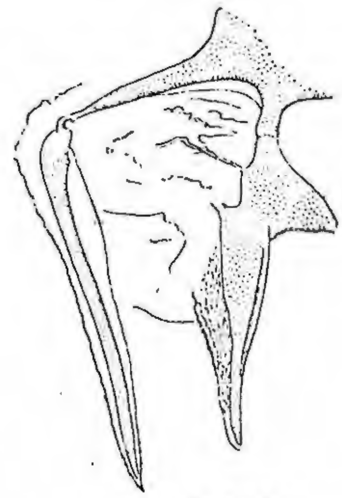


4.430

4.420 Amphipsocus facetus Smithers. Lacinia
4.421 Amphipsocus facetus Smithers. Fore wing
4.422 Amphipsocus fasciatus Badonnel. Hind wing
4.423 Amphipsocus facetus Smithers. Gonapophyses
4.424 Amphipsocus hyalinus Smithers. Phallosome
4.425 Xenopsocus hageni Kolbe. Fore wing
4.426 Harpezoneura limbata Badonnel. Fore wing
4.427 Harpezoneura ambigua Badonnel. Phallosome
4.428 Pentathyrsus vespertilio Enderlein. Fore wing
4.429 Pentathyrsus vespertilio Enderlein. Head
4.430 Pentathyrsus vespertilio Enderlein. Hind wing



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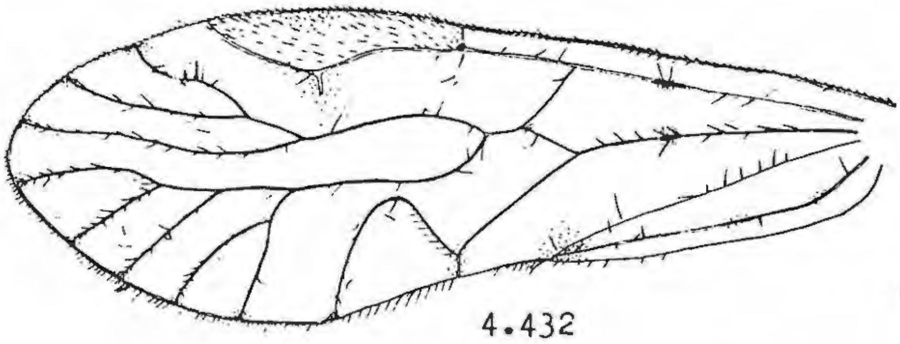

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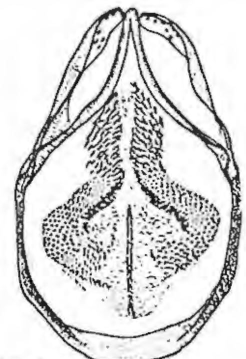

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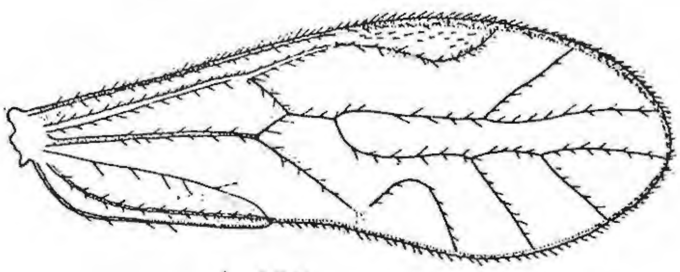

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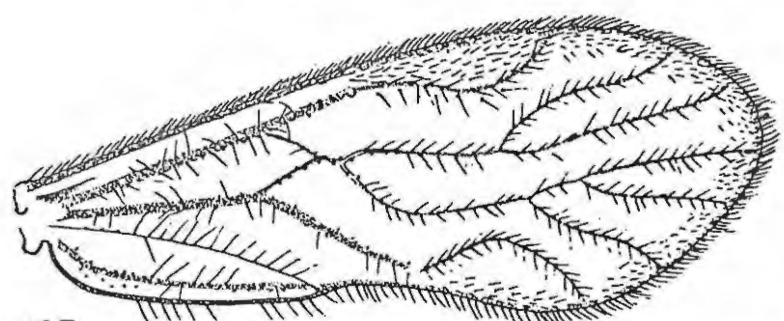

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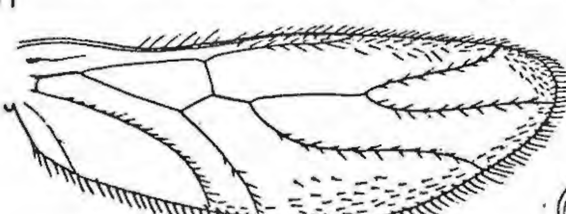

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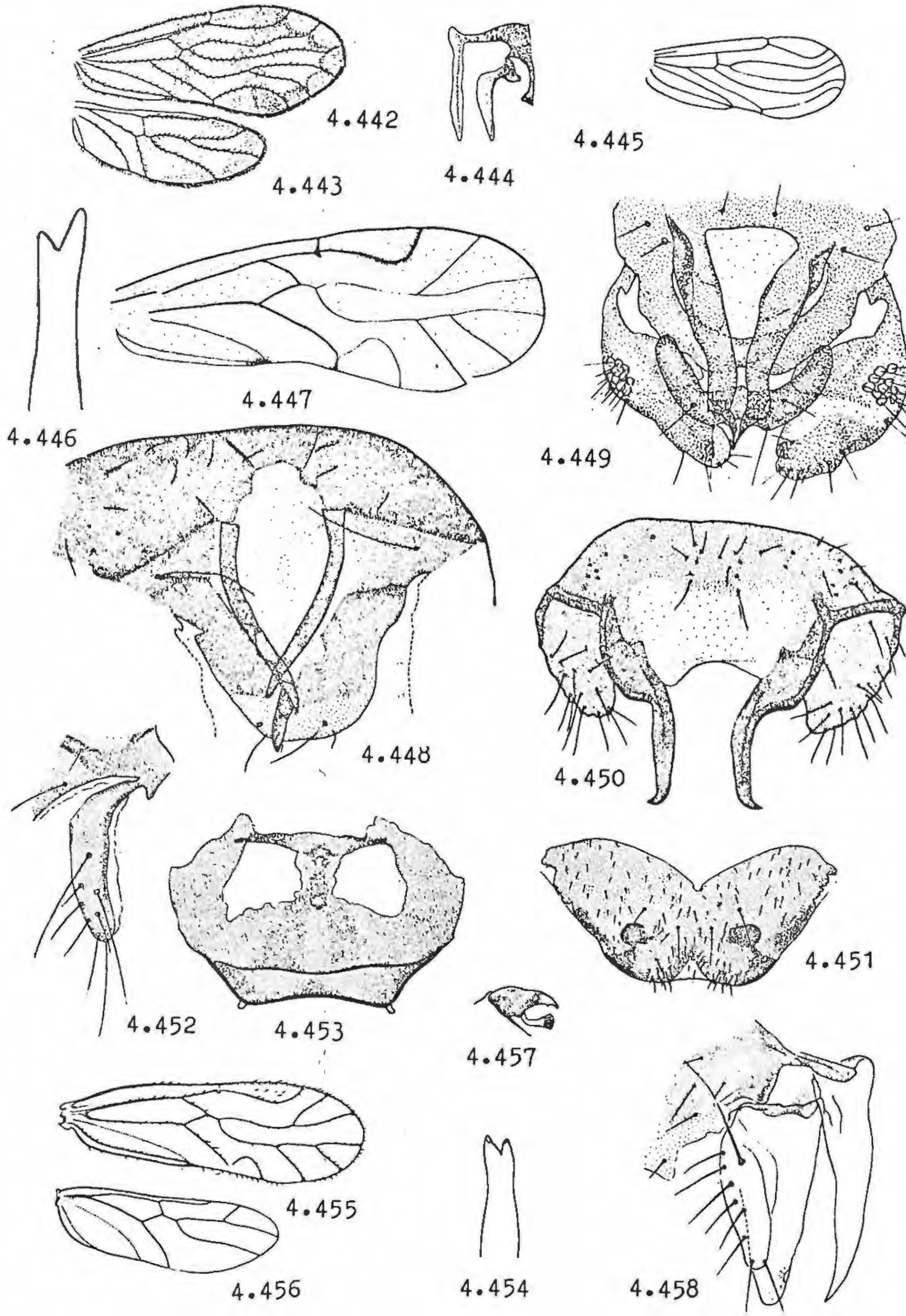
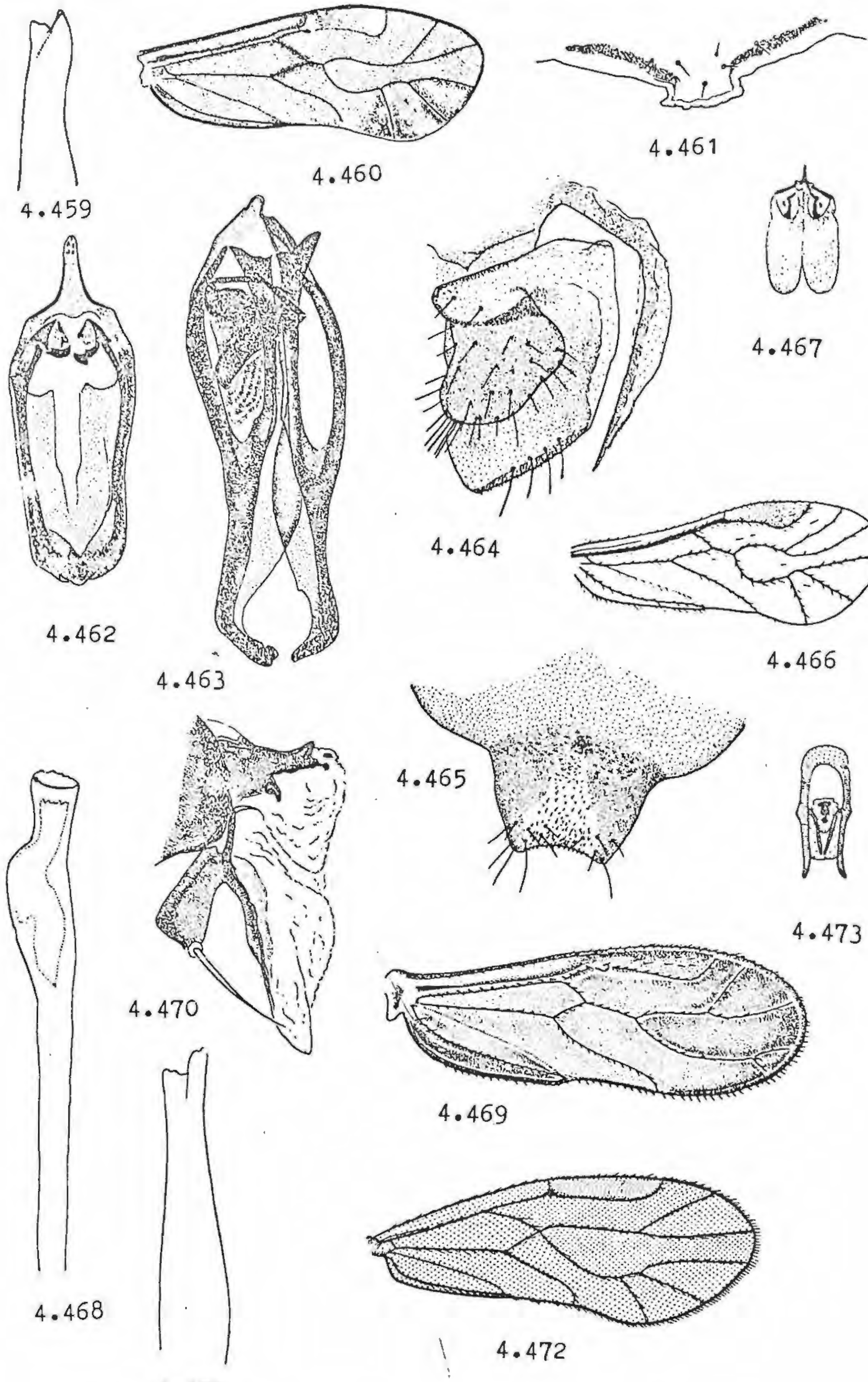
4.431 Pentathyrsus vespertilio Enderlein. Gonapophyses
4.432 Amphipsocopsis surculosus Smithers. Fore wing
4.433 Amphipsocopsis surculosus Smithers. Lacinia
4.434 Kolbea madagascariensis Badonnel. Lacinia
4.435 Kolbea madagascariensis Badonnel. Fore wing
4.436 Kolbea madagascariensis Badonnel. Phallosome
4.437 Dasypsocus angolensis Badonnel. Fore wing
4.438 Dasypsocus angolensis Badonnel. Hind wing
4.439 Dasypsocus angolensis Badonnel. Lacinia
4.440 Dasypsocus angolensis Badonnel. Gonapophyses
4.441 Dasypsocus angolensis Badonnel. Phallosome

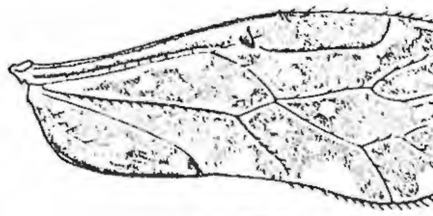


4.442 *Polypsocus fastosus* Roesler. Fore wing
4.443 *Polypsocus fastosus* Roesler. Hind wing
4.444 *Polypsocus coleopterus* Roesler. Gonapophyses
4.445 *Monocladellus ohausianus* Enderlein. Fore wing
4.446 *Lachesilla annulata* Smithers. Lacinia
4.447 *Lachesilla annulata* Smithers. Fore wing
4.448 *Lachesilla annulata* Smithers. 9th tergite and epiproct
4.449 *Lachesilla bugiriana* Smithers. Apex of abdomen
4.450 *Lachesilla annulata* Smithers. Hypandrium
4.451 *Lachesilla annulata* Smithers. Subgenital plate
4.452 *Lachesilla annulata* Smithers. Gonapophyses
4.453 *Lachesilla annulata* Smithers. Entrance to spermatheca
4.454 *Eolachesilla chilensis* Badonnel. Lacinia
4.455 *Eolachesilla chilensis* Badonnel. Fore wing
4.456 *Eolachesilla chilensis* Badonnel. Hind wing
4.457 *Eolachesilla chilensis* Badonnel. Claw
4.458 *Eolachesilla chilensis* Badonnel. Gonapophyses



4.459 *Peripsocus madecassus* Badonnel. Lacinia
4.460 *Peripsocus angolensis* Smithers. Fore wing
4.461 *Peripsocus angolensis* Smithers. Ninth tergite ♂
4.462 *Peripsocus angolensis* Smithers. Phallosome
4.463 *Peripsocus badonneli* Smithers. Phallosome
4.464 *Peripsocus setosus* Smithers. Gonapophyses
4.465 *Peripsocus setosus* Smithers. Subgenital plate
4.466 *Kaestneriella pilosa* Roesler. Fore wing
4.467 *Kaestneriella pilosa* Roesler. Phallosome
4.468 *Notiopsocus machadoi* Badonnel. Lacinia
4.469 *Notiopsocus machadoi* Badonnel. Fore wing
4.470 *Notiopsocus machadoi* Badonnel. Gonapophyses
4.471 *Interpsocus brunneus* Edwards. Lacinia
4.472 *Interpsocus brunneus* Edwards. Fore wing
4.473 *Interpsocus brunneus* Edwards. Phallosome

4.476



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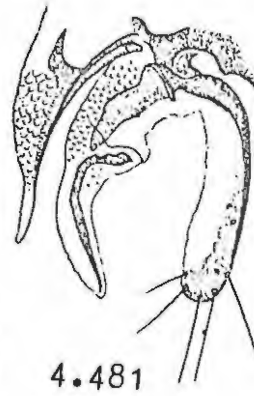

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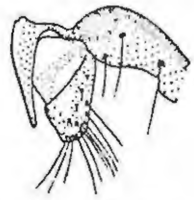

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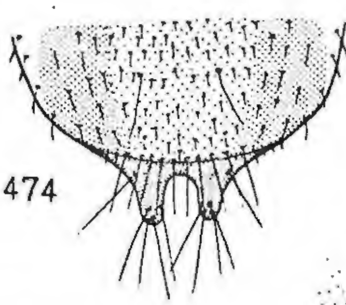

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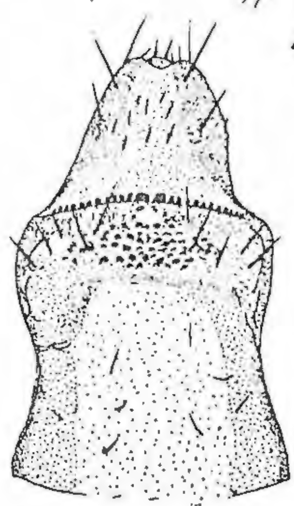

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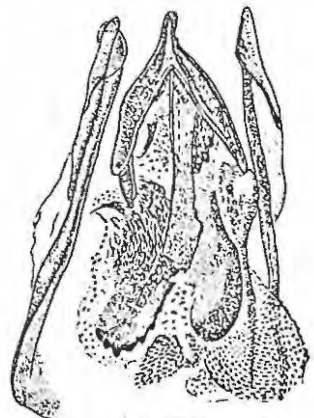

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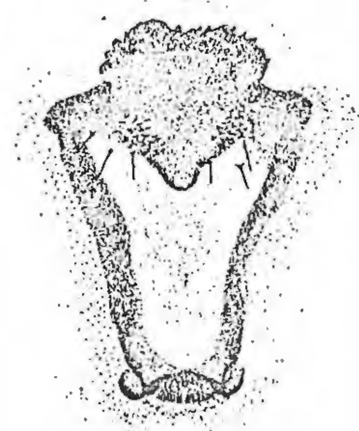

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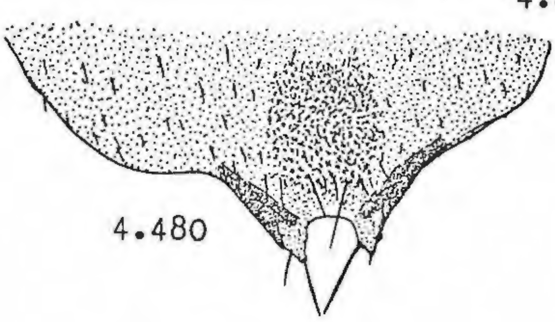

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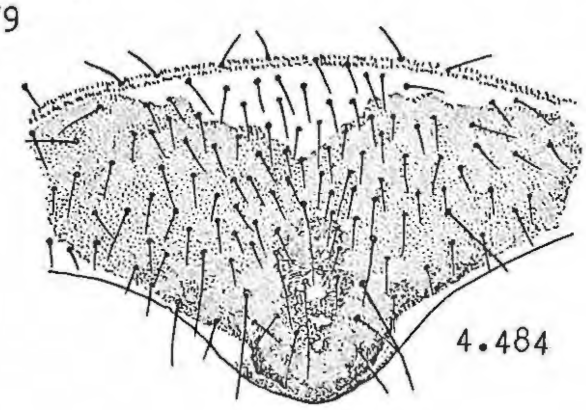

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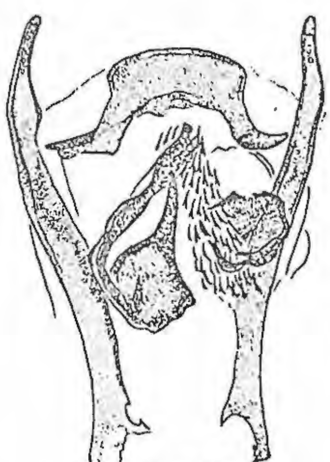

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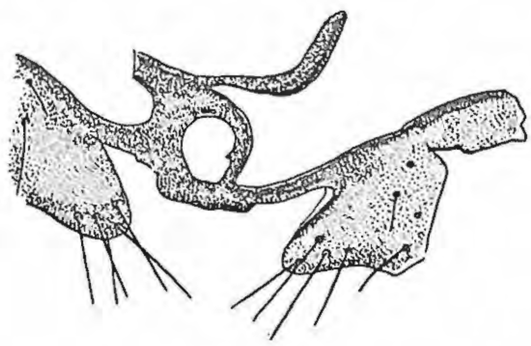
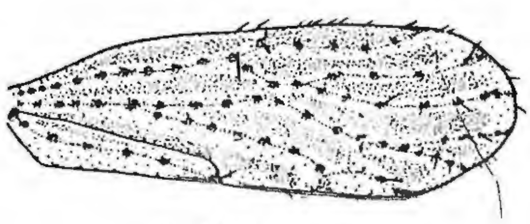


4.485

4.474 Interpsocus brunneus Edwards. Subgenital plate
4.475 Interpsocus brunneus Edwards. Gonapophyses
4.476 Ectopsocus maculatus Smithers. Lacinia
4.477 Ectopsocus maculatus Smithers. Fore wing
4.478 Ectopsocus pectinatus Smithers. 9th tergite and epiproct ♂
4.479 Ectopsocus maculatus Smithers. Phallosome
4.480 Ectopsocus maculatus Smithers. Subgenital plate
4.481 Ectopsocus pectinatus Smithers. Gonapophyses
4.482 Ectopsocopsis mozambicus (Badonnel). 9th tergite ♂
4.483 Ectopsocopsis anurus Badonnel. Phallosome
4.484 Ectopsocopsis terricolis Badonnel. Subgenital plate
4.485 Ectopsocopsis annulatus Badonnel. Gonapophyses and spermathecal opening



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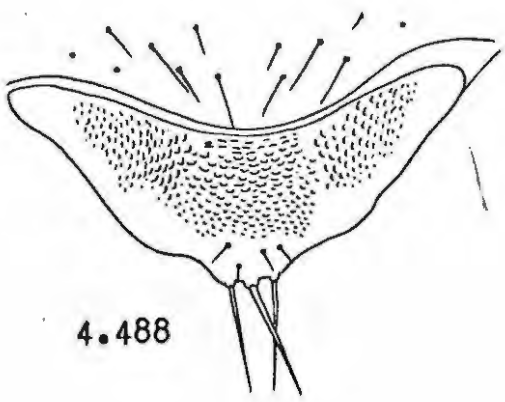

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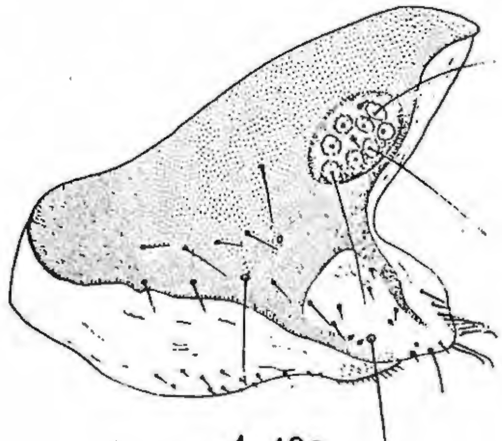

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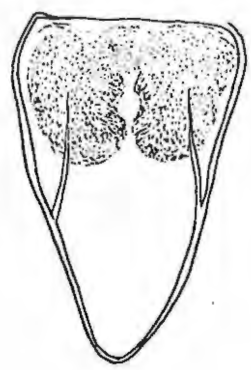

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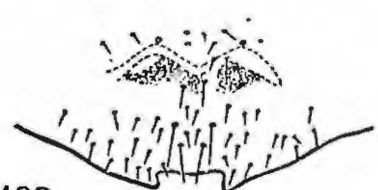

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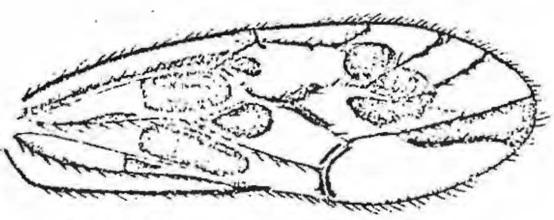
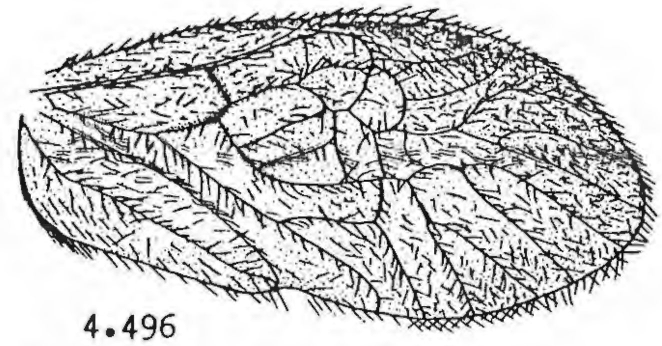


4.493

4.486 *Hemipsocus pardus* Smithers. Lacinia
4.487 *Hemipsocus pardus* Smithers. Fore wing
4.488 *Hemipsocus selysianus* Enderlein. Epiproct
4.489 *Hemipsocus fasciatus* Badonnel. Paraproct
4.490 *Hemipsocus* sp. Phallosome
4.491 *Hemipsocus selysianus* Enderlein. Phallosome
4.492 *Hemipsocus africanus* Enderlein. Subgenital plate
4.493 *Anopistoscena specularifrons* Enderlein. Fore wing



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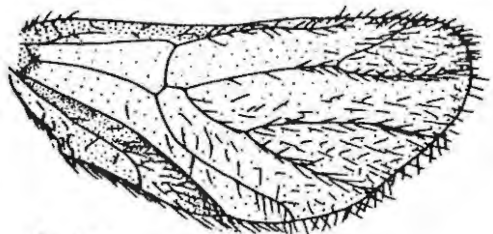

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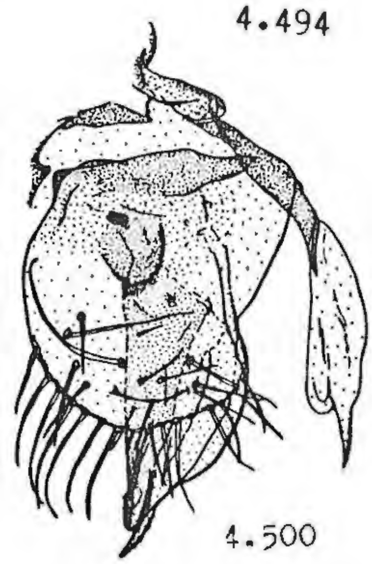

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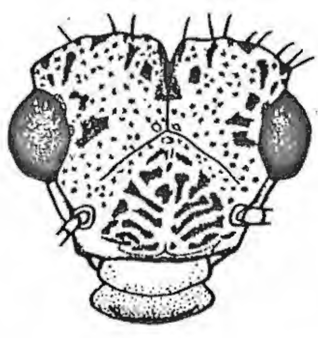

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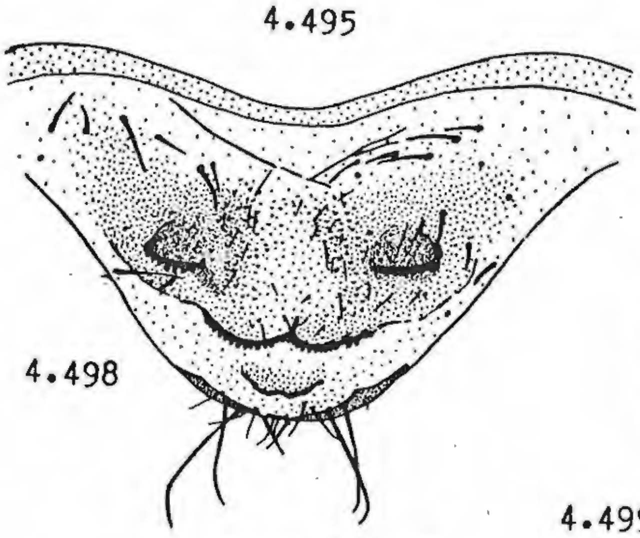

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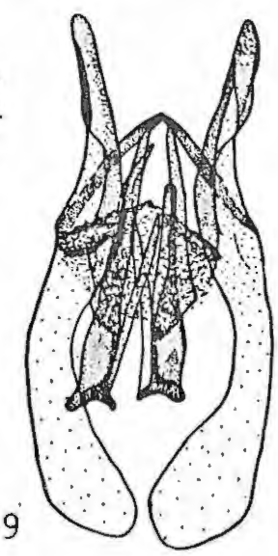

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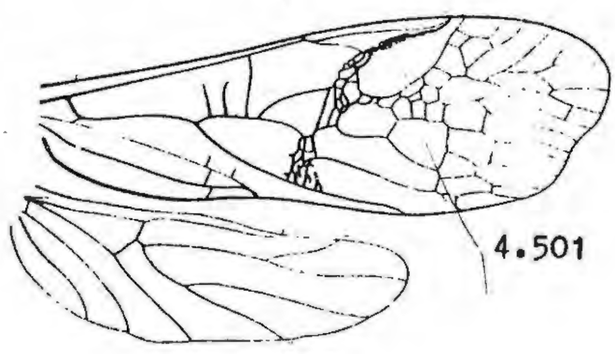

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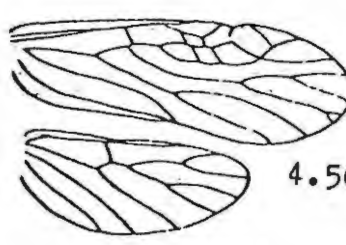

4.503

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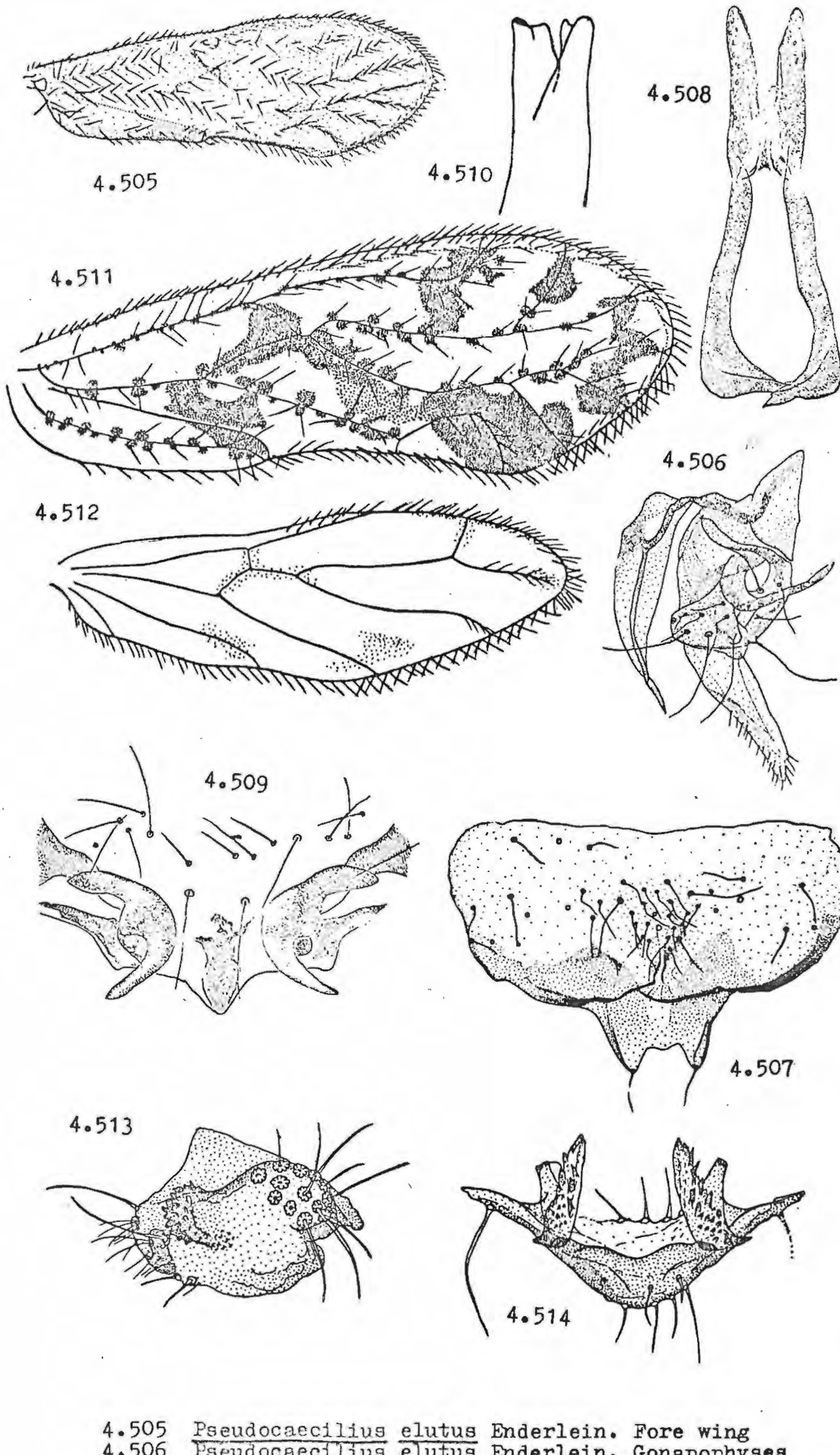
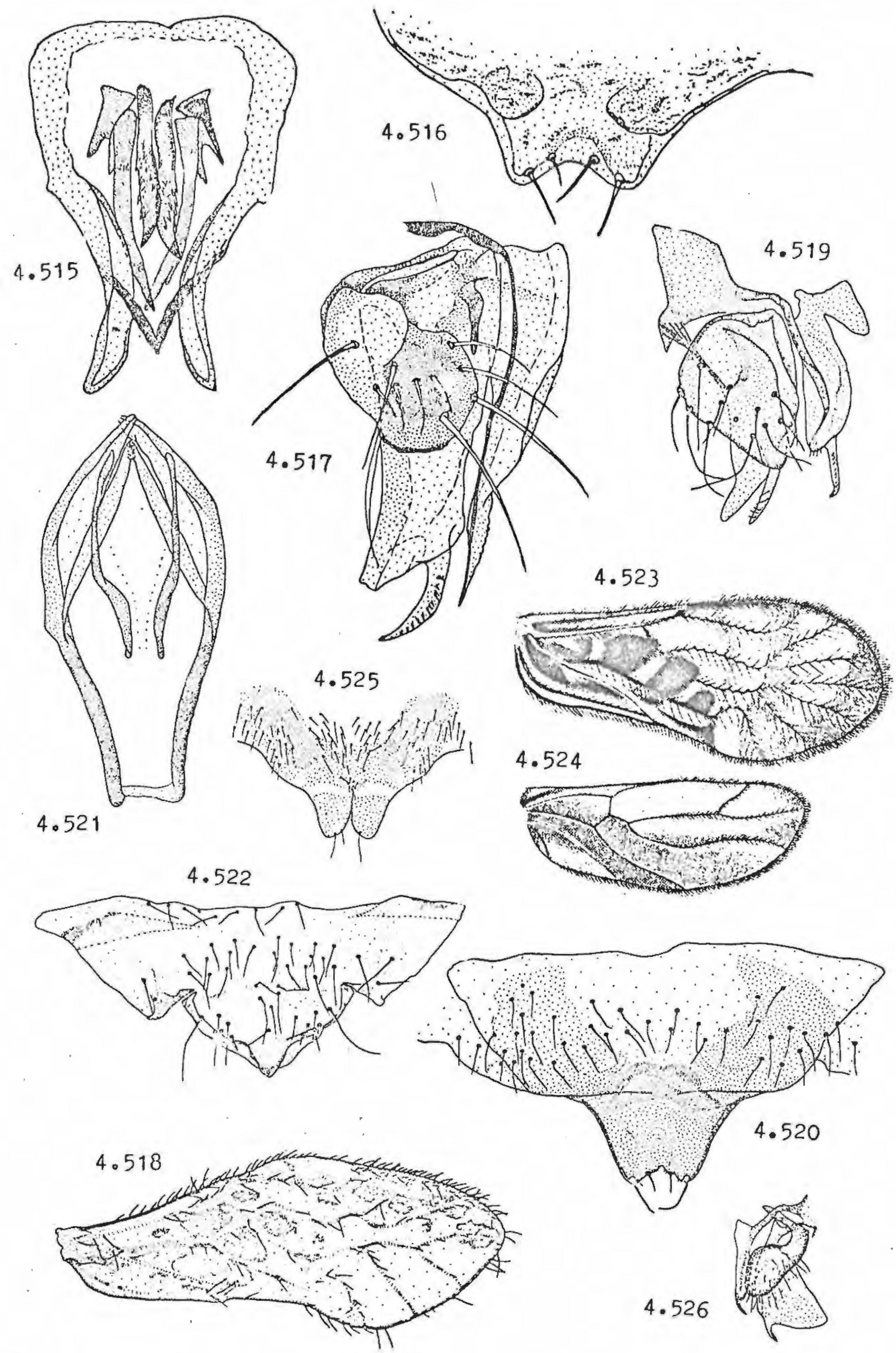
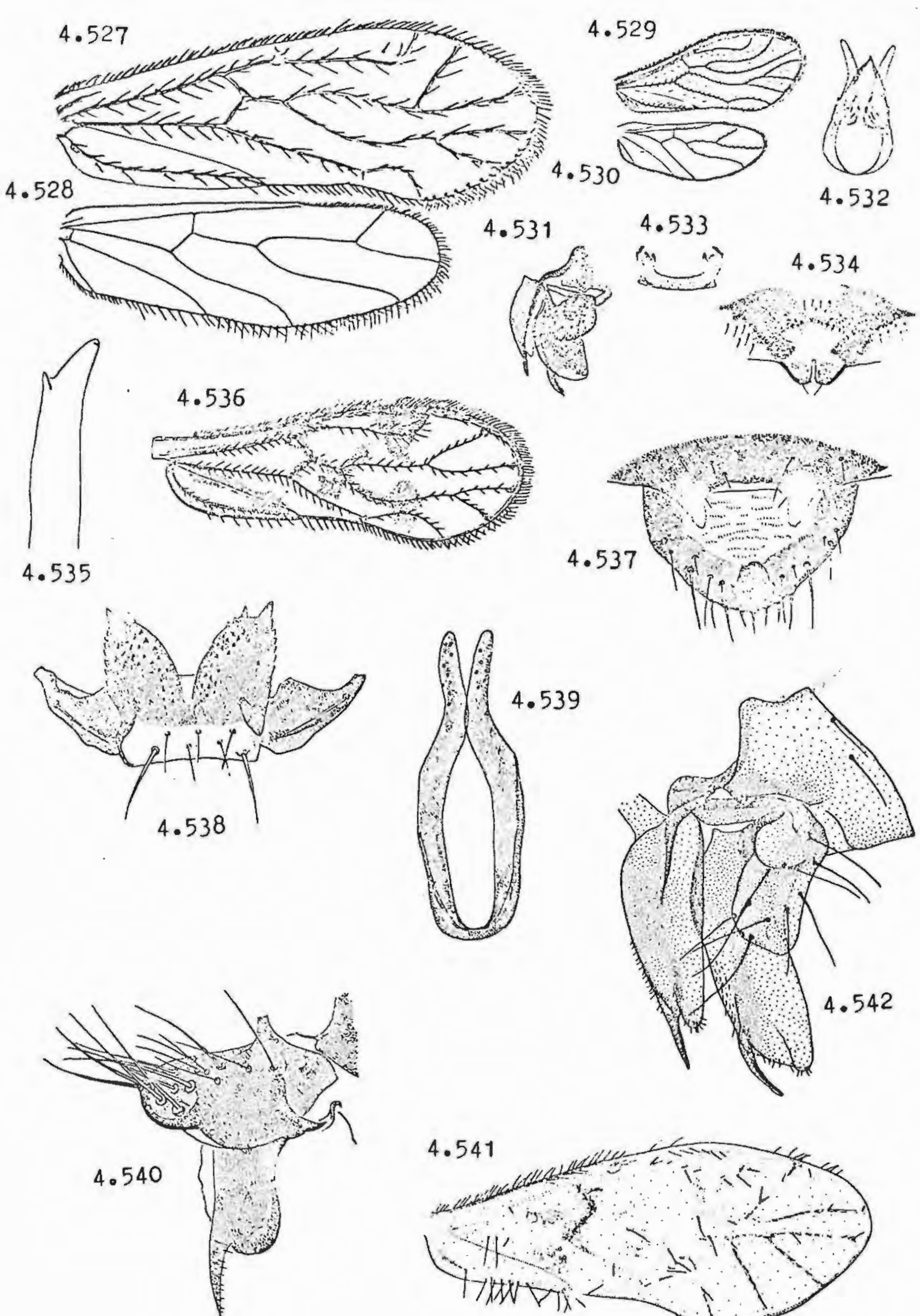
4.494 *Calopsocus guttatus* Smithers. Lacinia
4.495 *Calopsocus guttatus* Smithers. Head
4.496 *Calopsocus guttatus* Smithers. Fore wing
4.497 *Calopsocus guttatus* Smithers. Hind wing
4.498 *Calopsocus guttatus* Smithers. Ninth tergite and epiproct ♂
4.499 *Calopsocus guttatus* Smithers. Phallosome
4.500 *Calopsocus guttatus* Smithers. Gonapophyses
4.501 *Neurosema apicalis* McLachlan. Fore wing
4.502 *Neurosema apicalis* McLachlan. Hind wing
4.503 *Dirla javana* Navas. Fore wing
4.504 *Dirla javana* Navas. Hind wing



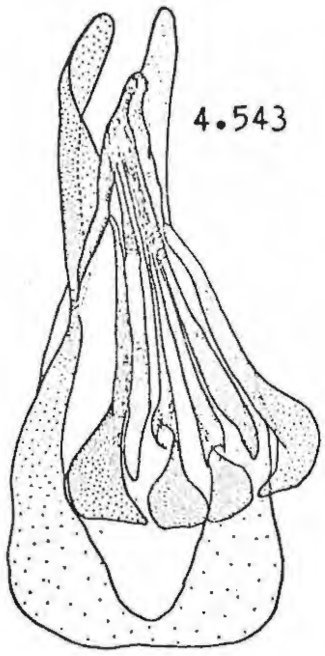
4.505 Pseudocaecilius elutus Enderlein. Fore wing
4.506 Pseudocaecilius elutus Enderlein. Gonapophyses
4.507 Pseudocaecilius elutus Enderlein. Subgenital plate
4.508 Pseudocaecilius elutus Enderlein. Phallosome
4.509 Pseudocaecilius elutus Enderlein. Hypandrium
4.510 Cladioneura pulchripennis Enderlein. Lacinia
4.511 Cladioneura pulchripennis Enderlein. Fore wing
4.512 Cladioneura pulchripennis Enderlein. Hind wing
4.513 Cladioneura pulchripennis Enderlein. Paraproct
4.514 Cladioneura pulchripennis Enderlein. Hypandrium



4.515 Cladioneura pulchripennis Enderlein. Phallosome
4.516 Cladioneura pulchripennis Enderlein. Subgenital plate
4.517 Cladioneura pulchripennis Enderlein. Gonapophyses
4.518 Ophiodopelma pictipenna Lee & Thornton. Fore wing
4.519 Ophiodopelma pictipenna Lee & Thornton. Gonapophyses
4.520 Ophiodopelma pictipenna Lee & Thornton. Subgenital plate
4.521 Ophiodopelma permaculatum Lee & Thornton. Phallosome
4.522 Ophiodopelma permaculatum Lee & Thornton. Hypandrium
4.523 Mesocaecilius quadrimaculatus Okamoto. Fore wing
4.524 Mesocaecilius quadrimaculatus Okamoto. Hind wing
4.525 Mesocaecilius quadrimaculatus Okamoto. Subgenital plate
4.526 Mesocaecilius quadrimaculatus Okamoto. Gonapophyses



4.527 Scottiella micans Enderlein. Fore wing
4.528 Scottiella micans Enderlein. Hind wing
4.529 Scytopsocus coriaceus Roesler. Fore wing
4.530 Scytopsocus coriaceus Roesler. Hind wing
4.531 Scytopsocus coriaceus Roesler. Gonapophyses
4.532 Scytopsocus coriaceus Roesler. Phallosome
4.533 Scytopsocus coriaceus Roesler. Hypandrium
4.534 Scytopsocus coriaceus Roesler. Subgenital plate
4.535 Pseudoscotiella immaculata Badonnel. Lacinia
4.536 Pseudoscotiella megops Badonnel. Fore wing
4.537 Pseudoscotiella tuberculata Badonnel. Ninth tergite & epiproct ♂
4.538 Pseudoscotiella megops Badonnel. Hypandrium
4.539 Pseudoscotiella tuberculata Badonnel. Phallosome
4.540 Pseudoscotiella immaculata Badonnel. Gonapophyses
4.541 Allocaecilius heterothorax Lee & Thornton. Fore wing
4.542 Allocaecilius heterothorax Lee & Thornton. Gonapophyses



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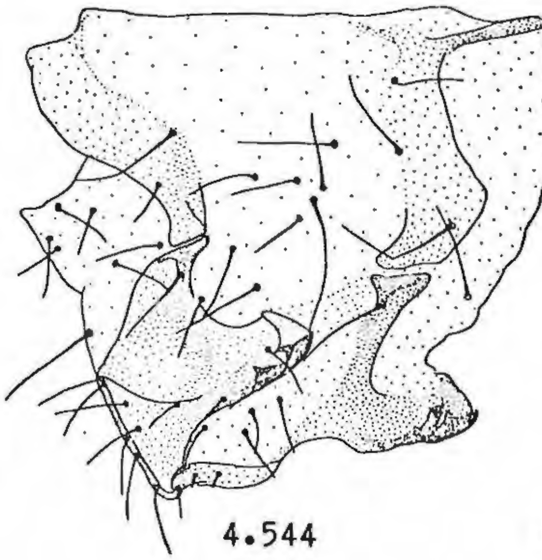

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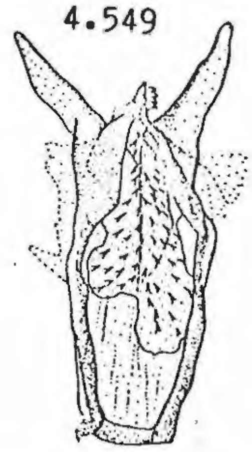

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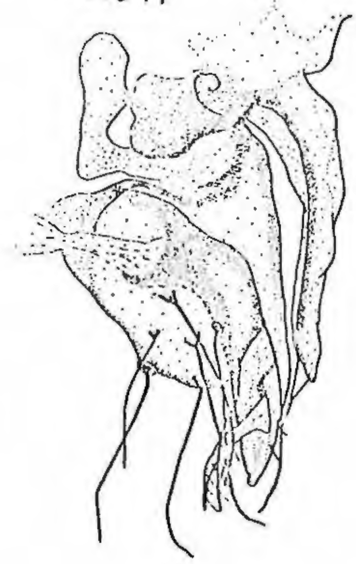

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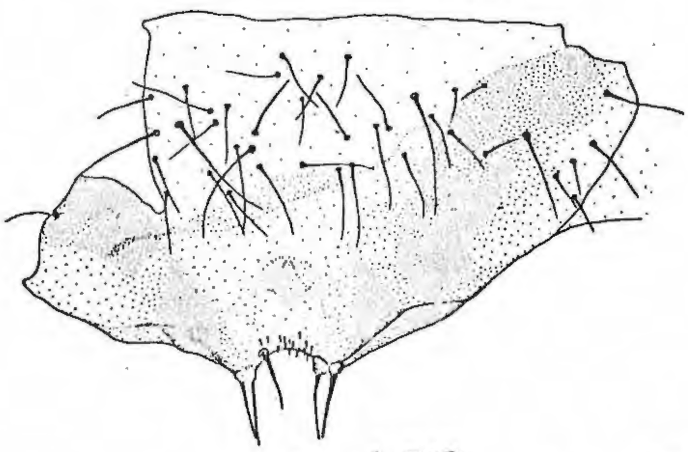

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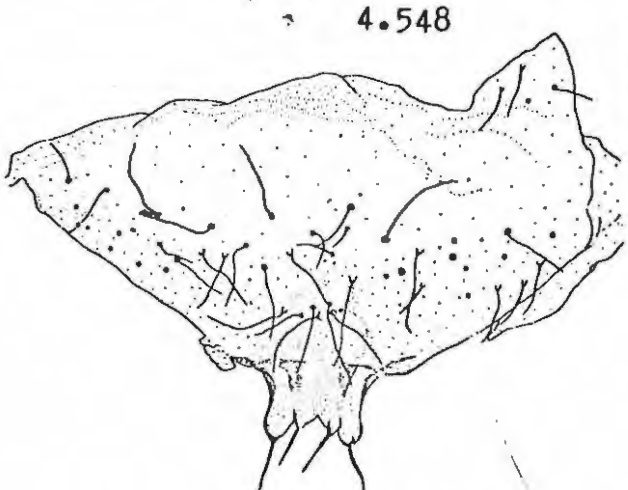

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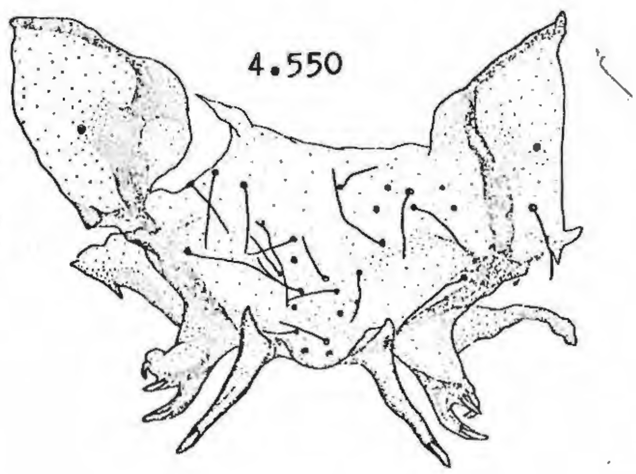

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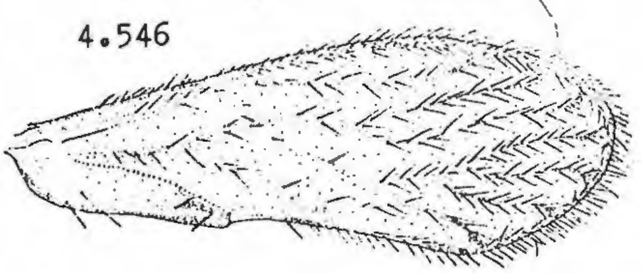

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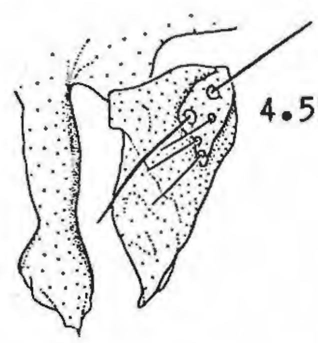
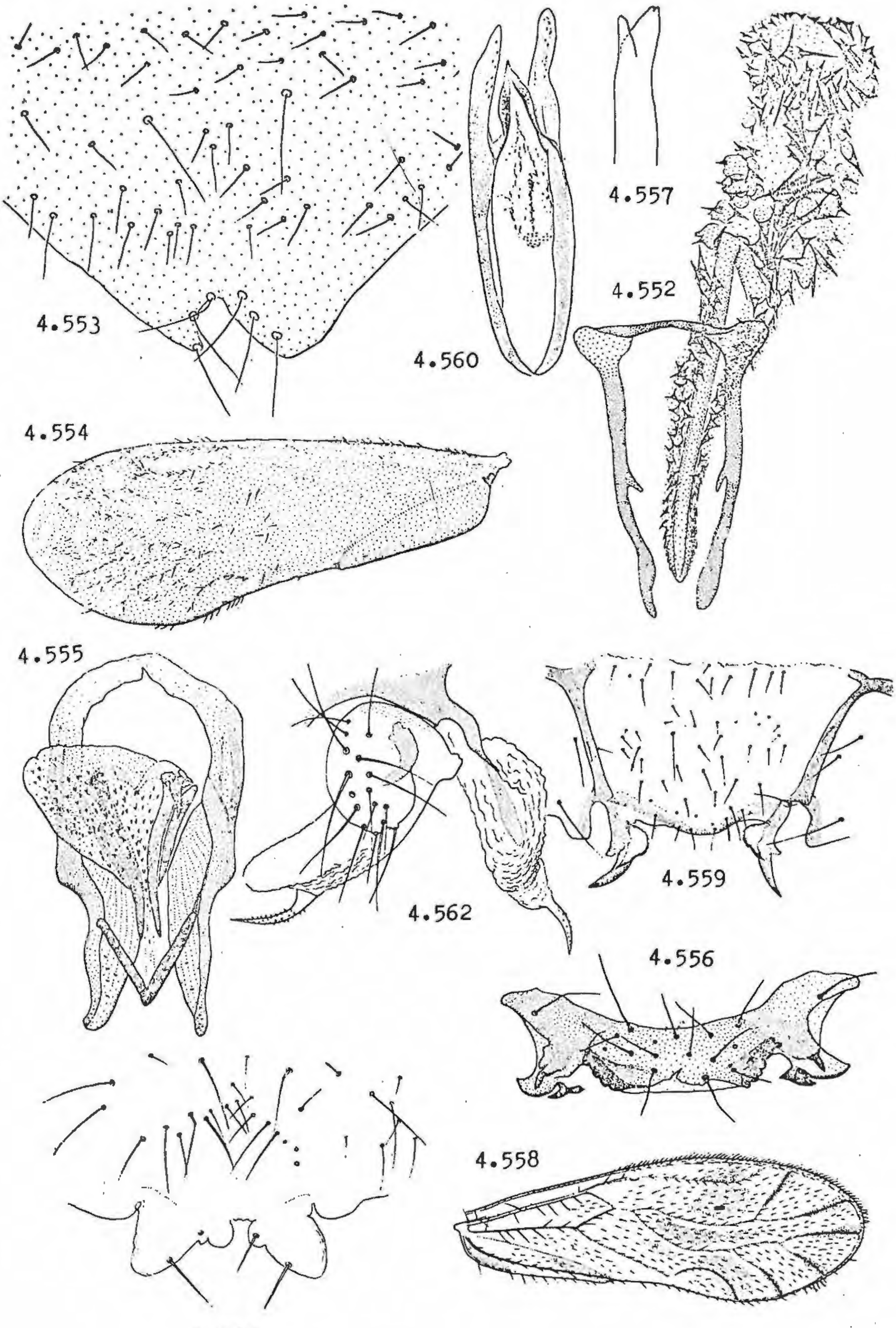
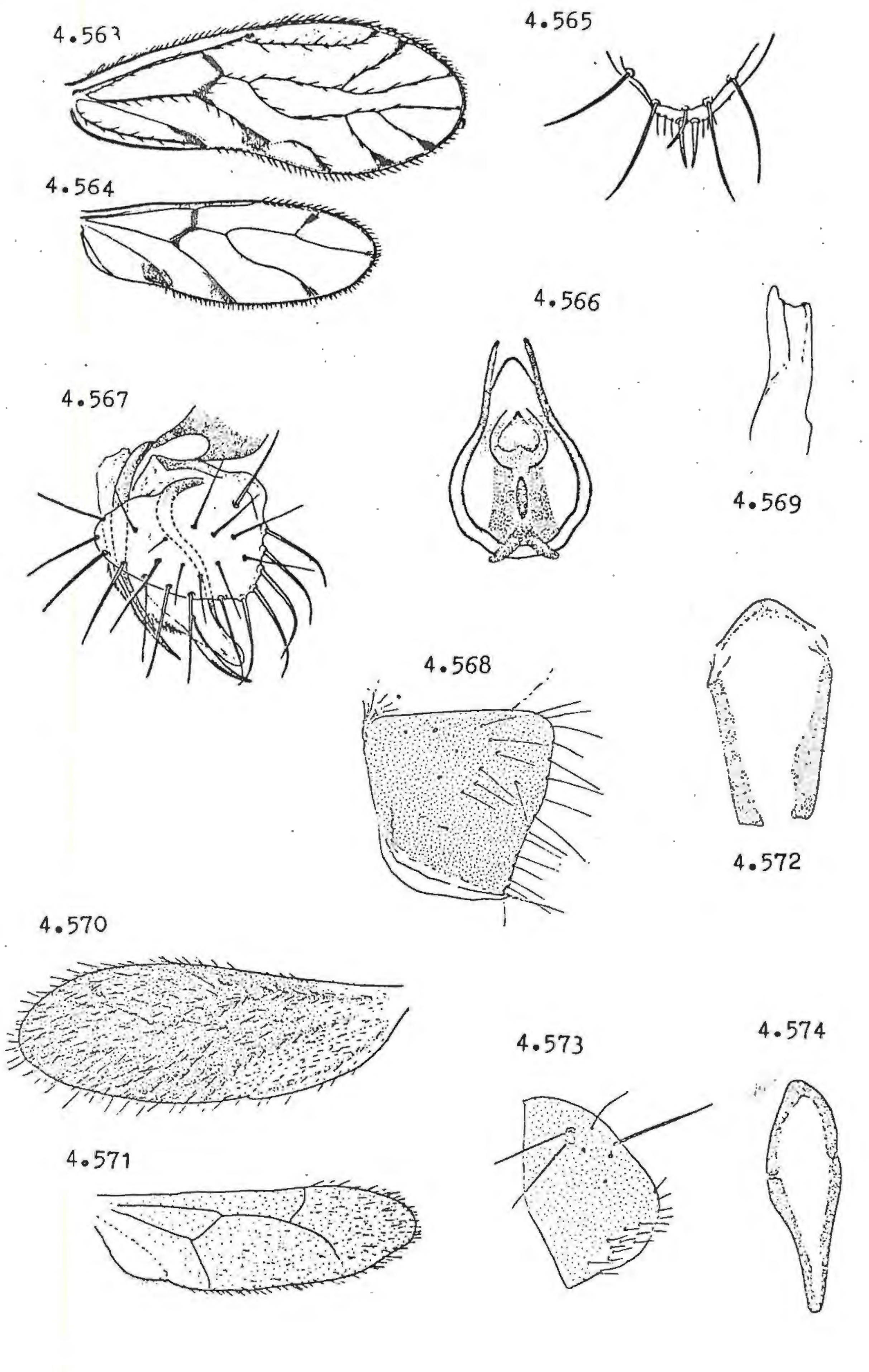


4.543 Allocaecilius heterothorax Lee & Thornton. Phallosome
4.544 Allocaecilius heterothorax Lee & Thornton. Hypandrium
4.545 Allocaecilius heterothorax Lee & Thornton. Subgenital plate

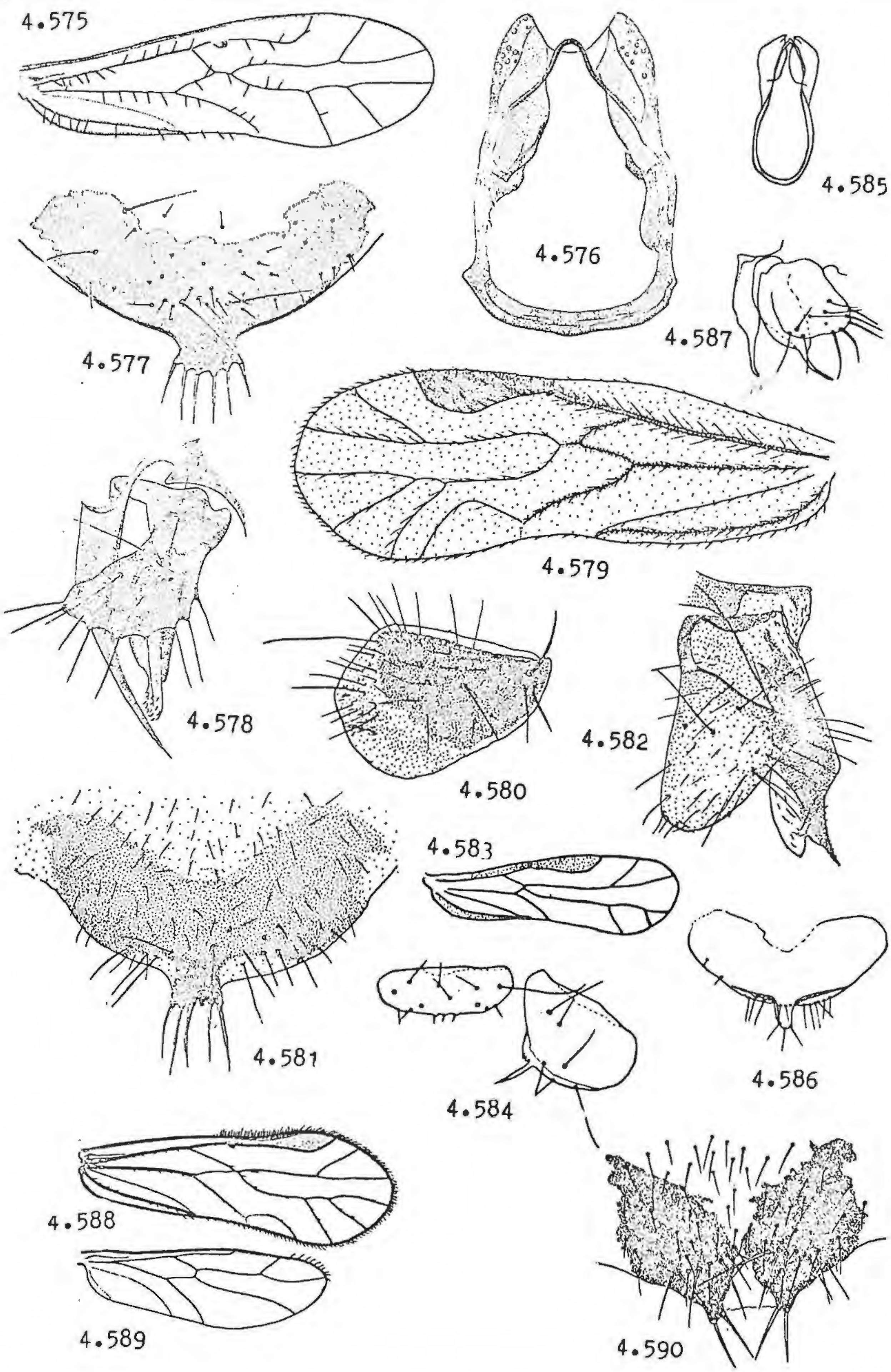
4.546 Lobocaecilius cynara Lee & Thornton. Fore wing
4.547 Lobocaecilius cynara Lee & Thornton. Gonapophyses
4.548 Lobocaecilius cynara Lee & Thornton. Subgenital plate
4.549 Lobocaecilius cynara Lee & Thornton. Phallosome
4.550 Lobocaecilius cynara Lee & Thornton. Hypandrium
4.551 Phallocaecilius hirsutus (Thornton). Gonapophyses



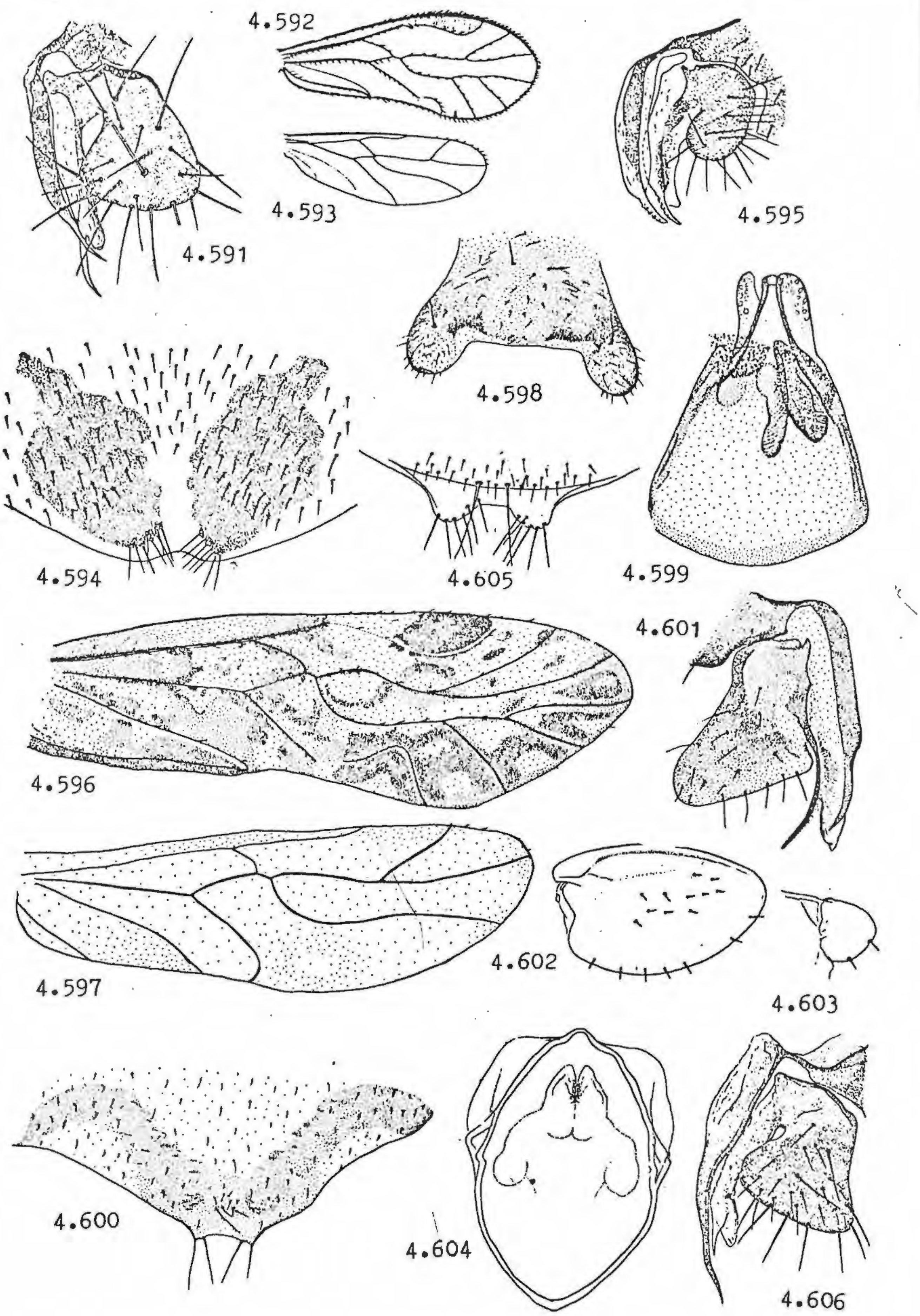
4.552 *Phallocaecilius hirsutus* (Thornton). Phallosome
4.553 *Phallocaecilius hirsutus* (Thornton). Subgenital plate
4.554 *Scytopsocopsis hirtipenna* Thornton. Fore wing
4.555 *Scytopsocopsis hirtipenna* Thornton. Phallosome
4.556 *Scytopsocopsis hirtipenna* Thornton. Hypandrium
4.557 *Trichocaecilius delicatus* Badonnel. Lacinia
4.558 *Trichocaecilius delicatus* Badonnel. Fore wing
4.559 *Trichocaecilius delicatus* Badonnel. Hypandrium
4.560 *Trichocaecilius delicatus* Badonnel. Phallosome
4.561 *Trichocaecilius delicatus* Badonnel. Subgenital plate
4.562 *Trichocaecilius delicatus* Badonnel. Gonapophyses



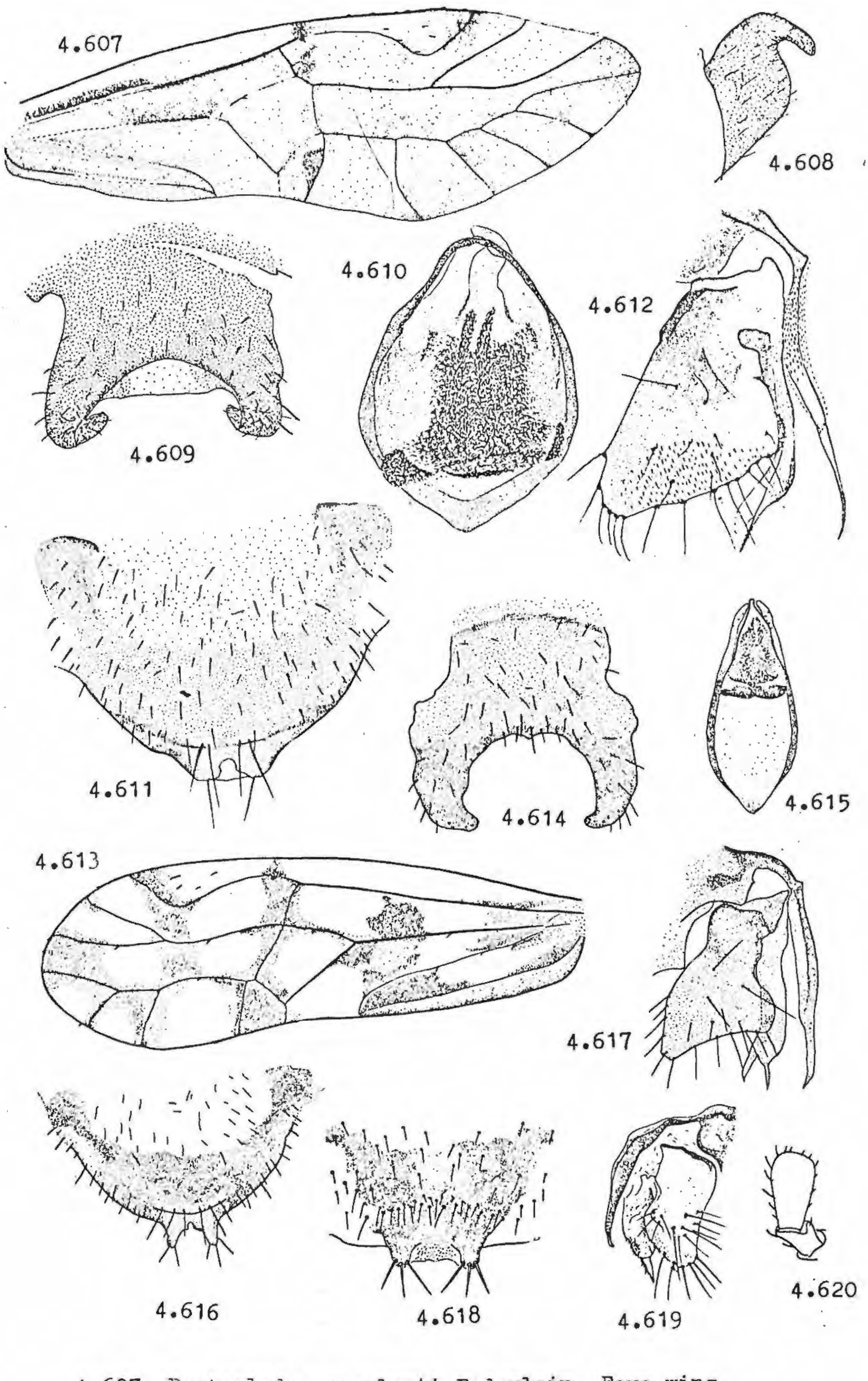
4.563 Trichopsocus acuminatus Badonnel. Fore wing
4.564 Trichopsocus acuminatus Badonnel. Hind wing
4.565 Trichopsocus dalii McLachlan. Epiproct ♀
4.566 Trichopsocus kolosvaryi Danks. Phallosome
4.567 Trichopsocus acuminatus Badonnel. Gonapophyses
4.568 Archipsocus corbetae Smithers. Gonapophyses
4.569 Archipsocus corbetae Smithers. Lacinia
4.570 Archipsocus corbetae Smithers. Fore wing
4.571 Archipsocus corbetae Smithers. Hind wing
4.572 Archipsocus corbetae Smithers. Phallosome
4.573 Archipsocus corbetae Smithers. Paraproct
4.574 Archipsocopsis intermedius Smithers. Phallosome



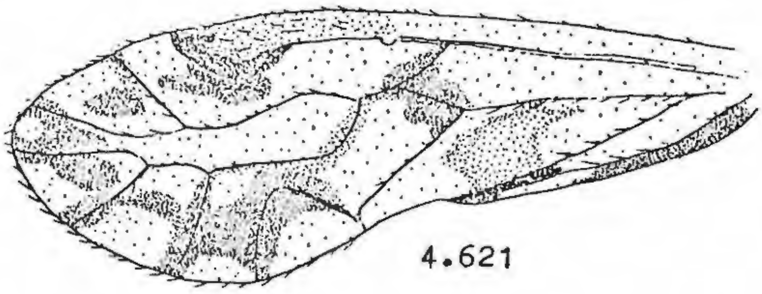
4.575 Nepiomorpha crucifera Pearman. Fore wing
4.576 Nepiomorpha annulata Badonnel. Phallosome
4.577 Nepiomorpha crucifera Pearman. Subgenital plate
4.578 Nepiomorpha crucifera Pearman. Gonapophyses
4.579 Paedomorpha gayi Smithers. Fore wing
4.580 Paedomorpha gayi Smithers. Paraproct
4.581 Paedomorpha gayi Smithers. Subgenital plate
4.582 Paedomorpha gayi Smithers. Gonapophyses
4.583 Palmicola aphrodite Mockford. Fore wing
4.584 Palmicola aphrodite Mockford. Paraproct
4.585 Palmicola aphrodite Mockford. Phallosome
4.586 Palmicola aphrodite Mockford. Subgenital plate
4.587 Palmicola aphrodite Mockford. Gonapophyses
4.588 Reuterella helvimacula (Enderlein). Fore wing
4.589 Reuterella helvimacula (Enderlein). Hind wing
4.590 Reuterella helvimacula (Enderlein). Subgenital plate



4.591 Reuterella helvimacula (Enderlein). Gonapophyses
4.592 Pseudopsocus fusciceps (Reuter). Fore wing
4.593 Pseudopsocus fusciceps (Reuter). Hind wing
4.594 Pseudopsocus rostocki Kolbe. Subgenital plate
4.595 Pseudopsocus rostocki Kolbe. Gonapophyses
4.596 Spilopsocus ruidus Smithers. Fore wing
4.597 Spilopsocus ruidus Smithers. Hind wing
4.598 Spilopsocus ruidus Smithers. Hypandrium
4.599 Spilopsocus ruidus Smithers. Phallosome
4.600 Spilopsocus ruidus Smithers. Subgenital plate
4.601 Spilopsocus ruidus Smithers. Gonapophyses
4.602 Antarctopsocus jeanneli Badonnel. Fore wing
4.603 Antarctopsocus jeanneli Badonnel. Hind wing
4.604 Antarctopsocus jeanneli Badonnel. Phallosome
4.605 Antarctopsocus jeanneli Badonnel. Subgenital plate
4.606 Antarctopsocus jeanneli Badonnel. Gonapophyses



4.607 Pentacladus eucalypti Enderlein. Fore wing
4.608 Pentacladus eucalypti Enderlein. Hypandrium
4.609 Pentacladus eucalypti Enderlein. Hypandrium
4.610 Pentacladus eucalypti Enderlein. Phallosome
4.611 Pentacladus eucalypti Enderlein. Subgenital plate
4.612P Pentacladus eucalypti Enderlein. Gonapophyses
4.613 Propsocus pulchripennis (Perkins). Fore wing
4.614 Propsocus pulchripennis (Perkins). Hypandrium
4.615 Propsocus pulchripennis (Perkins). Phallosome
4.616 Propsocus pulchripennis (Perkins). Subgenital plate
4.617 Propsocus pulchripennis (Perkins). Gonapophyses
4.618 Cuneopalpus cyanops (Rostock). Subgenital plate
4.619 Cuneopalpus cyanops (Rostock). Gonapophyses
4.620 Cuneopalpus cyanops (Rostock). Palp apex



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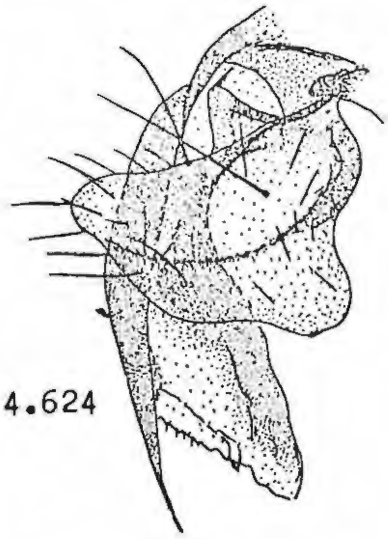

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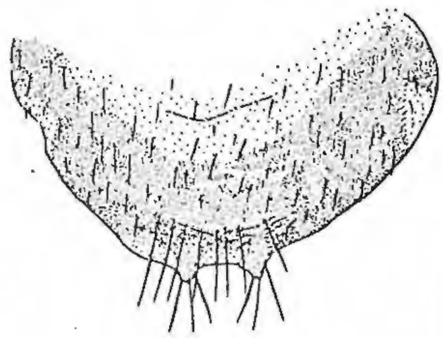

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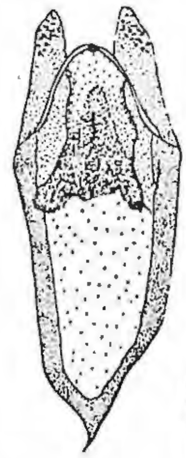

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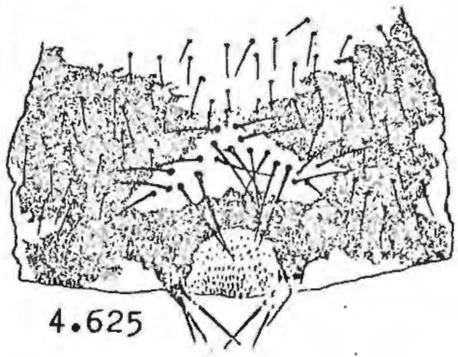

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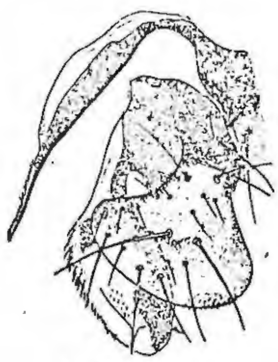

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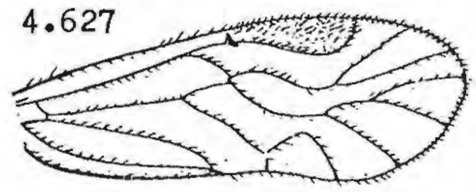

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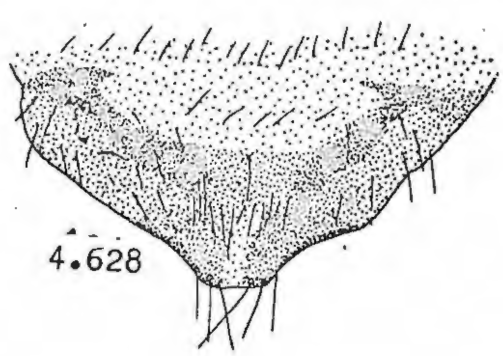

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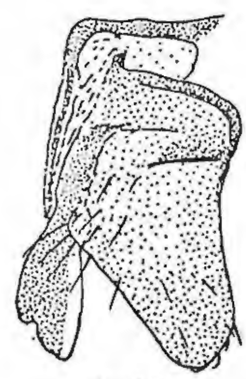

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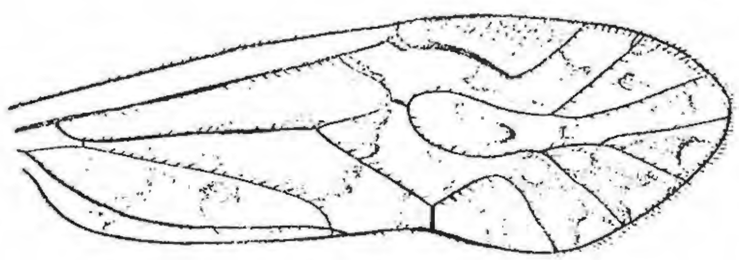

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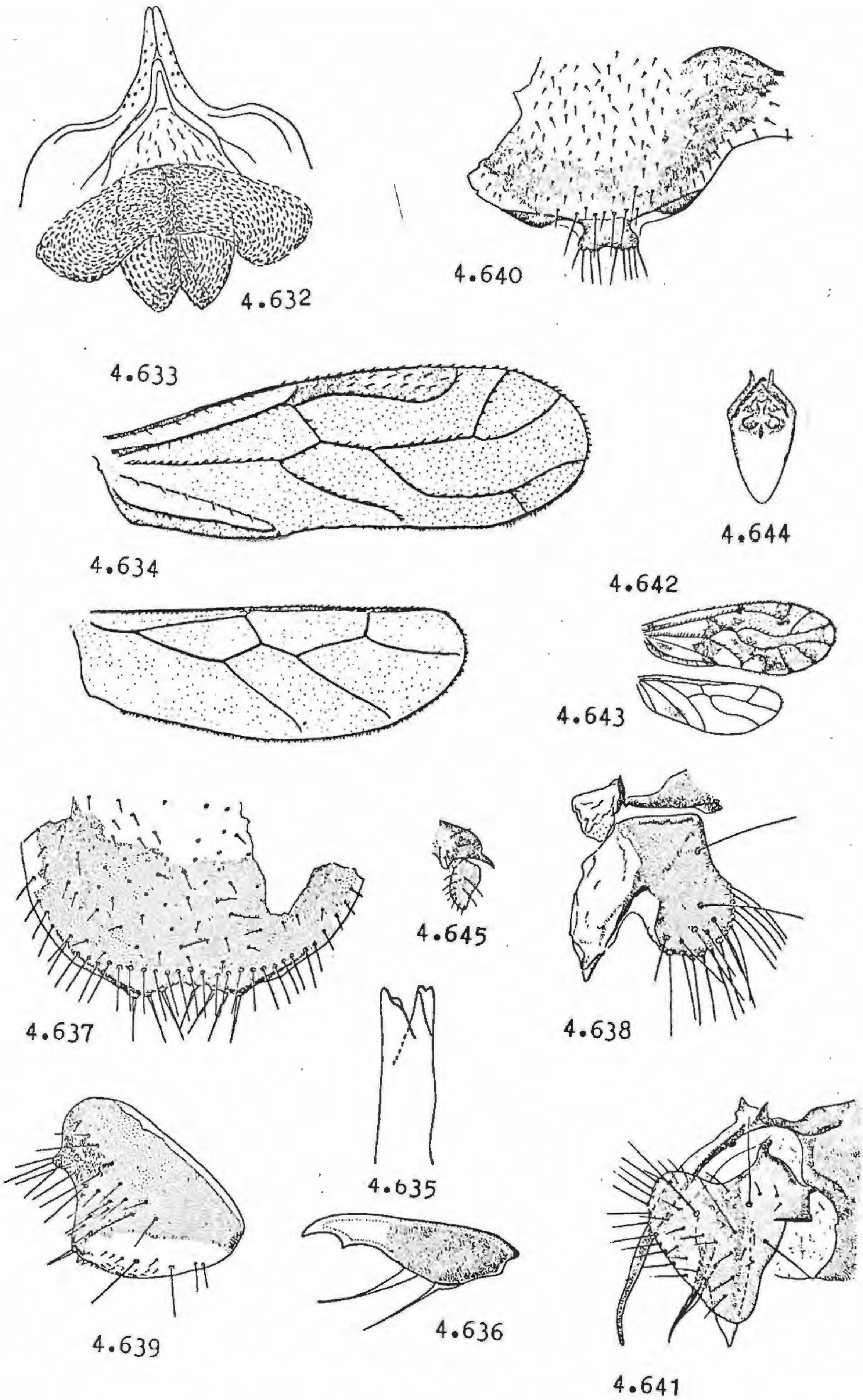
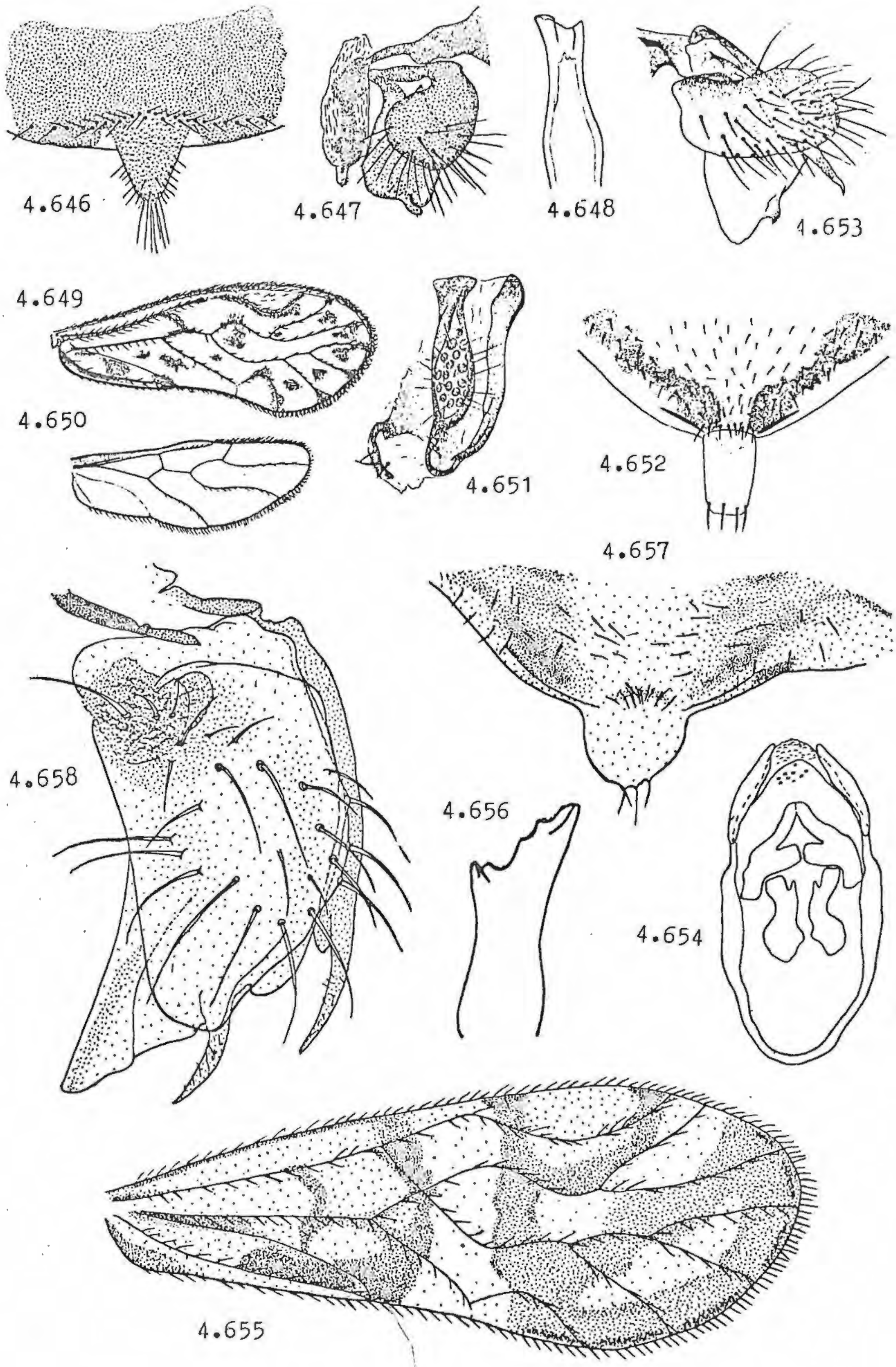
4.621 Elipsocus alettae Smithers. Fore wing
4.622 Elipsocus mbizianus Smithers. Phallosome
4.623 Elipsocus alettae Smithers. Subgenital plate
4.624 Elipsocus alettae Smithers. Gonapophyses
4.625 Hemineura hispanica (Enderlein). Subgenital plate
4.626 Hemineura hispanica (Enderlein). Gonapophyses
4.627 Kilauella vinosa (McLachlan). Fore wing
4.628 Drymopsocus brunneus Smithers. Subgenital plate
4.629 Drymopsocus brunneus Smithers. Gonapophyses
4.630 Palistreptus inconstans (Perkins).Fore wing
4.631 Lesneia stuckenbergi Badonnel. Lacinia



4.632 Lesneia stuckenbergi Badonnel. Phallosome
4.633 Lenkoella neotropica Machado-Allison & Papevero. Fore wing
4.634 Lenkoella neotropica Machado-Allison & Papevero. Hind wing
4.635 Roesleria chilensis Badonnel. Lacinia
4.636 Roesleria chilensis Badonnel. Claw
4.637 Roesleria chilensis Badonnel. Subgenital plate
4.638 Roesleria chilensis Badonnel. Gonapophyses
4.639 Roesleria chilensis Badonnel. Paraproct
4.640 Nothopsocus oxyurus Badonnel. Subgenital plate
4.641 Nothopsocus oxyurus Badonnel. Gonapophyses
4.642 Graphocaecilius interpretatus Roesler. Fore wing
4.643 Graphocaecilius interpretatus Roesler. Hind wing
4.644 Graphocaecilius interpretatus Roesler. Phallosome
4.645 Graphocaecilius interpretatus Roesler. Gonapophyses



4.646 *Psoculus neglectus* (Roesler). Subgenital plate
4.647 *Psoculus neglectus* (Roesler). Gonapophyses
4.648 *Philotarsus flaviceps* (Stephens). Lacinia
4.649 *Philotarsus flaviceps* (Stephens). Fore wing
4.650 *Philotarsus flaviceps* (Stephens). Hind wing
4.651 *Philotarsus flaviceps* (Stephens). Paraproct
4.652 *Philotarsus flaviceps* (Stephens). Subgenital plate
4.653 *Philotarsus flaviceps* (Stephens). Gonapophyses
4.654 *Philotarsus kwakiutl* Mockford. Phallosome
4.655 *Zelandopsocus formosellus* Tillyard. Fore wing
4.656 *Zelandopsocus formosellus* Tillyard. Lacinia
4.657 *Zelandopsocus formosellus* Tillyard. Subgenital plate
4.658 *Zelandopsocus formosellus* Tillyard. Gonapophyses

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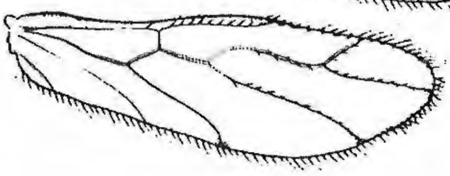
4.661



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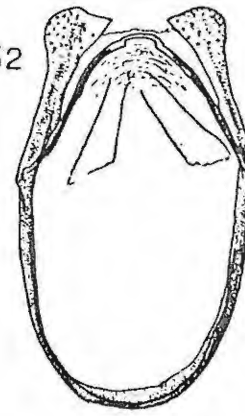

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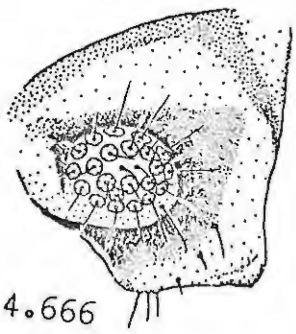

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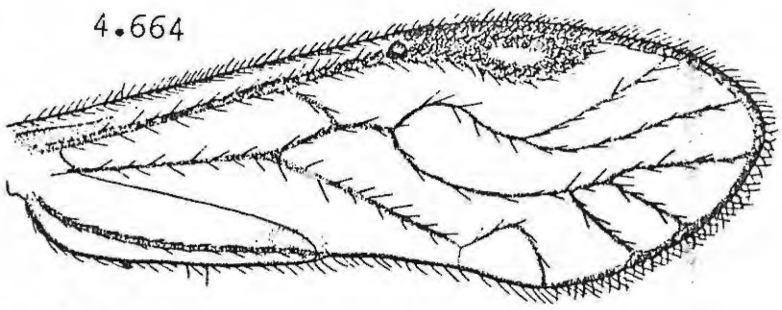

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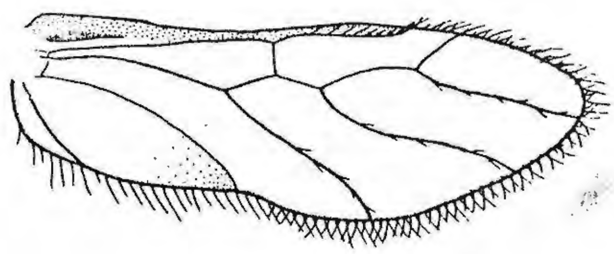

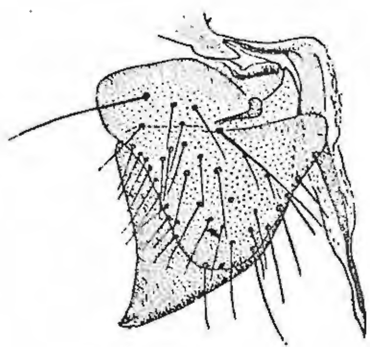

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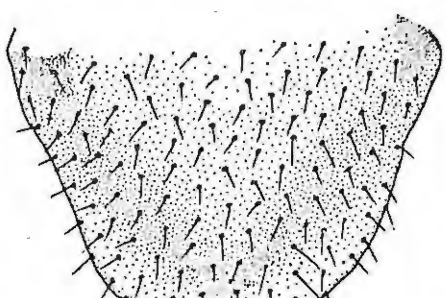

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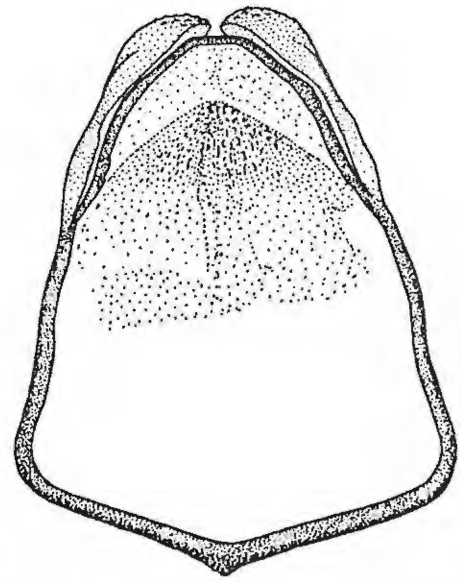
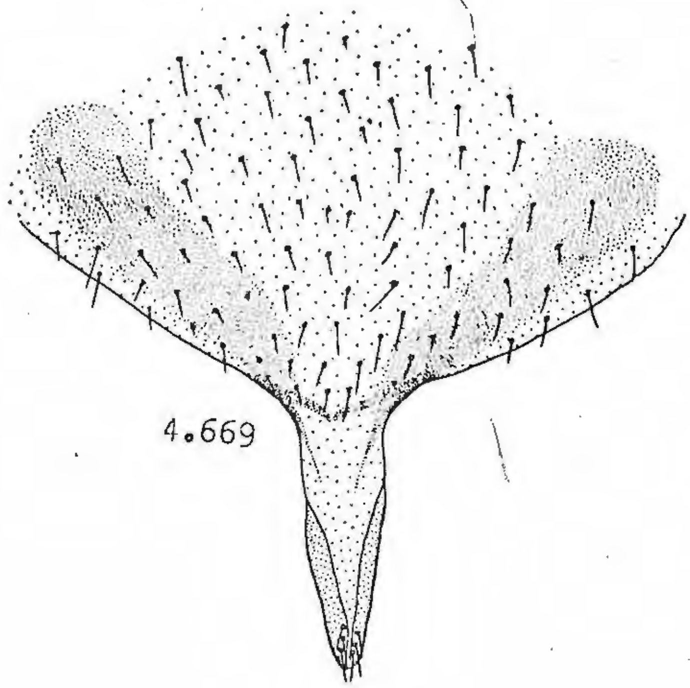


4.668

4.659 Aaroniella montana Badonnel. Lacinia
4.660 Aaroniella montana Badonnel. Fore wing
4.661 Aaroniella montana Badonnel. Hind wing
4.662 Aaroniella montana Badonnel. Phallosome
4.663 Aaroniella madecassa Badonnel. Gonapophyses
4.664 Haplophallus orientalis Thornton. Fore wing
4.665 Haplophallus orientalis Thornton. Hind wing
4.666 Haplophallus orientalis Thornton. Paraproct
4.667 Haplophallus orientalis Thornton. Hypandrium
4.668 Haplophallus orientalis Thornton. Phallosome



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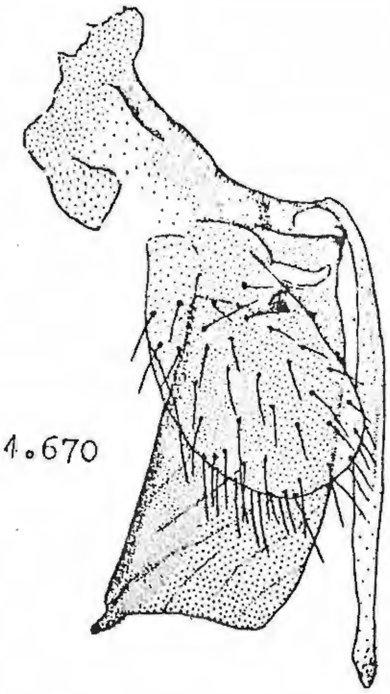

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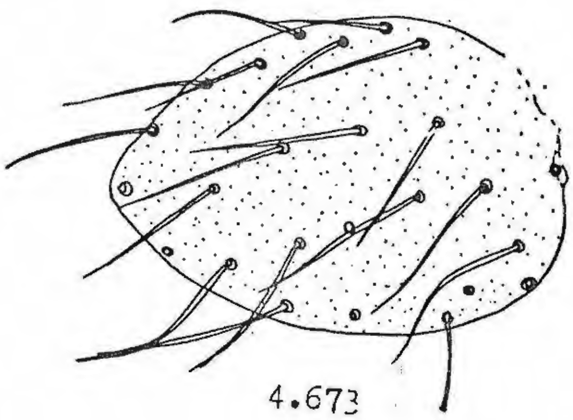

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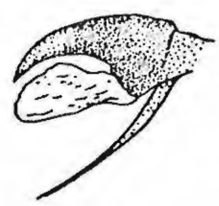

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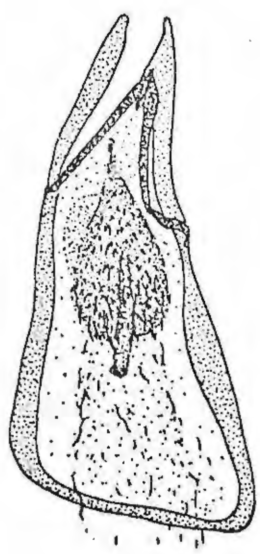

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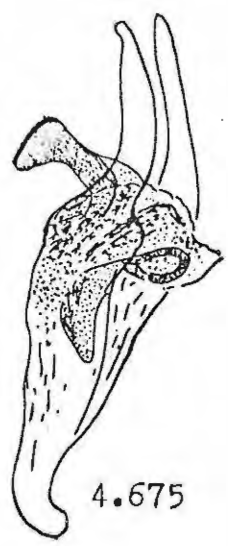

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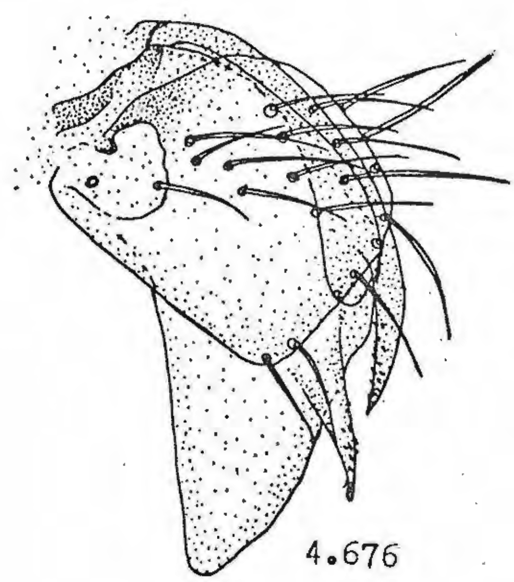

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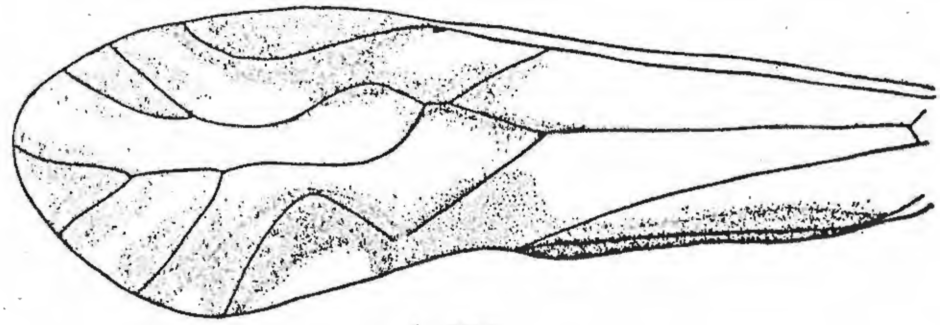
4.669 *Haplophallus orientalis* Thornton. Subgenital plate
4.670 *Haplophallus orientalis* Thornton. Gonapophyses
4.671 *Austropsocus insularis* Smithers. Lacinia
4.672 *Austropsocus insularis* Smithers. Claw
4.673 *Austropsocus insularis* Smithers. Fore wing
4.674 *Austropsocus insularis* Smithers. Phallosome
4.675 *Austropsocus insularis* Smithers. Phallosome
4.676 *Austropsocus insularis* Smithers. Gonapophyses



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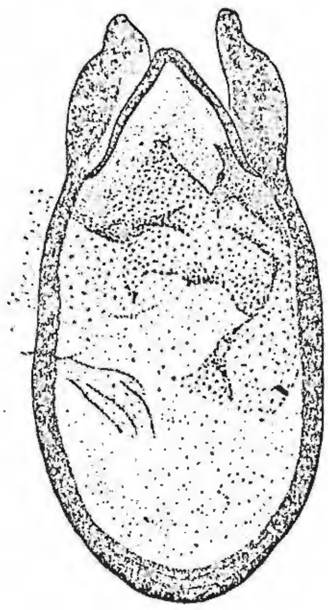

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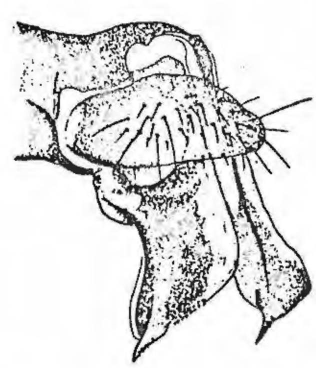

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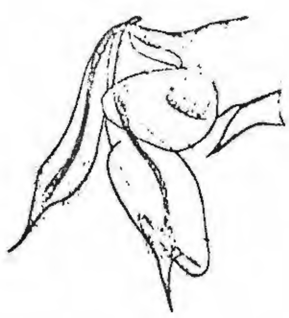

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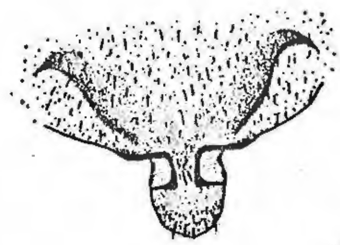

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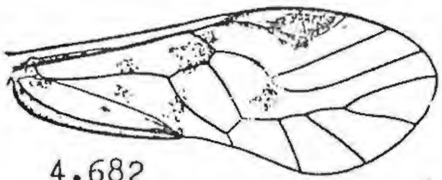
4.677 Mesopsocus distinctus Smithers. Fore wing
4.678 Mesopsocus distinctus Smithers. Phallosome
4.679 Mesopsocus shiffi Smithers. Subgenital plate
4.680 Mesopsocus unipunctatus (Muller). Gonapophyses
4.681 Hexacyrtoma capensis Enderlein. Gonapophyses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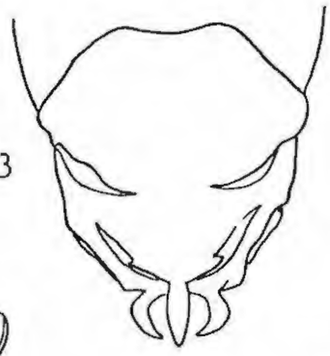
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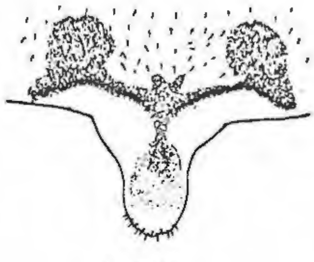
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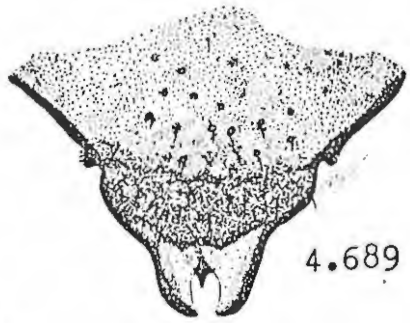
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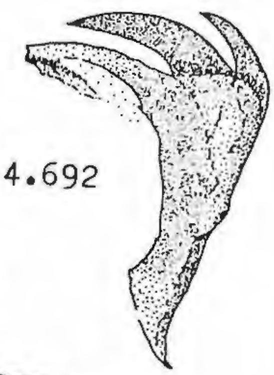
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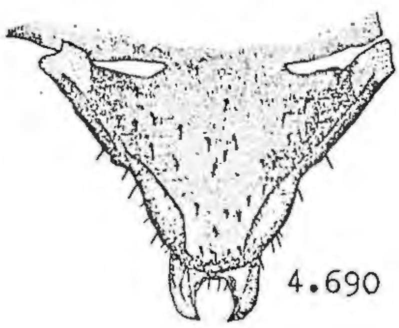
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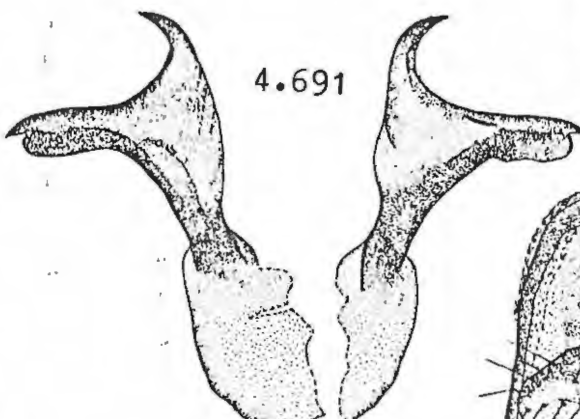
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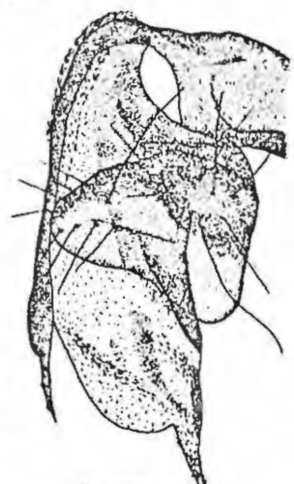
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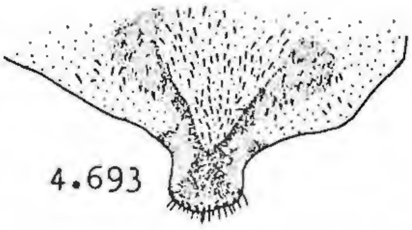
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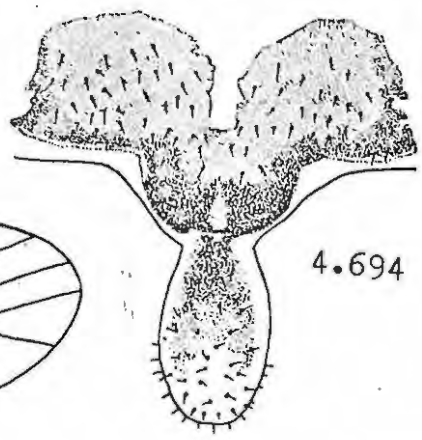
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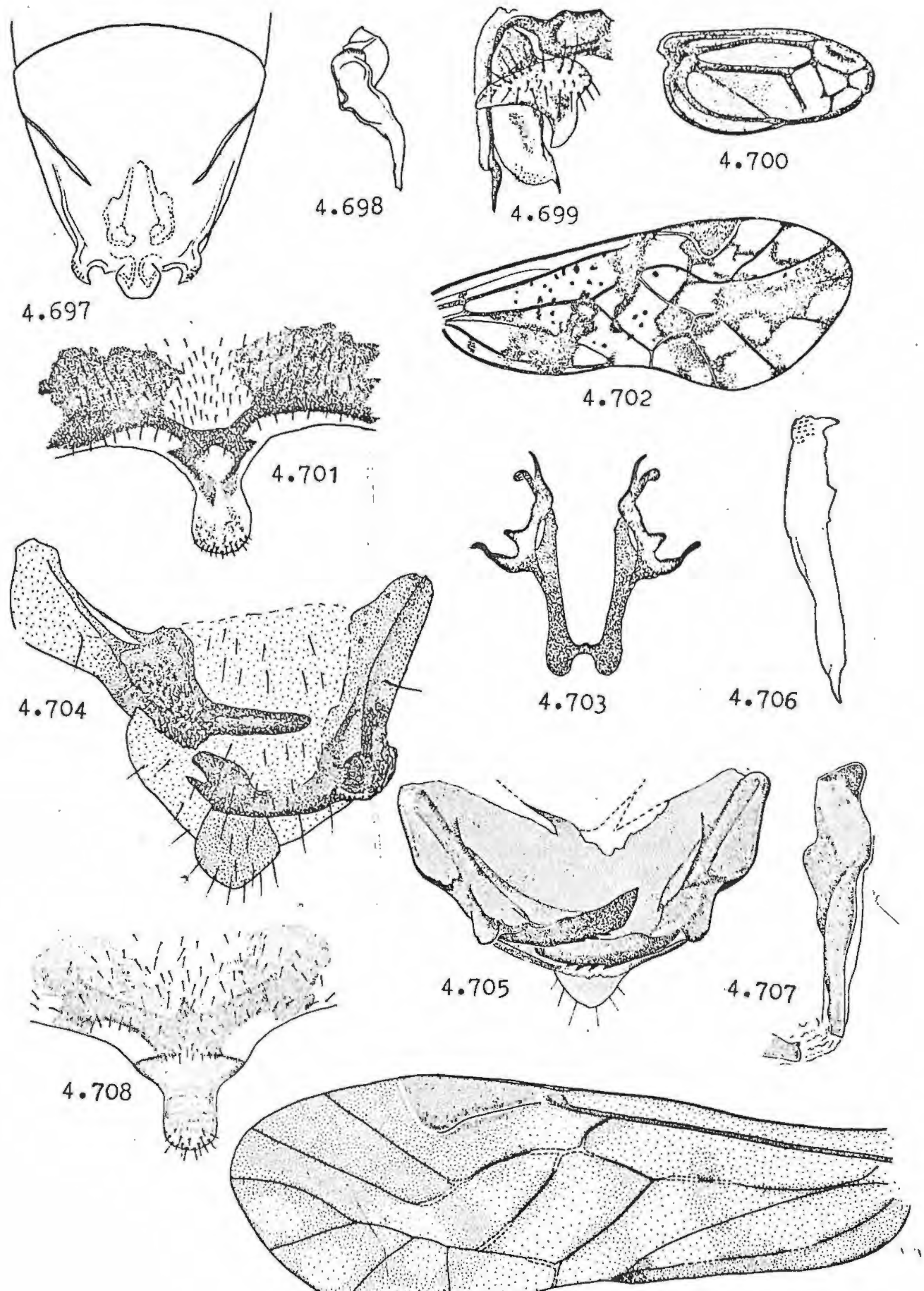
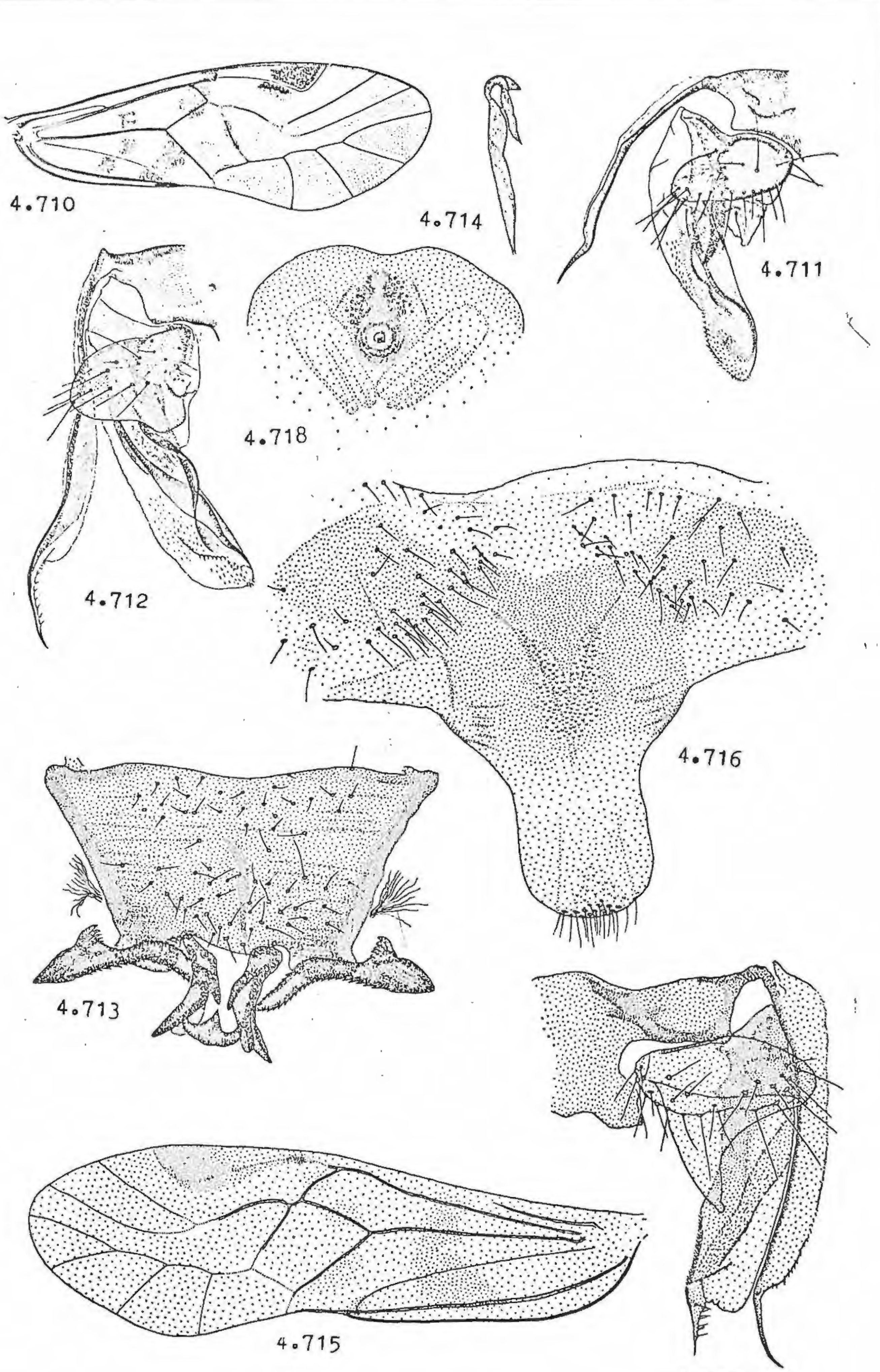
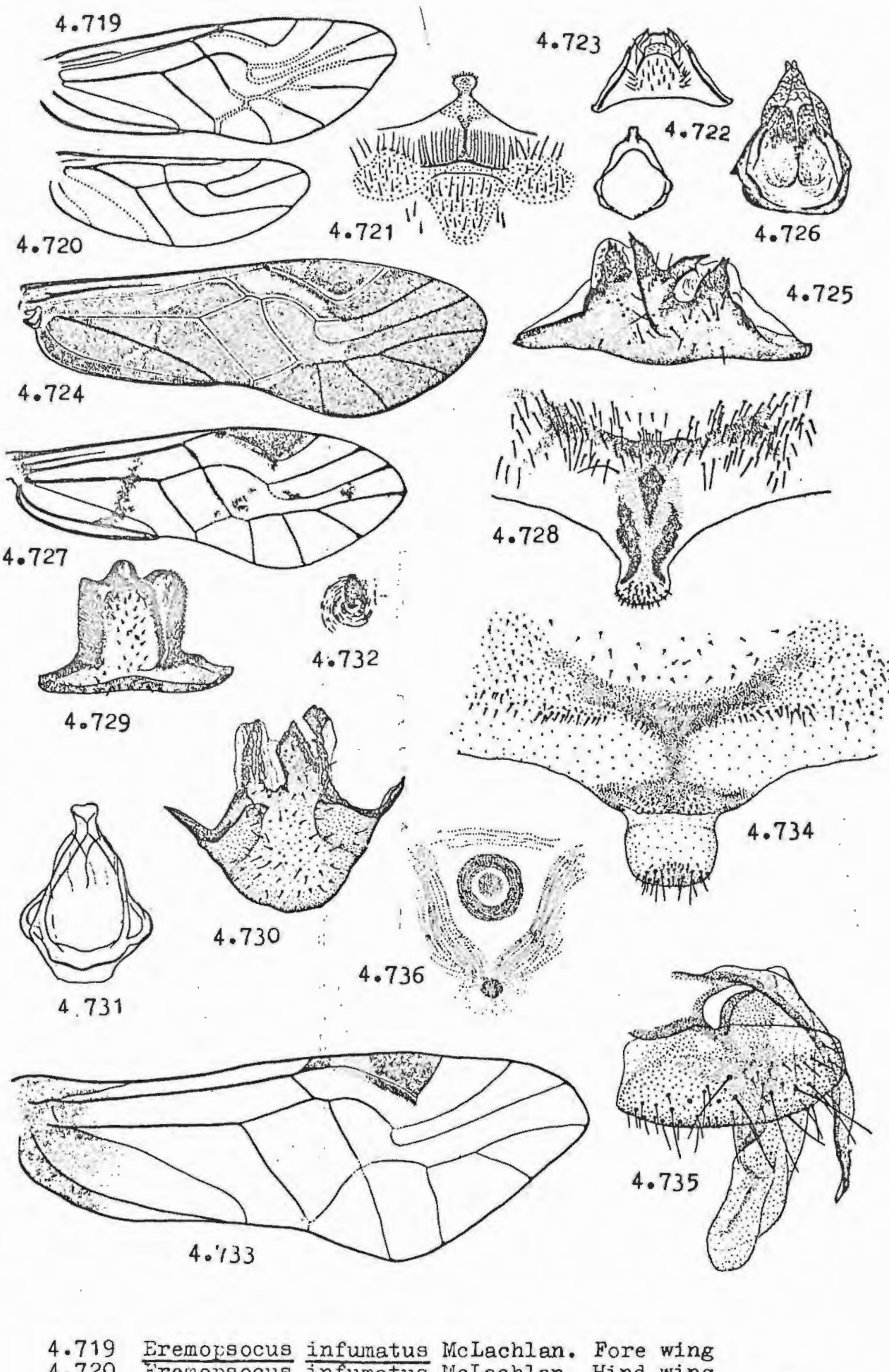
4.682 *Amphigerontia bifasciata* (Latreille). Fore wing
4.683 *Amphigerontia bifasciata* (Latreille). Hypandrium
4.684 *Amphigerontia bifasciata* (Latreille). Parameres
4.685 *Amphigerontia bifasciata* (Latreille). Subgenital plate
4.686 *Amphigerontia bifasciata* (Latreille). Gonapophyses
4.687 *Amphigerontia bifasciata* (Latreille). Spermathecal entrance
4.688 *Blaste polioptera* Smithers. Fore wing
4.689 *Blaste polioptera* Smithers. Hypandrium
4.690 *Blaste stuckenbergi* Smithers. Hypandrium
4.691 *Blaste bicuspis* Smithers. Paramere
4.692 *Blaste stuckenbergi* Smithers. Paramere
4.693 *Blaste stuckenbergi* Smithers. Subgenital plate
4.694 *Blaste machadoi* Badonnel. Subgenital plate
4.695 *Blaste stuckenbergi* Smithers. Gonapophyses
4.696 *Neopsocopsis pyrenaicus* Badonnel. Fore wing ♂



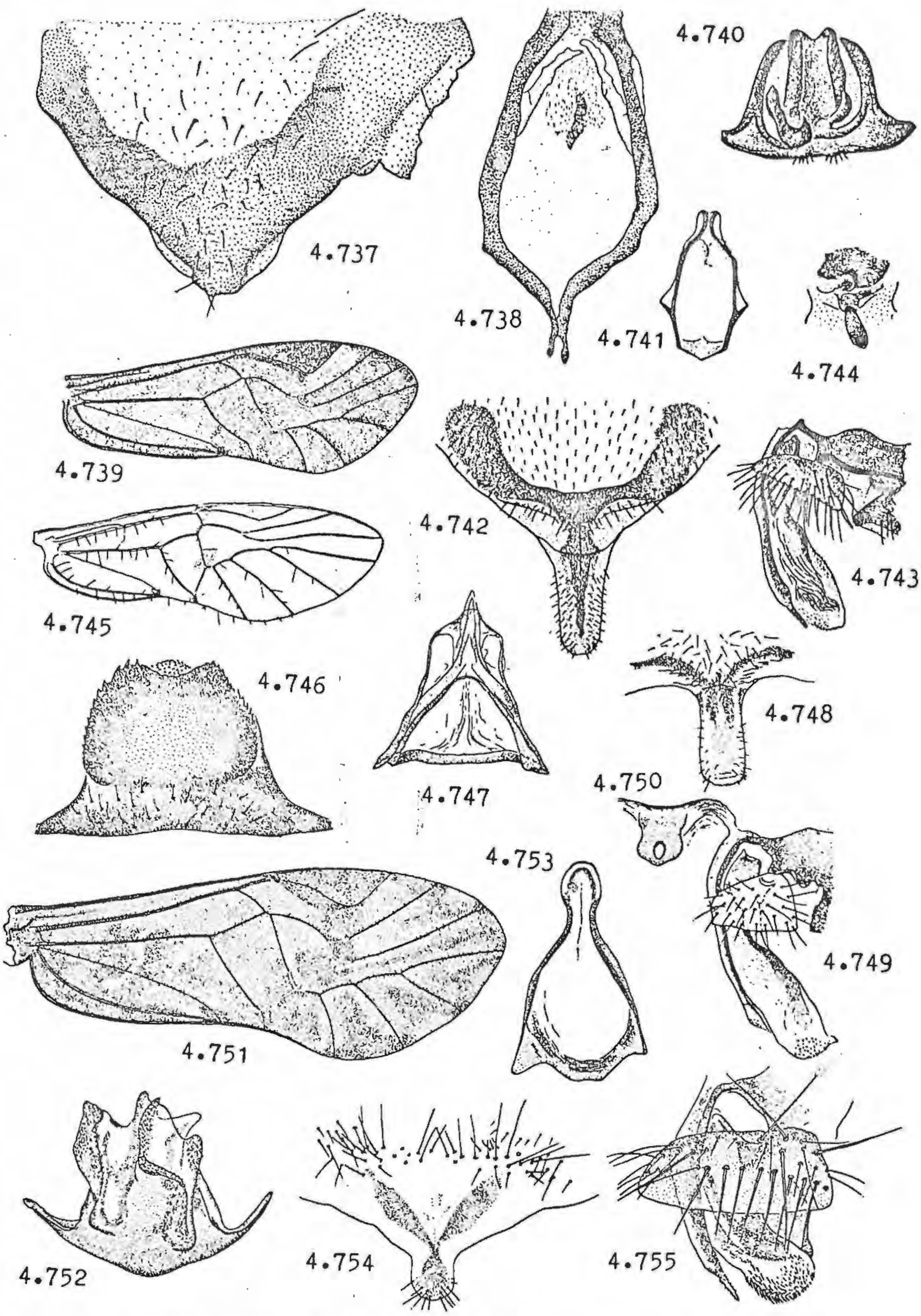
4.697 *Neopsocopsis pyrenaicus* Badonnel. Hypandrium
4.698 *Neopsocopsis pyrenaicus* Badonnel. Parameres
4.699 *Neopsocopsis pyrenaicus* Badonnel. Gonapophyses
4.700 *Neopsocopsis pyrenaicus* Badonnel. Fore wing ♀
4.701 *Neopsocopsis pyrenaicus* Badonnel. Subgenital plate
4.702 *Elaphopsocus glaphyrostigma* Roesler. Fore wing
4.703 *Elaphopsocus glaphyrostigma* Roesler. Parameres
4.704 *Blastopsocidus strictus* (Smithers). Hypandrium
4.705 *Blastopsocidus montanus* Badonnel. Hypandrium
4.706 *Blastopsocidus strictus* (Smithers). Paramere
4.707 *Blastopsocidus montanus* Badonnel. Paramere
4.708 *Blastopsocidus montanus* Badonnel. Subgenital plate
4.709 *Blastopsocidus strictus* (Smithers). Fore wing



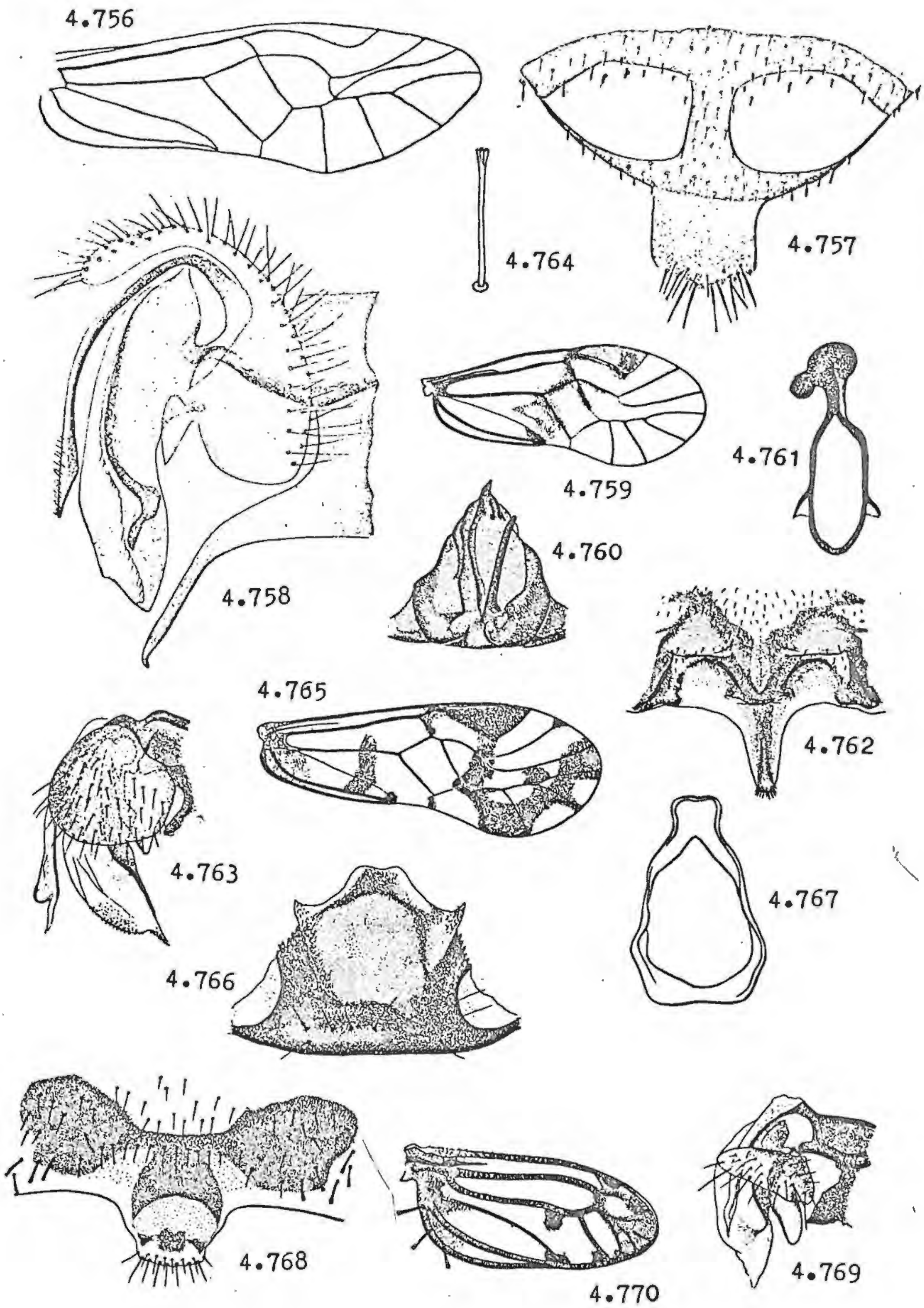
4.710 Blastopsocidus montanus Badonnel. Fore wing
4.711 Blastopsocidus montanus Badonnel. Gonapophyses
4.712 Blastopsocidus actus Badonnel. Gonapophyses
4.713 Neoblaste papillosus Thornton. Hypandrium
4.714 Neoblaste papillosus Thornton. Paramere
4.715 Neoblaste papillosus Thornton. Fore wing
4.716 Neoblaste papillosus Thornton. Subgenital plate
4.717 Neoblaste papillosus Thornton. Gonapophyses
4.718 Neoblaste papillosus Thornton. Spermathecal entrance



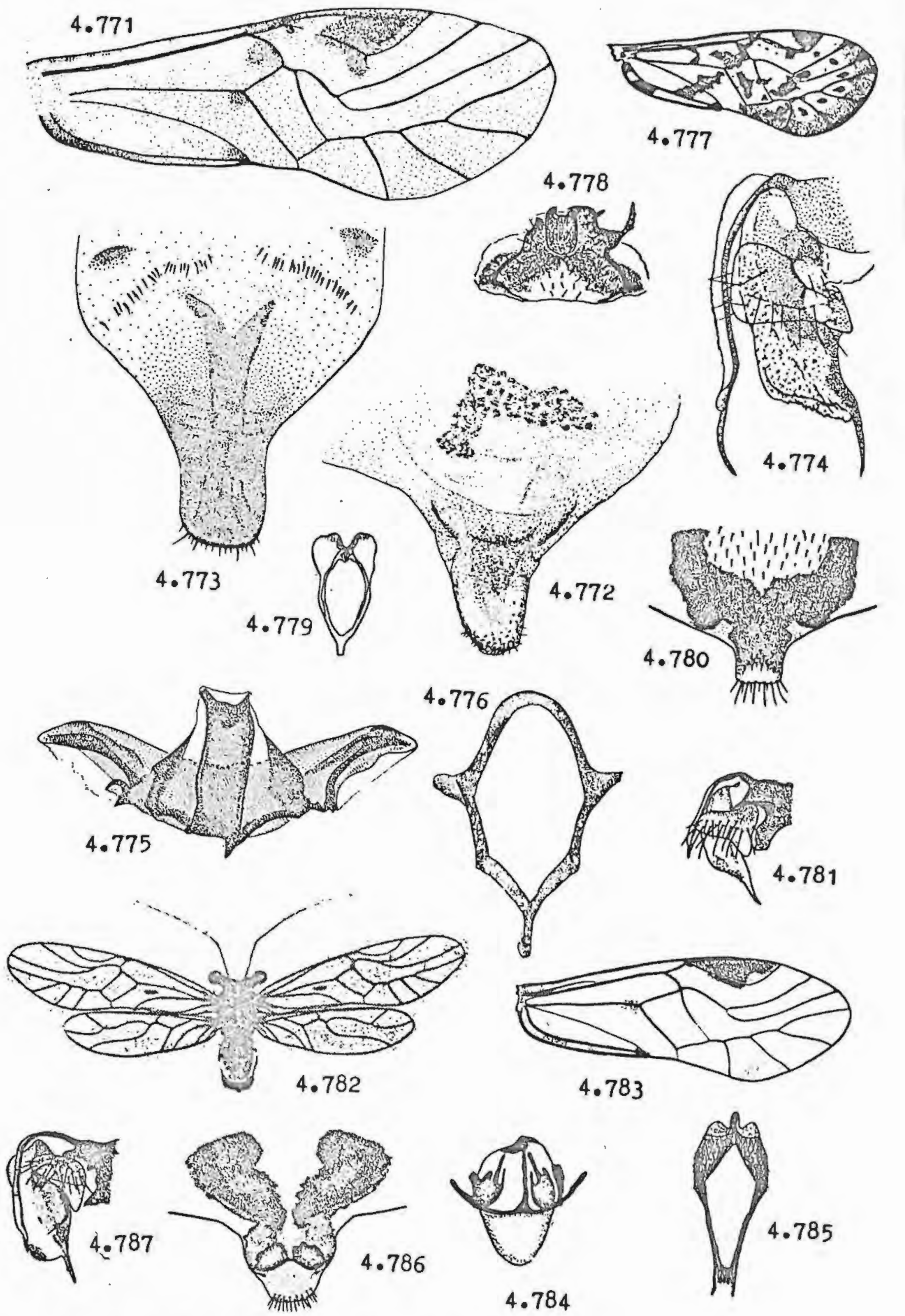
4.719 Eremopsocus infumatus McLachlan. Fore wing
4.720 Eremopsocus infumatus McLachlan. Hind wing
4.721 Eremopsocus infumatus McLachlan. Subgenital plate
4.722 Eremopsocus infumatus McLachlan. Phallosome
4.723 Eremopsocus infumatus McLachlan. Hypandrium
4.724 Cerastipsocus iguazuensis Williner. Fore wing
4.725 Cerastipsocus iguazuensis Williner. Hypandrium
4.726 Cerastipsocus iguazuensis Williner. Phallosome
4.727 Psococerastis gibbosa (Sulzer). Fore wing
4.728 Psococerastis gibbosa (Sulzer). Subgenital plate
4.729 Psococerastis gibbosa (Sulzer). Hypandrium
4.730 Psococerastis gibbosa (Sulzer). Hypandrium
4.731 Psococerastis gibbosa (Sulzer). Phallosome
4.732 Psococerastis gibbosa (Sulzer). Spermathecal opening
4.733 Scaphopsocus phaeotherus Smithers. Fore wing
4.734 Scaphopsocus kolbei (Enderlein). Subgenital plate
4.735 Scaphopsocus kolbei (Enderlein). Gonapophyses
4.736 Scaphopsocus kolbei (Enderlein). Spermathecal opening



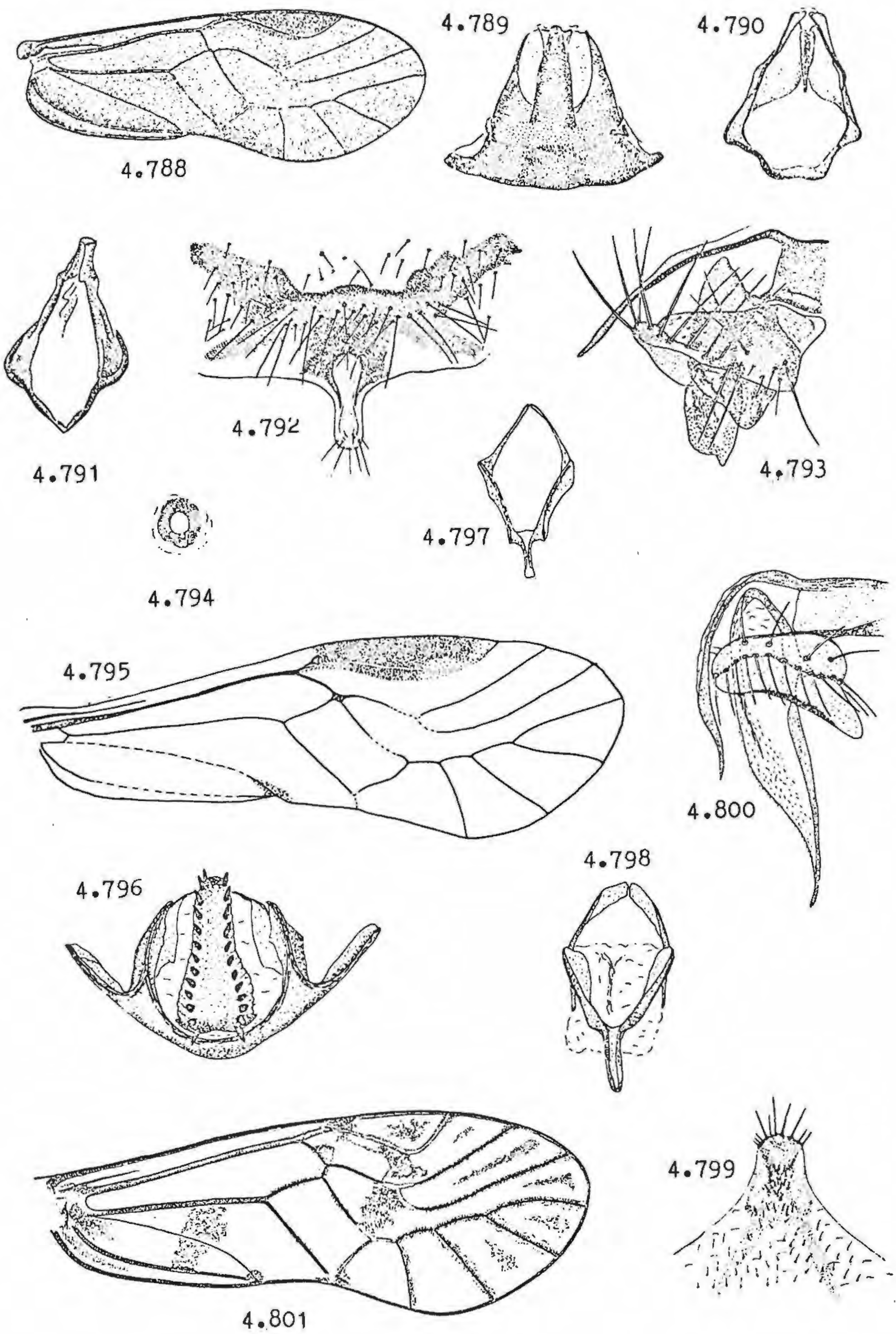
4.737 Scaphopsocus phaeotherus Smithers. Hypandrium
4.738 Scaphopsocus phaeotherus Smithers. Phallosome
4.739 Metylophorus nebulosus (Stephens). Fore wing
4.740 Metylophorus nebulosus (Stephens). Hypandrium
4.741 Metylophorus nebulosus (Stephens). Phallosome
4.742 Metylophorus nebulosus (Stephens). Subgenital plate
4.743 Metylophorus nebulosus (Stephens). Gonapophyses
4.744 Metylophorus nebulosus (Stephens). Spermathecal opening
4.745 Diplacanthoda bouvieri Enderlein. Fore wing
4.746 Diplacanthoda bouvieri Enderlein. Hypandrium
4.747 Diplacanthoda bouvieri Enderlein. Phallosome
4.748 Diplacanthoda bouvieri Enderlein. Subgenital plate
4.749 Diplacanthoda bouvieri Enderlein. Gonapophyses
4.750 Diplacanthoda bouvieri Enderlein. Spermathecal opening
4.751 Filipsocus congolensis Badonnel. Fore wing
4.752 Filipsocus congolensis Badonnel. Hypandrium
4.753 Filipsocus congolensis Badonnel. Phallosome
4.754 Filipsocus congolensis Badonnel. Subgenital plate
4.755 Filipsocus congolensis Badonnel. Gonapophyses



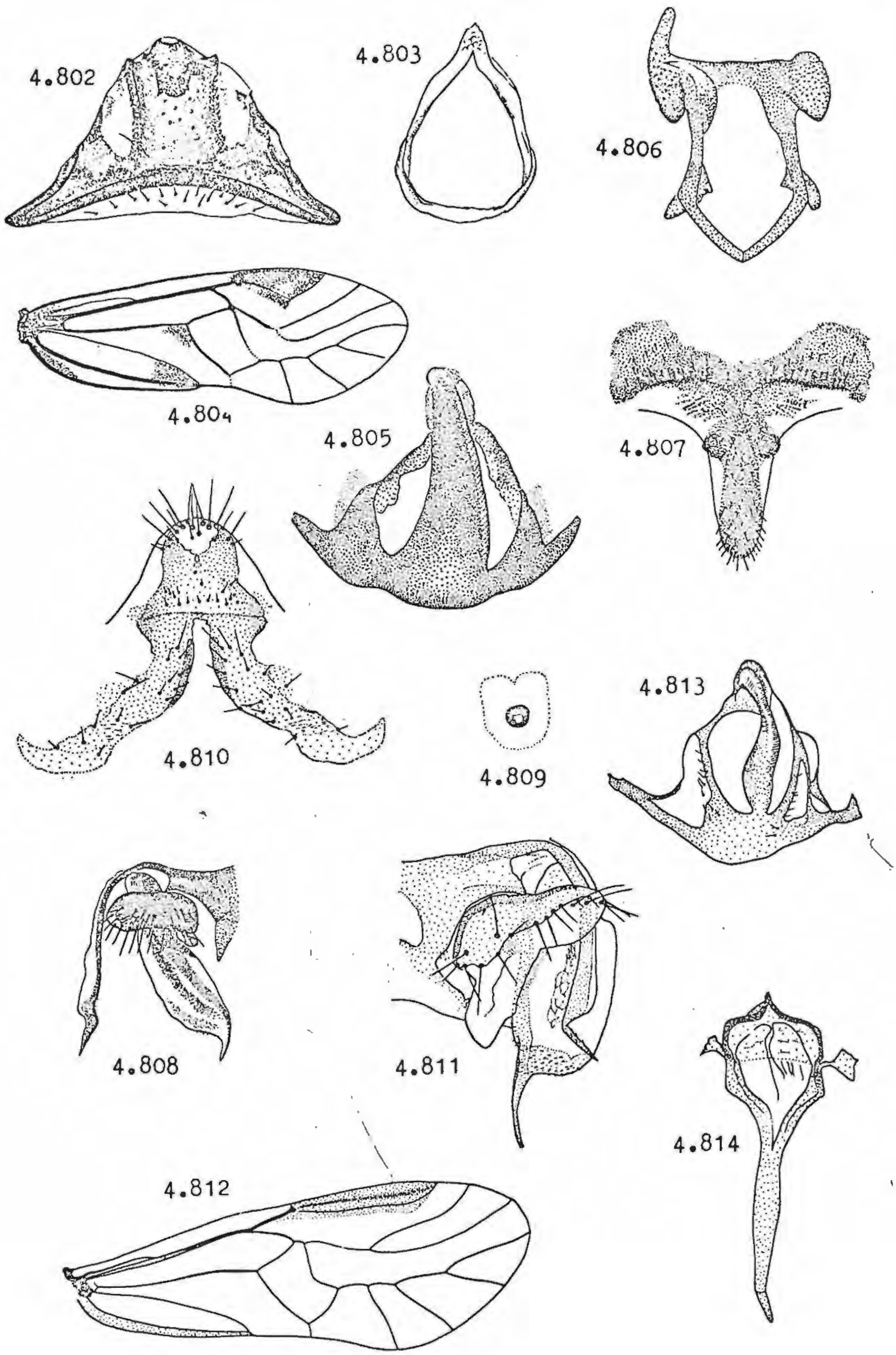
4.756 Cycetes thrysophoroides Enderlein. Fore wing
4.757 Cycetes thrysophoroides Enderlein. Subgenital plate
4.758 Cycetes thrysophoroides Enderlein. Gonapophyses
4.759 Psocus bipunctatus (Linnaeus). Fore wing
4.760 Psocus bipunctatus (Linnaeus). Hypandrium
4.761 Psocus bipunctatus (Linnaeus). Phallosome
4.762 Psocus bipunctatus (Linnaeus). Subgenital plate
4.763 Psocus bipunctatus (Linnaeus). Gonapophyses
4.764 Neopsocus rhenanus Kolbe. Glandular hair
4.765 Neopsocus rhenanus Kolbe. Fore wing ♂
4.766 Neopsocus rhenanus Kolbe. Hypandrium
4.767 Neopsocus rhenanus Kolbe. Phallosome
4.768 Neopsocus rhenanus Kolbe. Subgenital plate
4.769 Neopsocus rhenanus Kolbe. Gonapophyses
4.770 Neopsocus rhenanus Kolbe. Fore wing ♀



4.771 Ptycta longispinosa (Smithers). Fore wing
4.772 Ptycta longispinosa (Smithers). Subgenital plate
4.773 Ptycta lemniscata (Smithers). Subgenital plate
4.774 Ptycta quadrimaculata (Smithers). Gonapophyses
4.775 Ptycta longispinosa (Smithers). Hypandrium
4.776 Ptycta longispinosa (Smithers). Phallosome
4.777 Trichadenotecnum sexpunctatum (Linnaeus). Fore wing
4.778 Trichadenotecnum sexpunctatum (Linnaeus). Hypandrium
4.779 Trichadenotecnum sexpunctatum (Linnaeus). Phallosome
4.780 Trichadenotecnum sexpunctatum (Linnaeus). Subgenital plate
4.781 Trichadenotecnum sexpunctatum (Linnaeus). Gonapophyses
4.782 Steleops pedunculata Enderlein. Fore wing
4.783 Oreopsocus montanus (Kolbe). Fore wing
4.784 Oreopsocus montanus (Kolbe). Hypandrium
4.785 Oreopsocus montanus (Kolbe). Phallosome
4.786 Oreopsocus montanus (Kolbe). Subgenital plate
4.787 Oreopsocus montanus (Kolbe). Gonapophyses

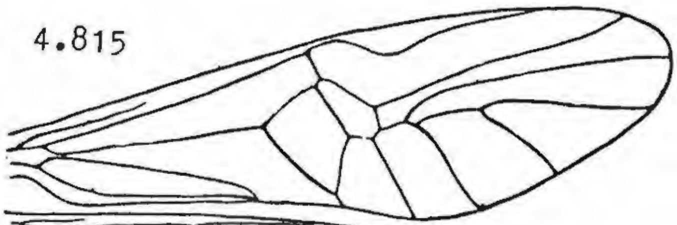


4.788 *Pearmania collarti* Badonnel. Fore wing
4.789 *Pearmania collarti* Badonnel. Hypandrium
4.790 *Pearmania collarti* Badonnel. Phallosome
4.791 *Pearmania wittei* Badonnel. Phallosome
4.792 *Pearmania rutshuruana* Badonnel. Subgenital plate
4.793 *Pearmania rutshuruana* Badonnel. Gonapophyses
4.794 *Pearmania rutshuruana* Badonnel. Spermathecal opening
4.795 *Atlantopsocus personatus* (Hagen). Fore wing
4.796 *Atlantopsocus adustus* (Hagen). Hypandrium
4.797 *Atlantopsocus personatus* (Hagen). Phallosome
4.798 *Atlantopsocus adustus* (Hagen). Phallosome
4.799 *Atlantopsocus personatus* (Hagen). Subgenital plate
4.800 *Atlantopsocus personatus* (Hagen). Gonapophyses
4.801 *Ghesquierella ealensis* Badonnel. Fore wing



4.802 Ghesquierella ealensis Badonnel. Hypandrium
4.803 Ghesquierella ealensis Badonnel. Phallosome
4.804 Hyalopsocus contrarius (Reuter). Fore wing
4.805 Hyalopsocus contrarius (Reuter). Hypandrium
4.806 Hyalopsocus contrarius (Reuter). Phallosome
4.807 Hyalopsocus contrarius (Reuter). Subgenital plate
4.808 Hyalopsocus contrarius (Reuter). Gonapophyses
4.809 Hyalopsocus contrarius (Reuter). Spermathecal opening
4.810 Camelopsocus monticolus Mockford. Subgenital plate
4.811 Camelopsocus similis Mockford. Gonapophyses
4.812 Camelopsocus similis Mockford. Fore wing
4.813 Camelopsocus monticolus Mockford. Hypandrium
4.814 Camelopsocus monticolus Mockford. Phallosome

4.815



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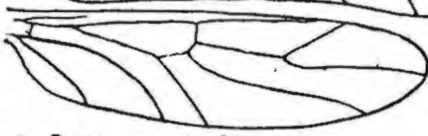

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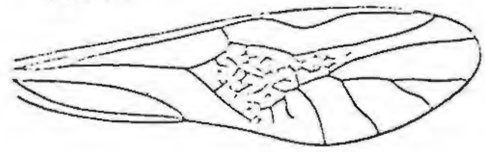

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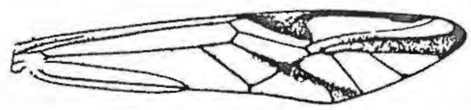

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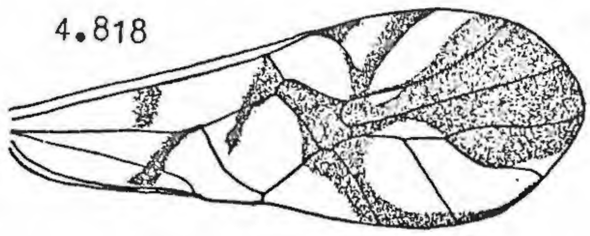
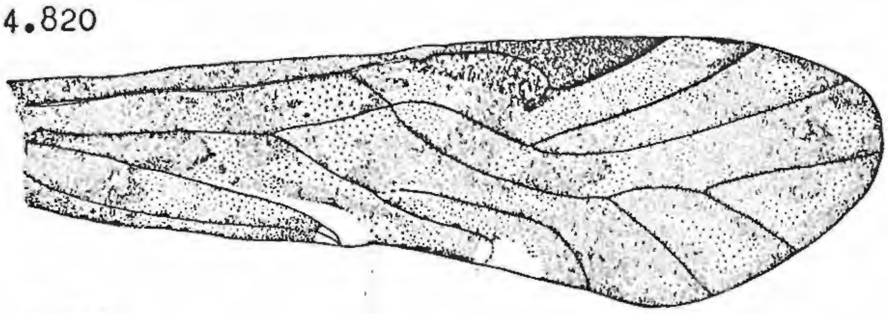


4.821

4.824

4.820



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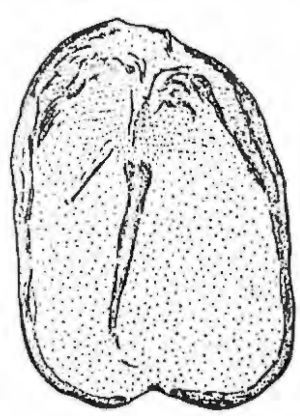

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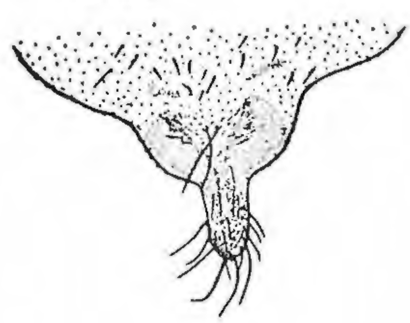
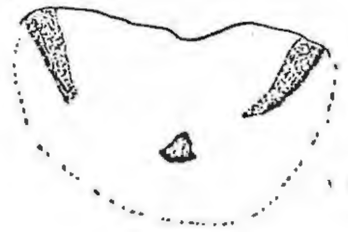
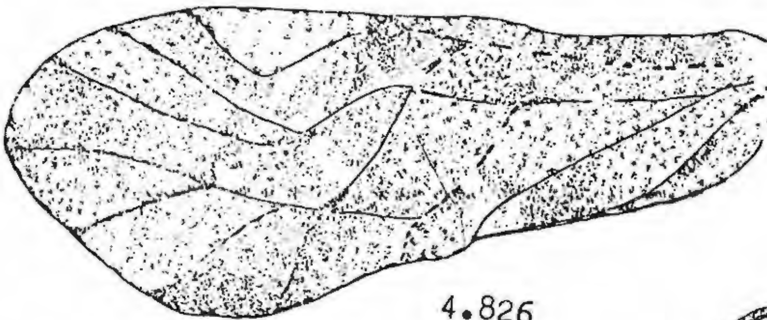


4.815 Thyrsophorus metallicus Enderlein. Fore wing
4.816 Thyrsophorus metallicus Enderlein. Hind wing
4.817 Dictyopsocus pennicornis (Burmeister). Fore wing
4.818 Thyrsopsocus pretiosus Banks. Fore wing
4.819 Thyrsopsocus cinctus (Enderlein). Fore wing
4.820 Psilopsocus mimulus Smithers. Fore wing
4.821 Psilopsocus mimulus Smithers. Lacinia
4.822 Psilopsocus mimulus Smithers. Subgenital plate
4.823 Psilopsocus mimulus Smithers. Gonapophyses
4.824 Psilopsocus mimulus Smithers. Sclerification of spermathecal opening
4.825 Psilopsocus mimulus Smithers. Phallosome

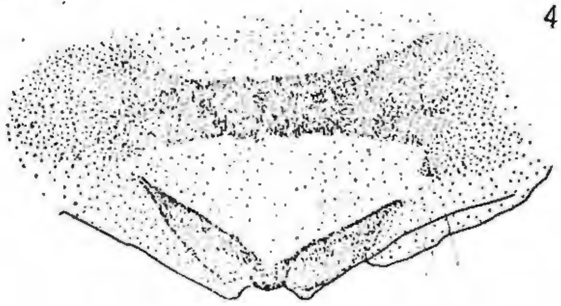
4.828





4.826

4.827



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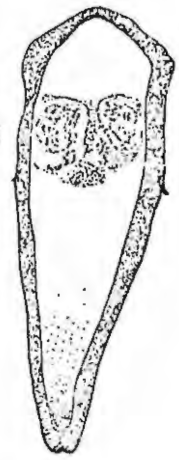
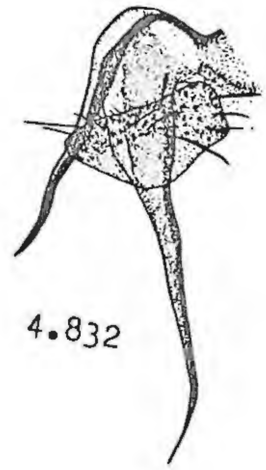
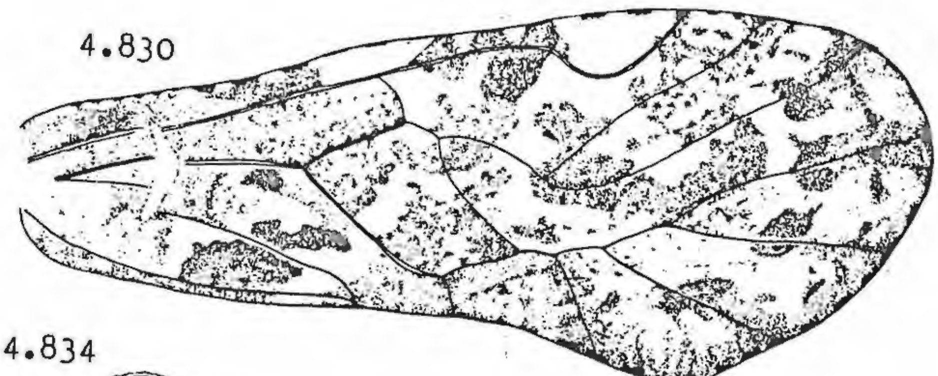




4.832

4.830



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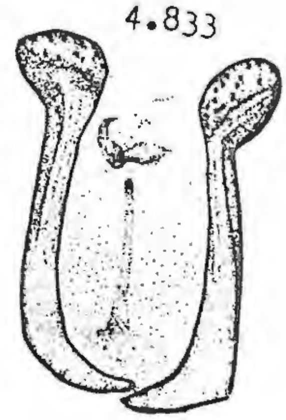

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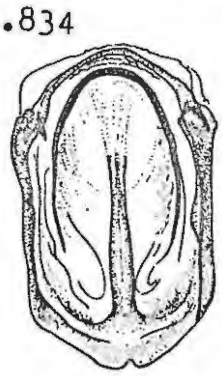

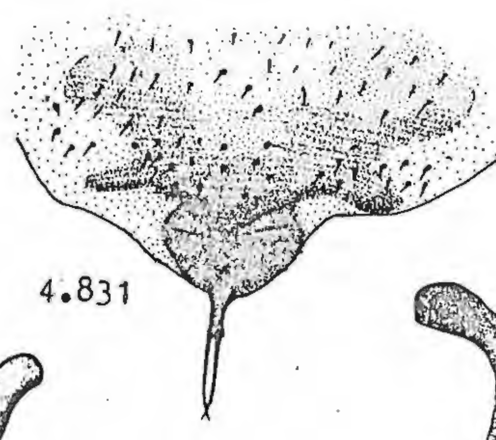

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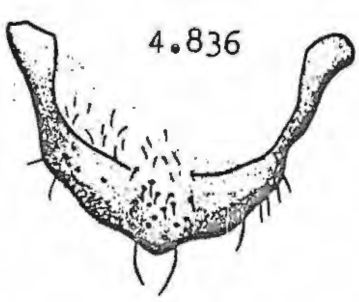
4.836



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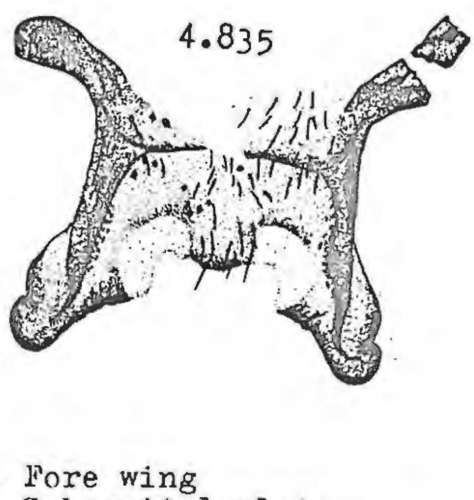
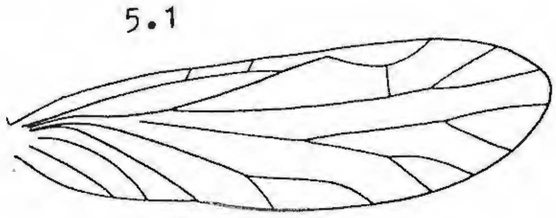


4.826 Myopsocus maxima (Smithers). Fore wing
4.827 Myopsocus maxima (Smithers). Subgenital plate
4.828 Myopsocus maxima (Smithers). Spermathecal opening
4.829 Myopsocus maxima (Smithers). Phallosome
4.830 Phlotodes corticosa Smithers. Fore wing
4.831 Phlotodes ciliifera (Smithers). Subgenital plate
4.832 Phlotodes setosa (Smithers). Gonapophyses
4.833 Phlotodes lyriifera Smithers. Phallosome
4.834 Phlotodes obscura Badonnel. Phallosome
4.835 Phlotodes speciosa (Smithers). Hypandrium
4.836 Phlotodes lyriifera Smithers. Hypandrium

5.1



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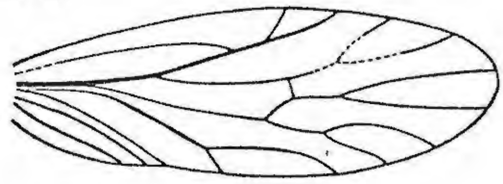

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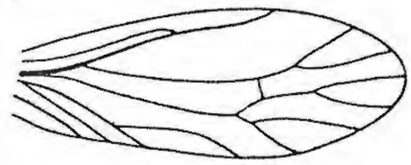

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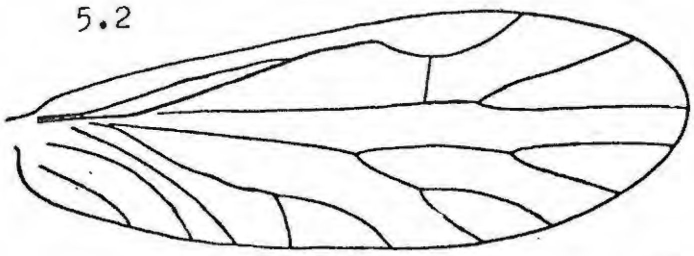

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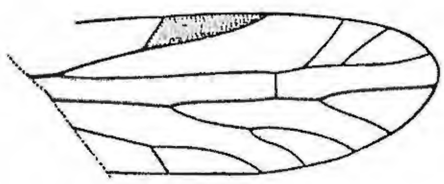

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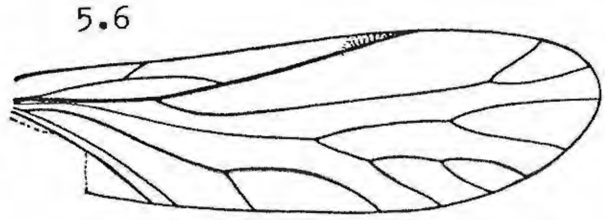

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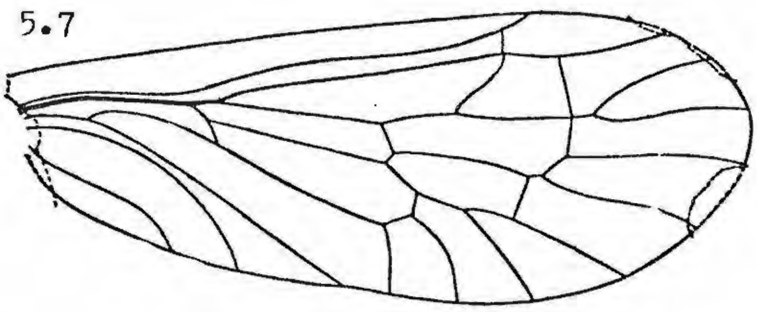

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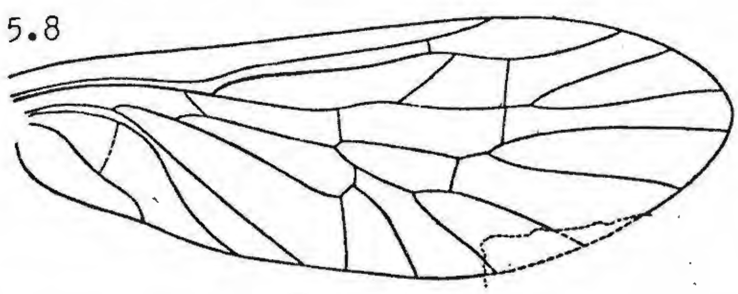

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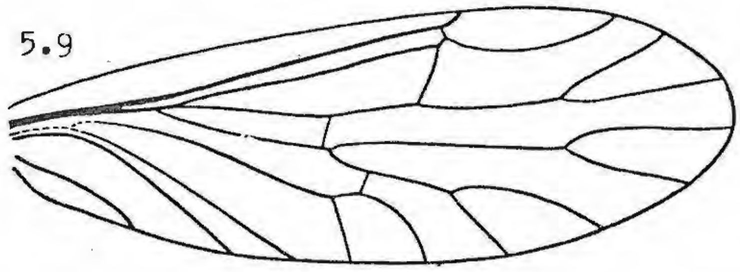
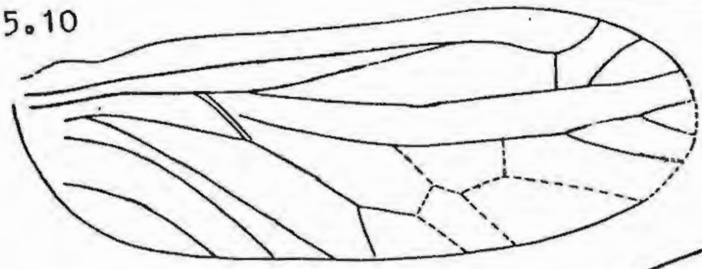


5.1 Dichentomum tinctum Tillyard. Fore wing
5.2 Dichentomum latum Carpenter. Hind wing
5.3 Austropsocidium pincombei Tillyard. Fore wing
5.4 Austropsocidium pincombei Tillyard. Hind wing
5.5 Austropsocidium stigmaticum Tillyard. Fore wing
5.6 Stenopsocidium elongatum Tillyard. Fore wing
5.7 Permopsocus latipennis Tillyard. Fore wing
5.8 Permopsocus congener Tillyard. Fore wing
5.9 Prognopsocus permianus Tillyard. Fore wing

5.10



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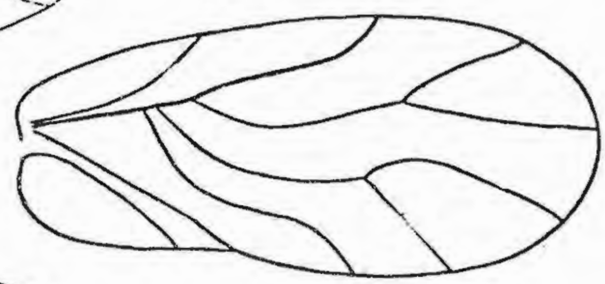

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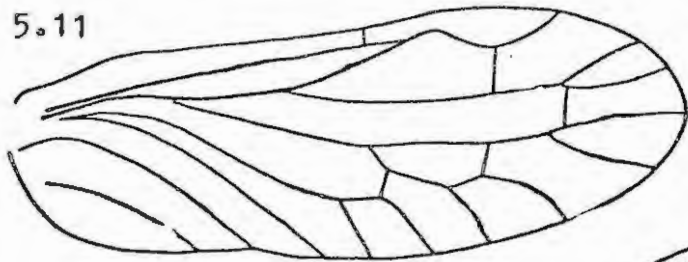

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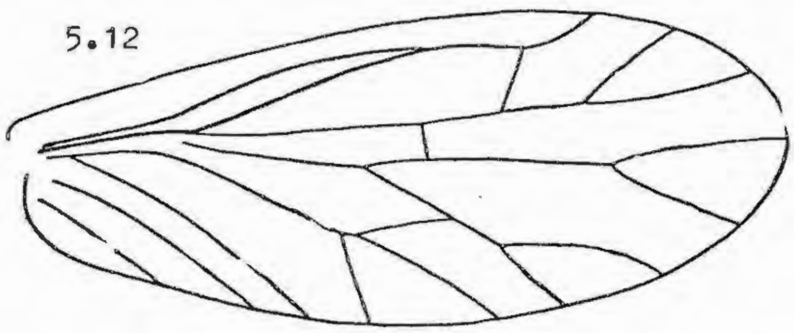
5.12



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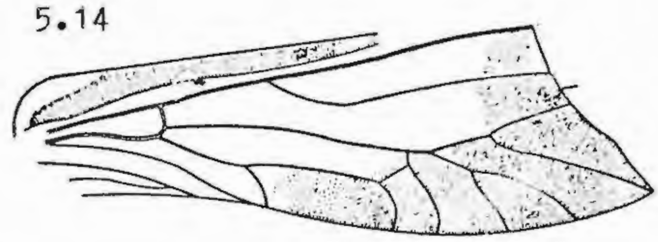

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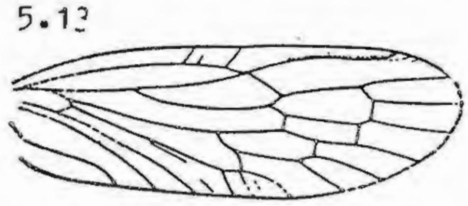

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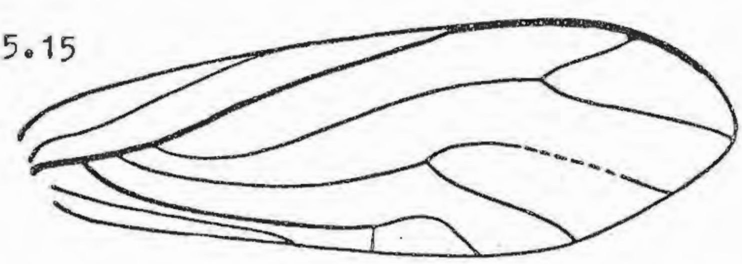
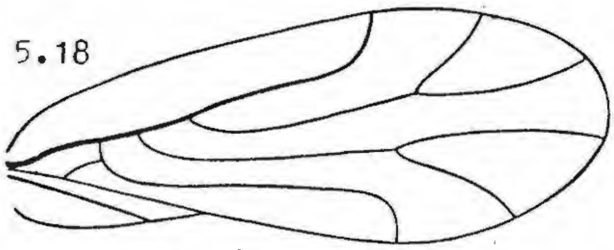


5.10 Lithopsocidium permianum Carpenter. Fore wing
5.11 Lithopsocidium permianum Carpenter. Hind wing
5.12 Orthopsocus singularis Carpenter. Hind wing
5.13 Martynopsocus arcuatus (Martynov). Fore wing
5.14 Surijokopsocus radtshenkoi Becker-Migdisova. Fore wing
5.15 Lophioneura ustulata Tillyard. Fore wing
5.16 Cyphoneura permiana Carpenter. Fore wing
5.17 Cyphoneurades reducta Carpenter. Fore wing

5.18



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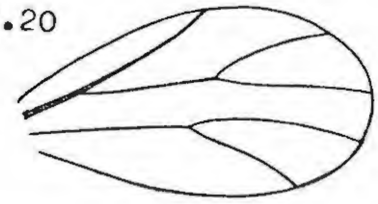

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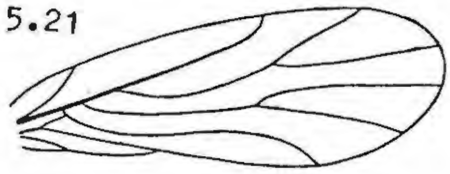

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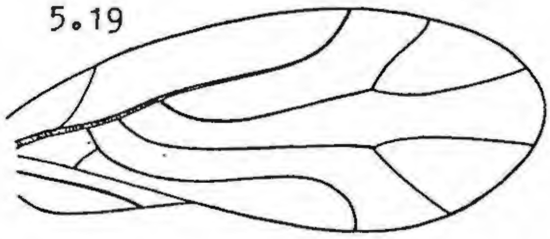

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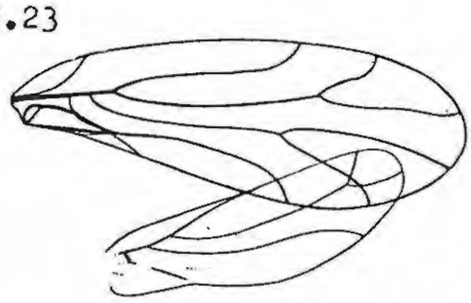

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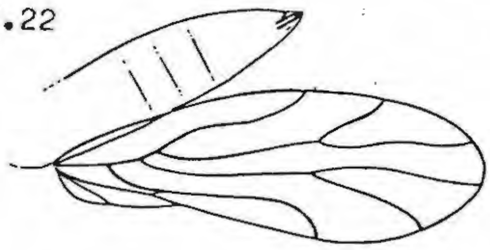

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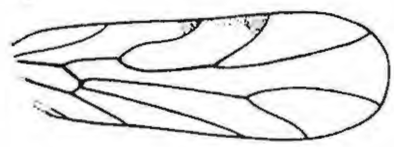

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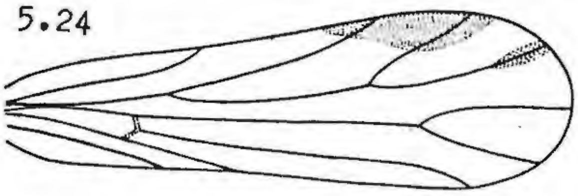

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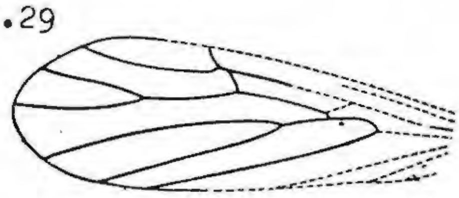

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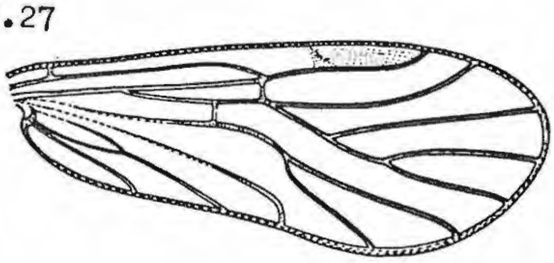

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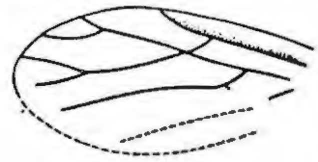

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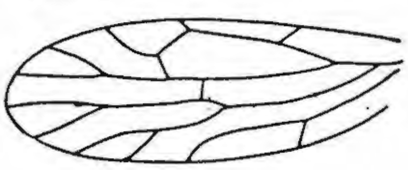

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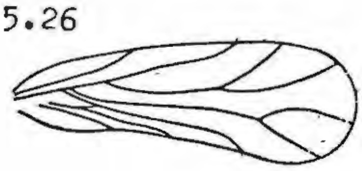
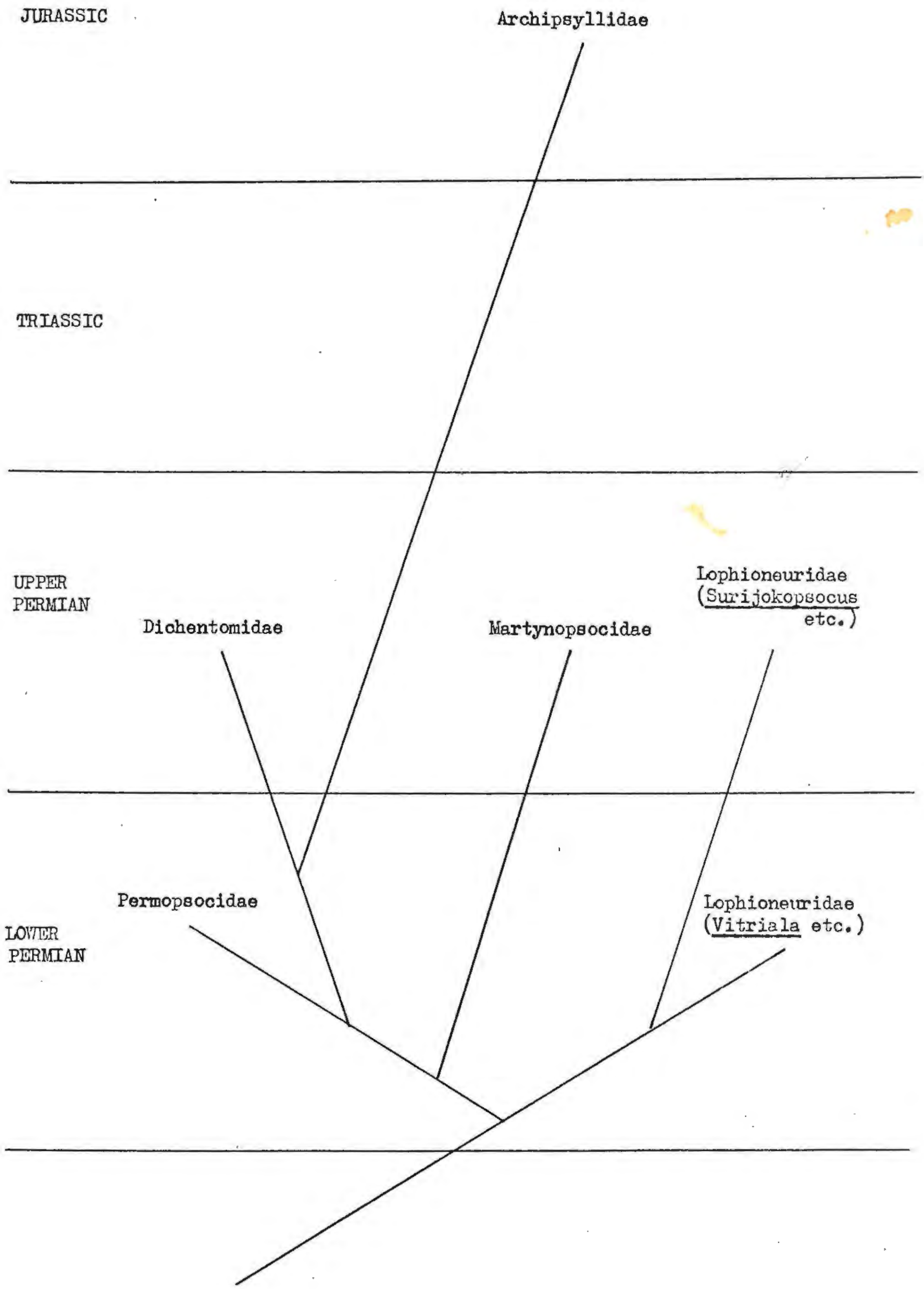
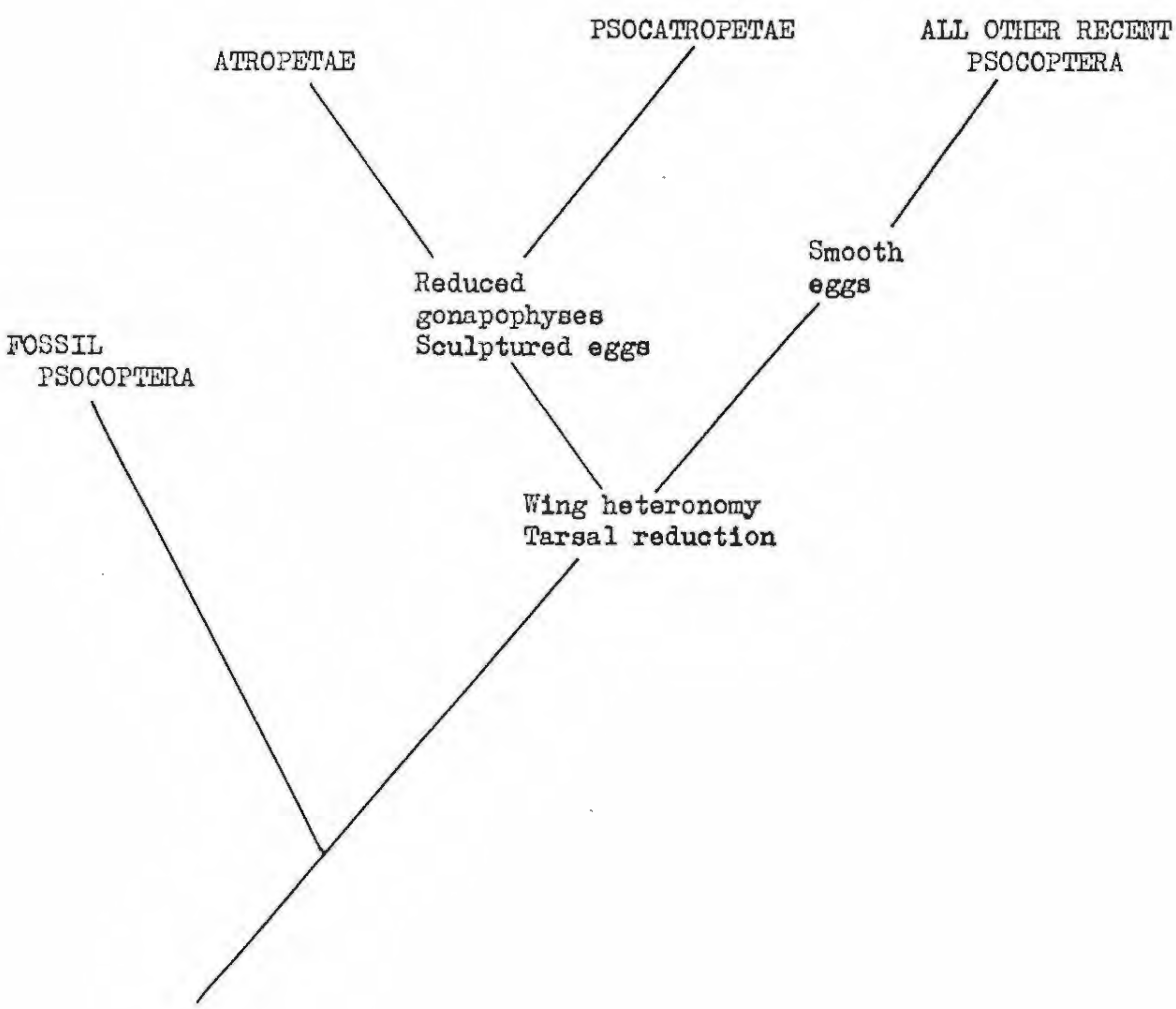


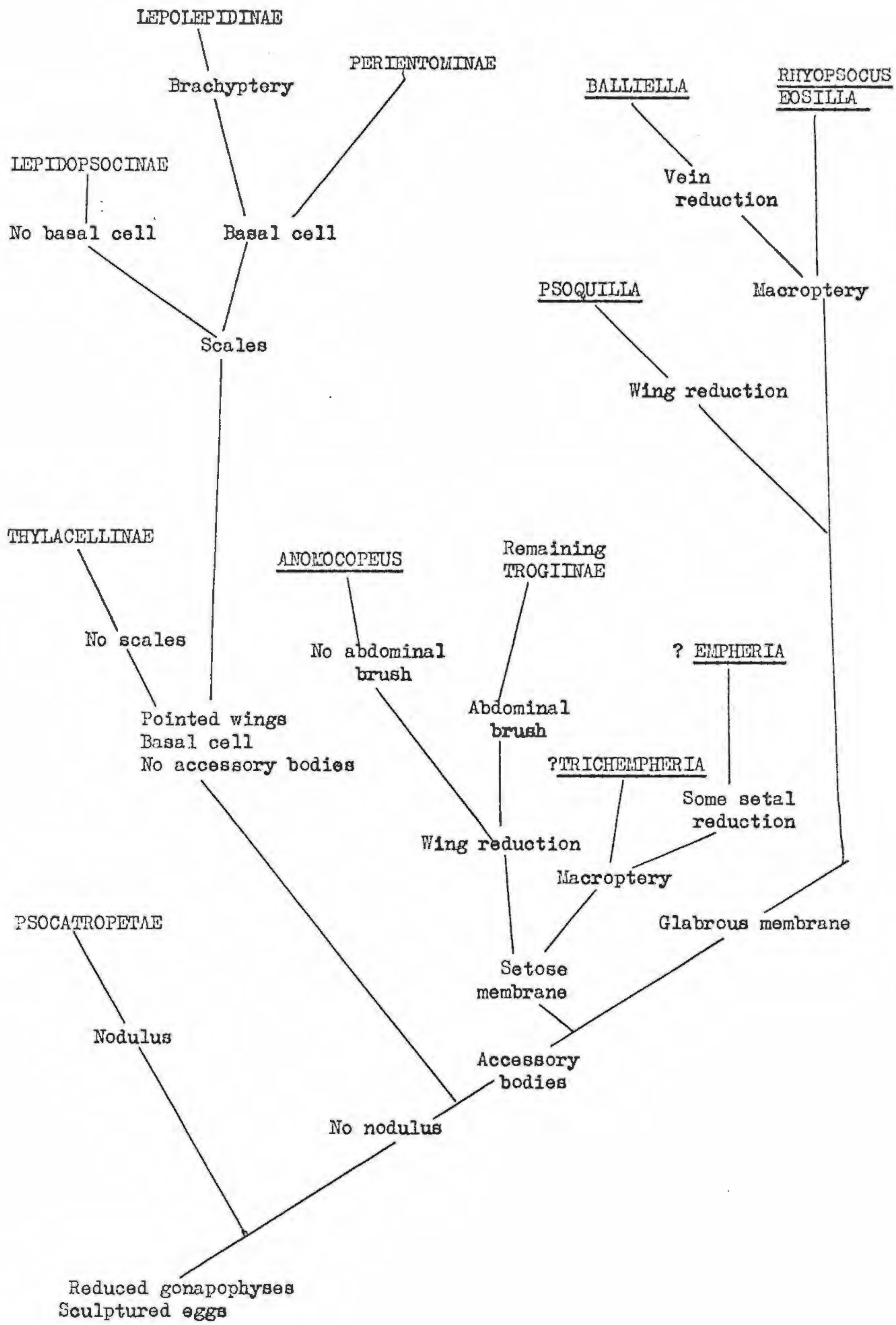
5.18 Austrocypha abrupta Tillyard. Fore wing
5.19 Austrocypha barretti Tillyard. Fore wing
5.20 Austrocypha sp. Fore wing
5.21 Lophiocypha stanleyi Tillyard. Fore wing
5.22 Lophiocypha permiana Tillyard. Fore wing
5.23 Lophiocypha stanleyi Tillyard. Fore & hind wings
5.24 Zoropsocus delicatulus Tillyard. Fore wing
5.25 Zoropsocus stanleyi Davis. Fore wing
5.26 Lophioneurodes sarbalensis Becker-Migdisova. Fore wing
5.27 Zygopsocus permianus Tillyard. Fore wing
5.28 Archipsylla turanica Martynov. Fore wing
5.29 Asientomum praecox (Martynov). Fore wing
5.30 Asientomum praecox (Martynov). Hind wing



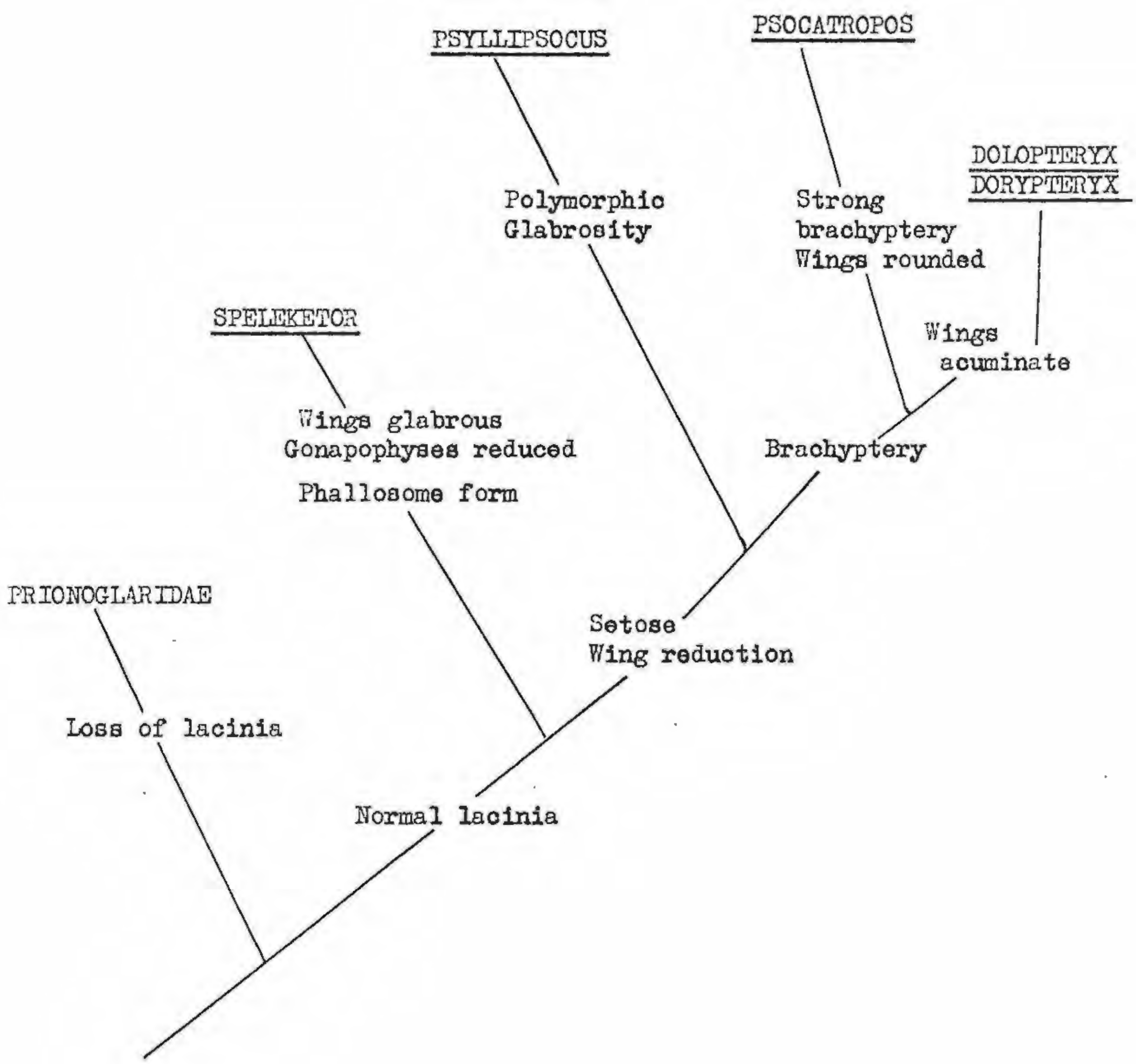
5.31 RELATIONSHIPS OF FAMILIES OF PERMOPSOCIDA



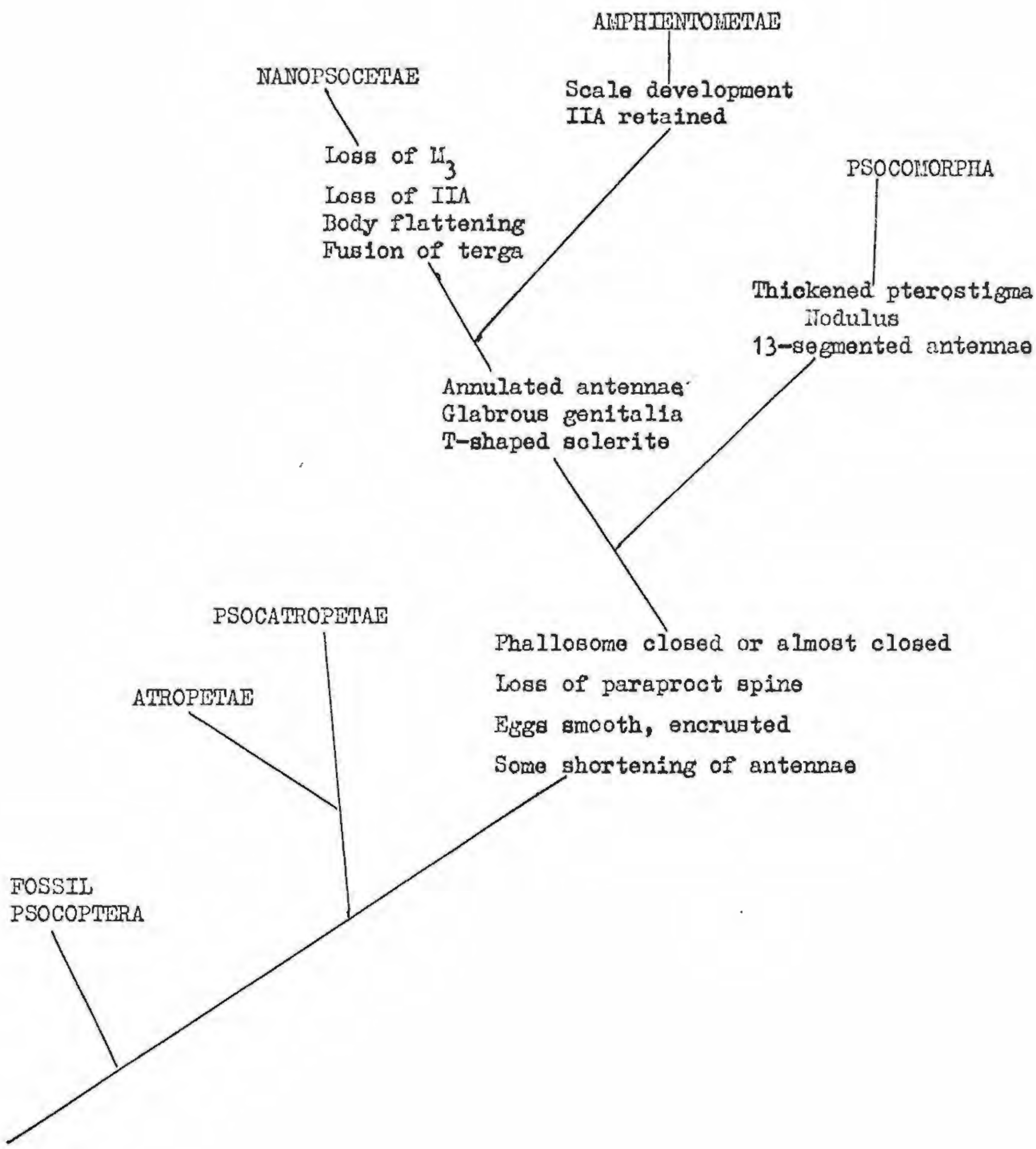
6.1 RELATIONSHIPS OF FOSSIL PSOCOPTERA TO RECENT GROUPS



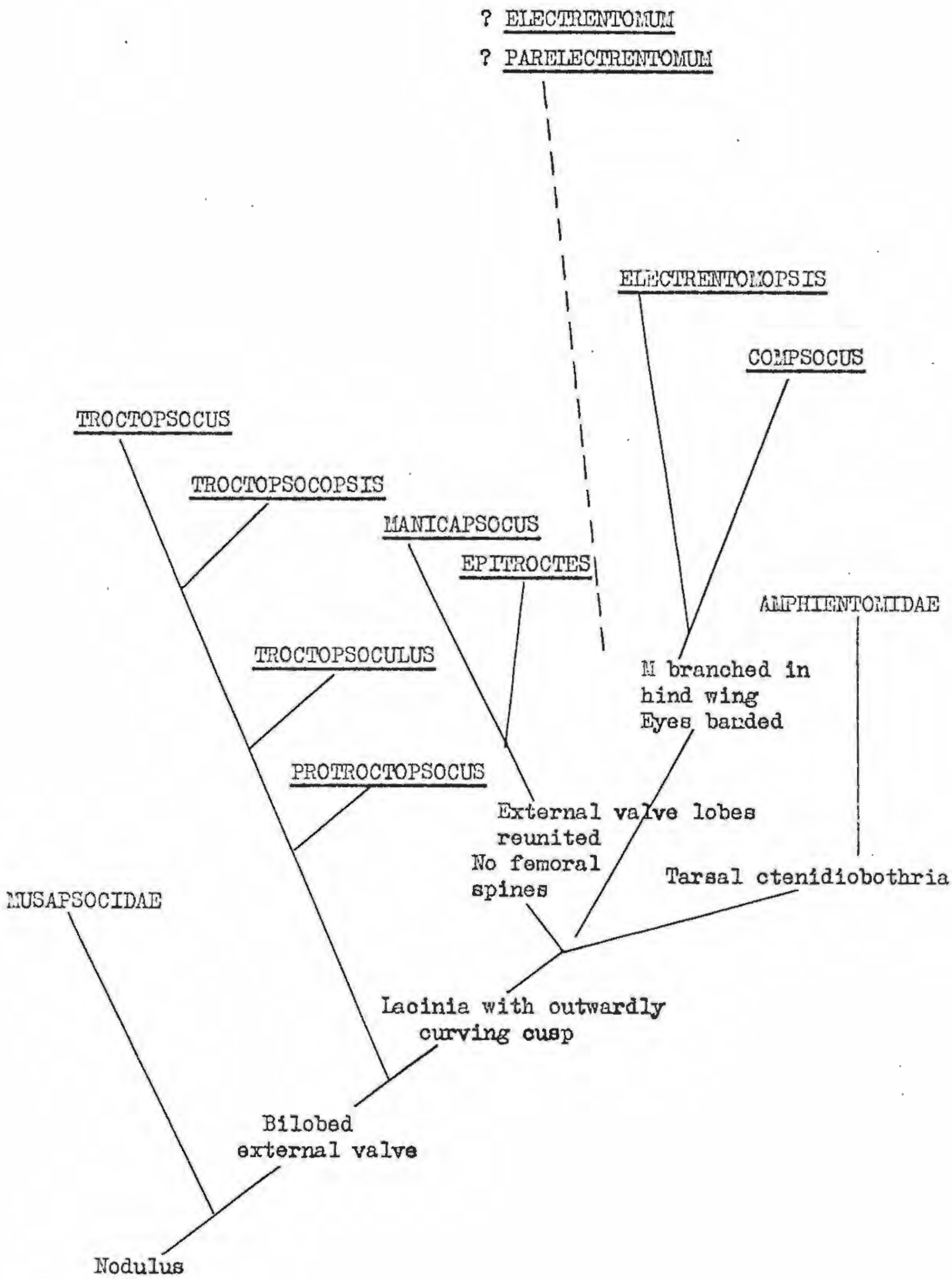
6.2 RELATIONSHIPS WITHIN THE ATROPETAE



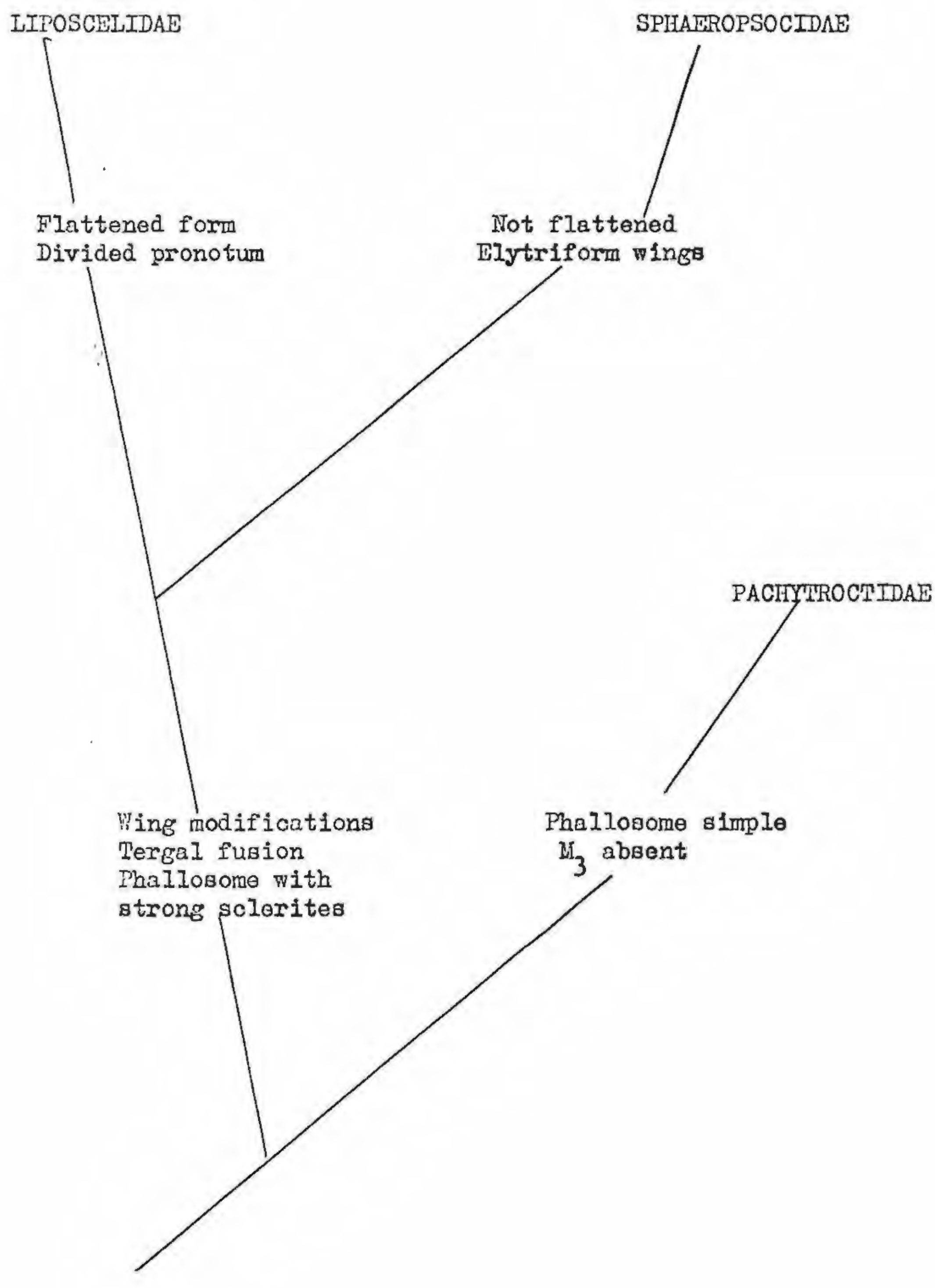
6.3 RELATIONSHIPS WITHIN THE PSOCATROPETAE



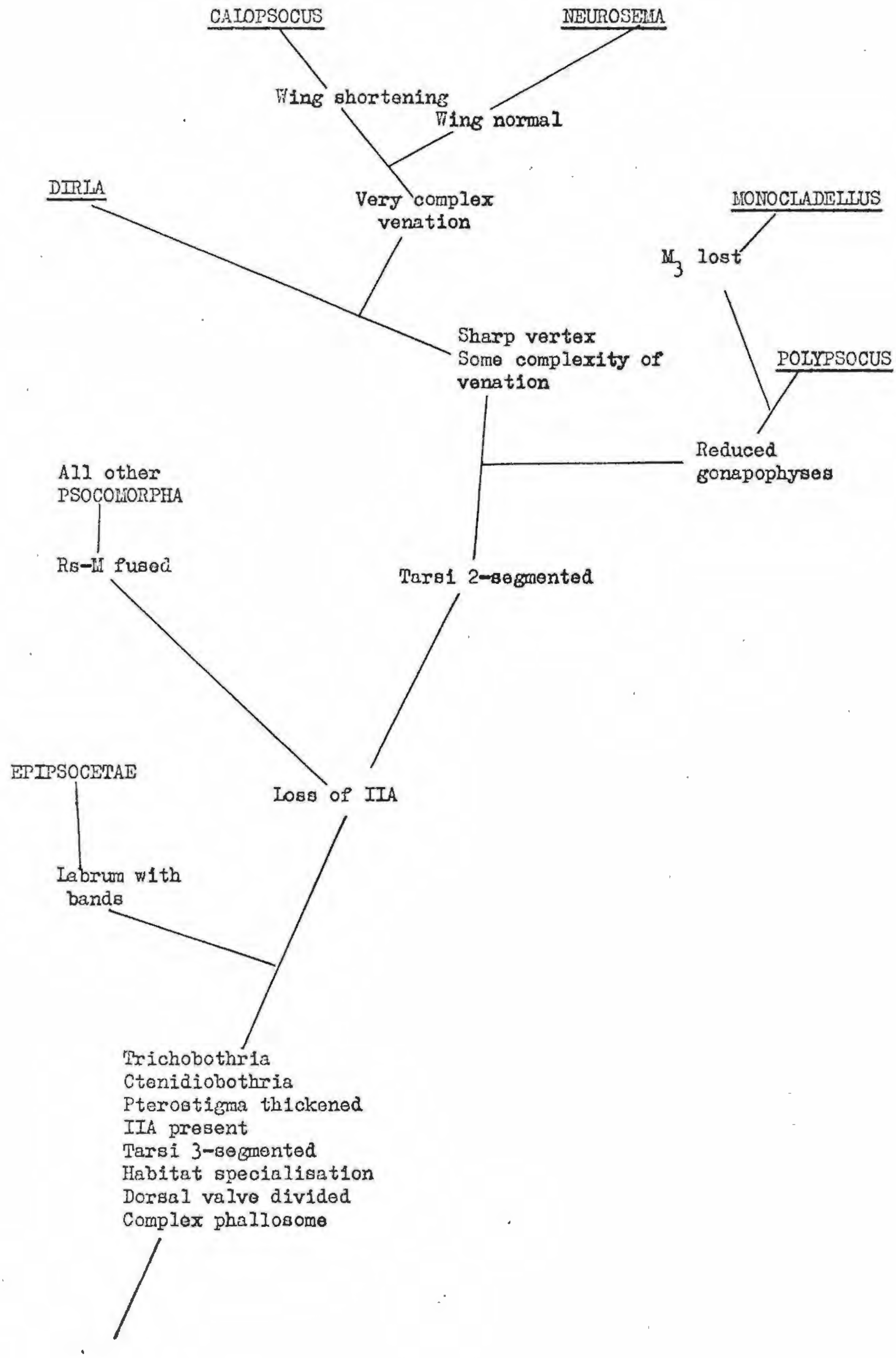
6.4 RELATIONSHIPS OF MAJOR GROUPS OF THE ORDER



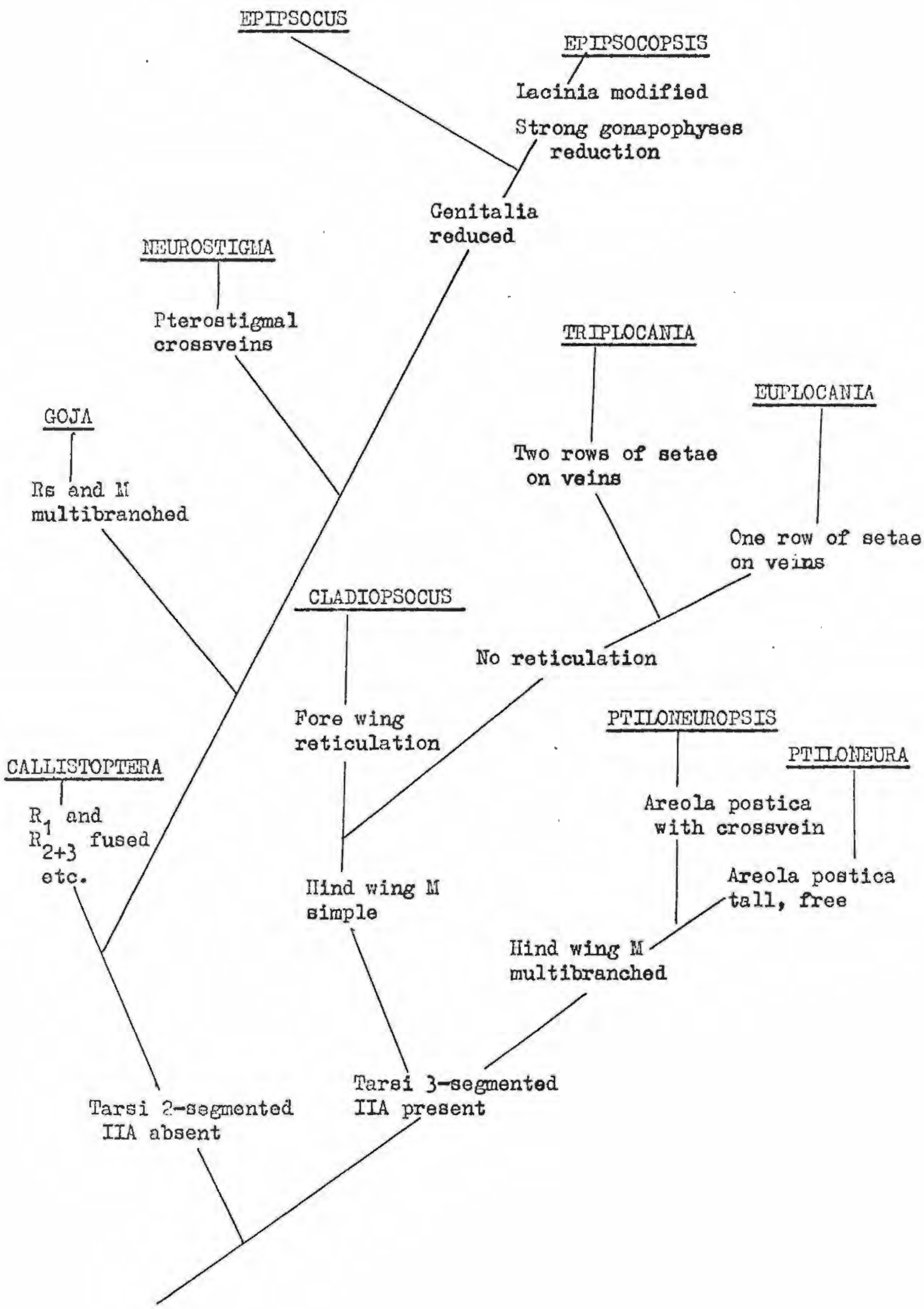
6.5 RELATIONSHIPS OF GROUPS WITHIN THE AMPHIENTOMETAE
(Based on Mockford, 1967)



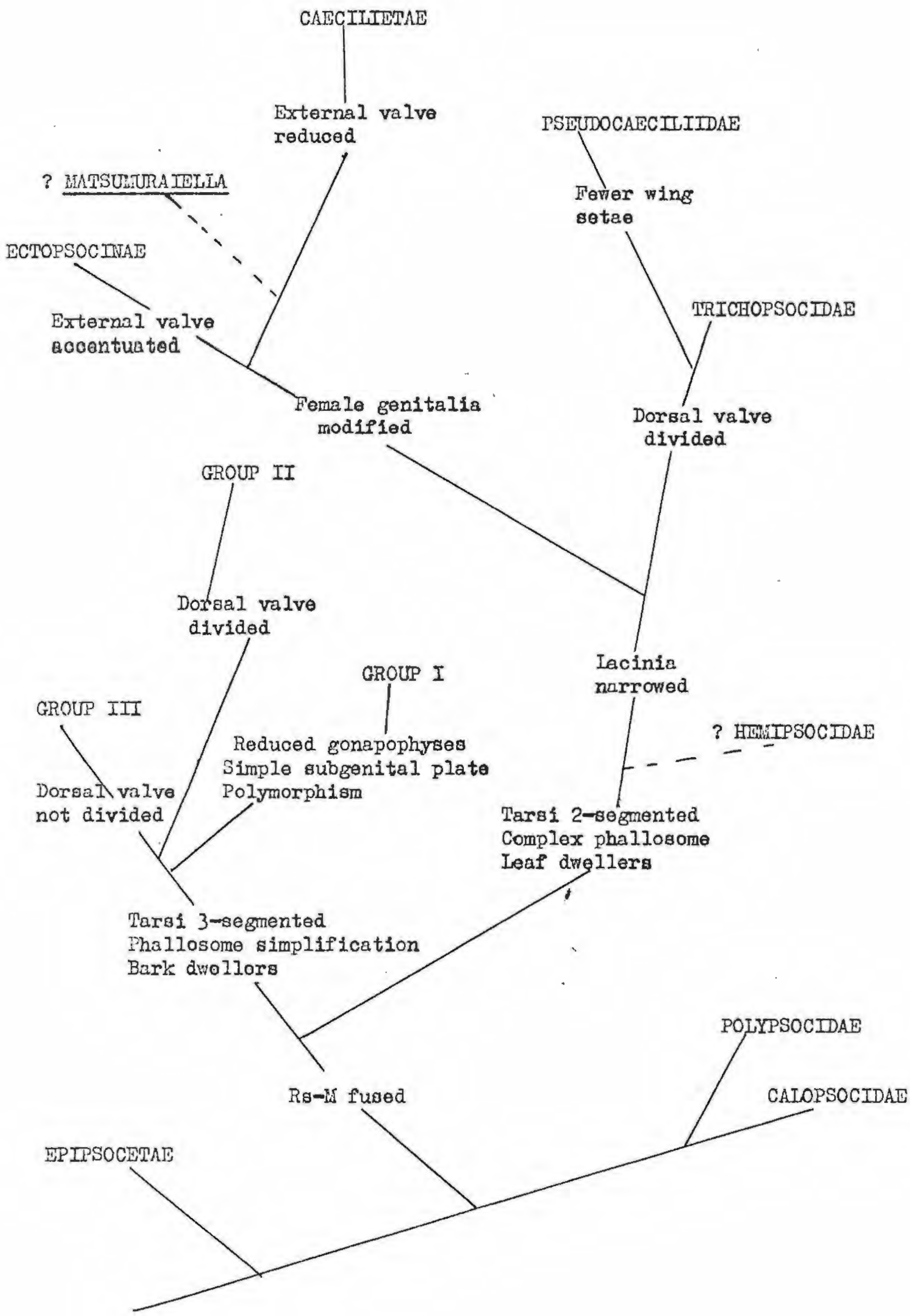
6.6 RELATIONSHIPS WITHIN THE NANOPSOCETAE



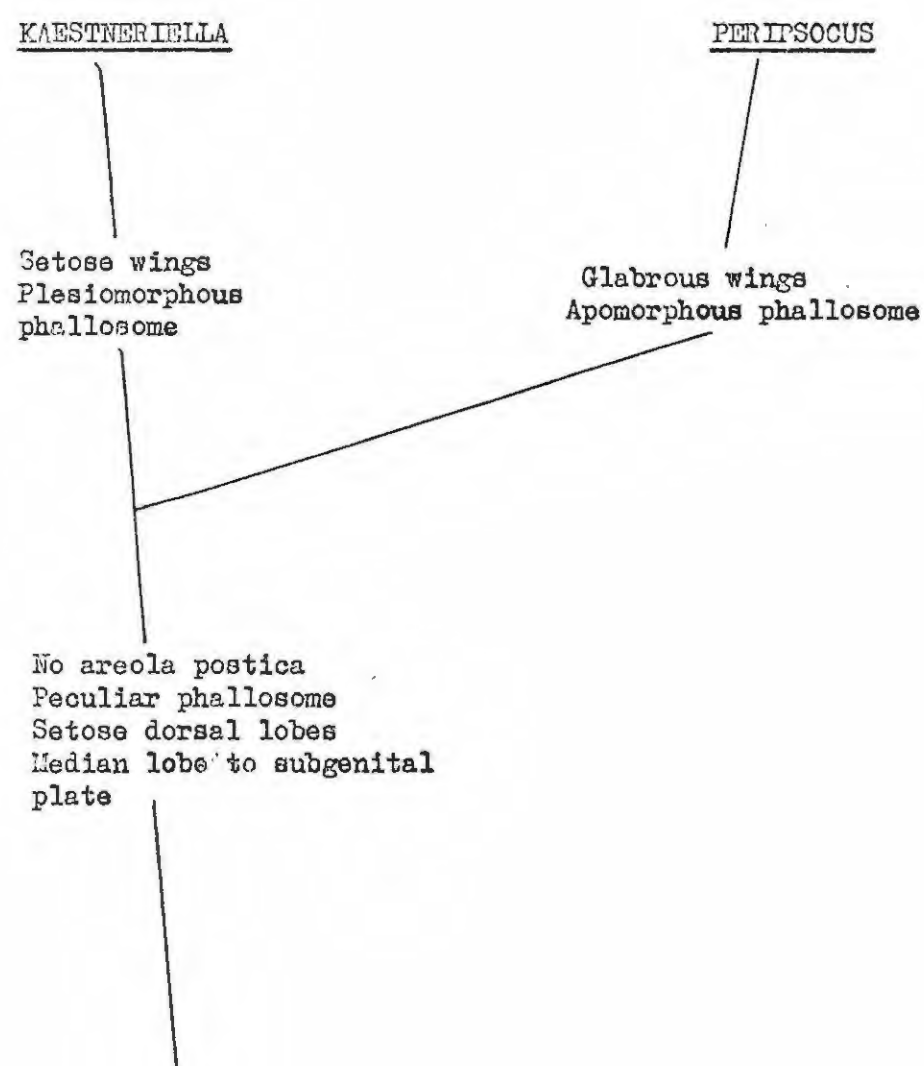
6.7 RELATIONSHIPS OF "PRIMITIVE" PSOCOMORPHA



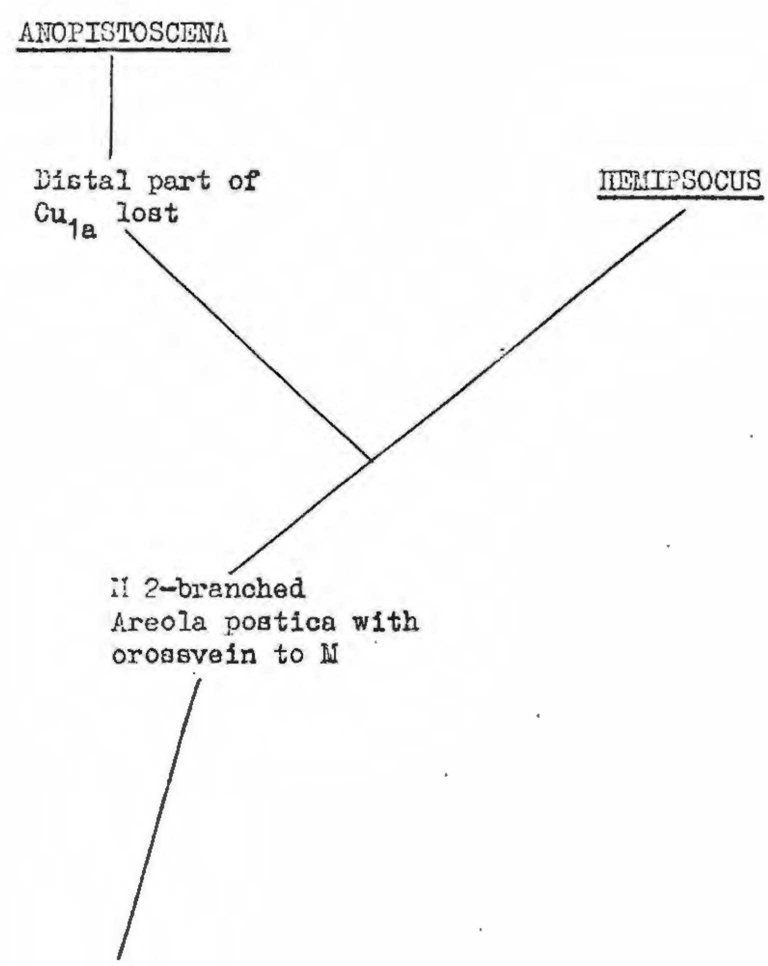
6.8 RELATIONSHIPS WITHIN THE EPIPSOCETAE



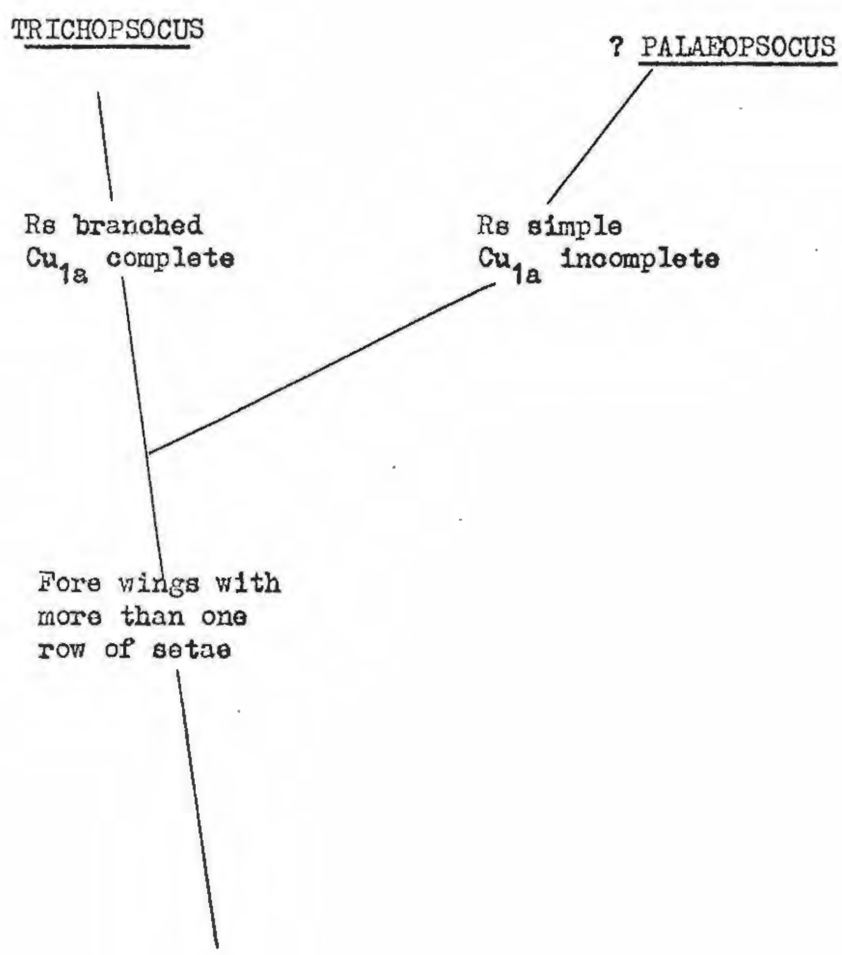
6.9 RELATIONSHIPS WITHIN THE PSOCOMORPHA



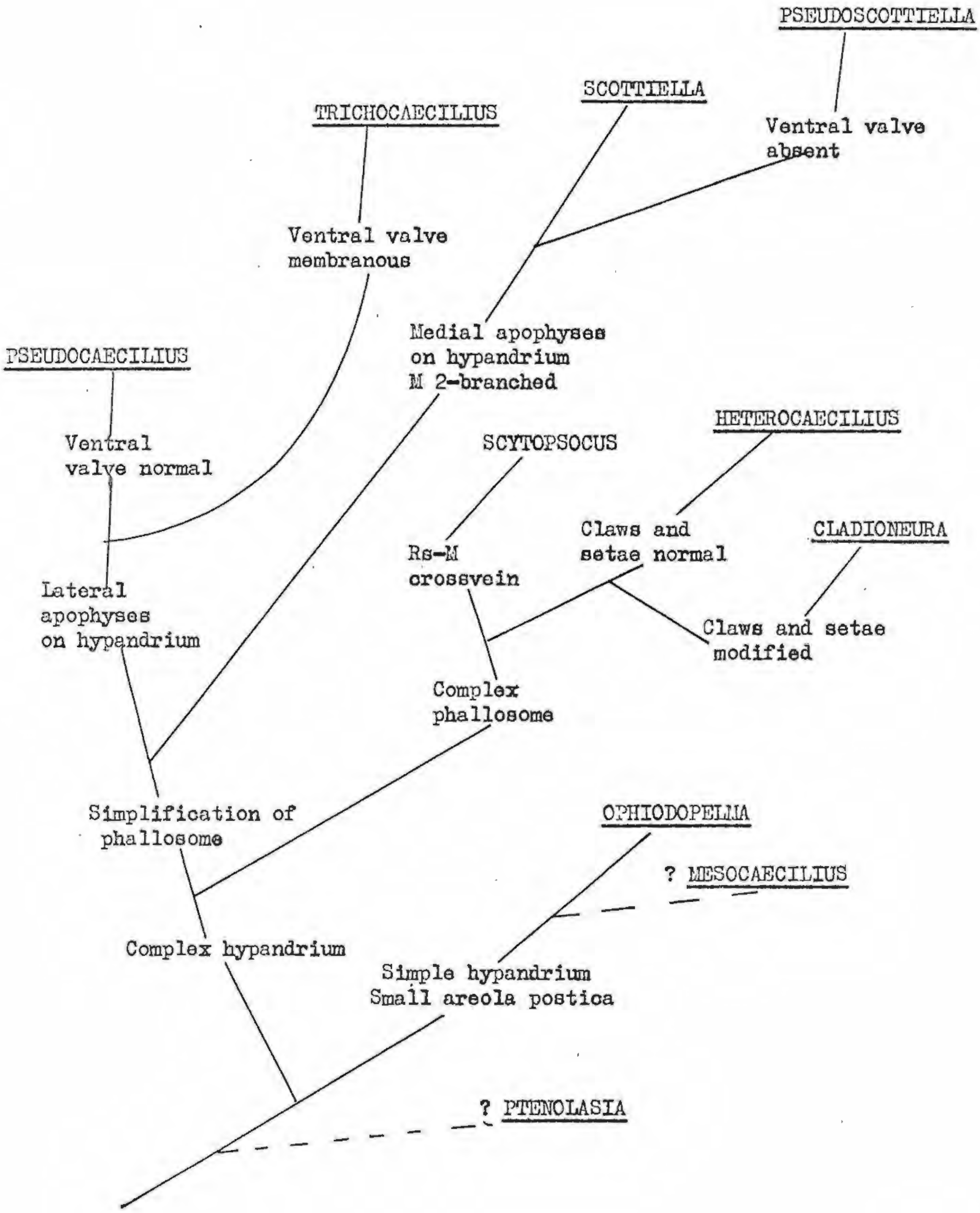
6.10 RELATIONSHIPS WITHIN THE PERIPSOCINAE



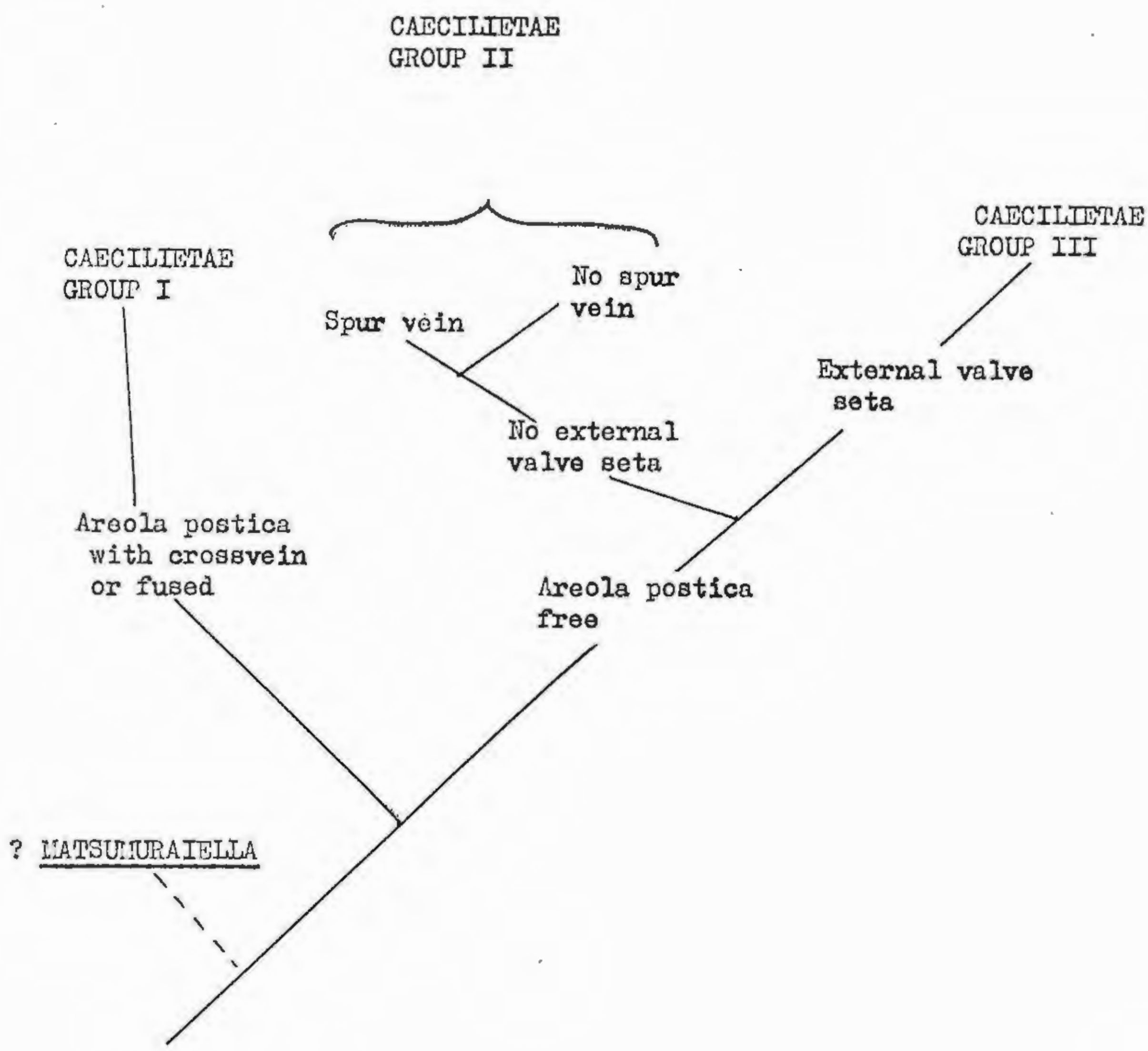
6.11 RELATIONSHIPS WITHIN THE HEMIPSOCIDAE



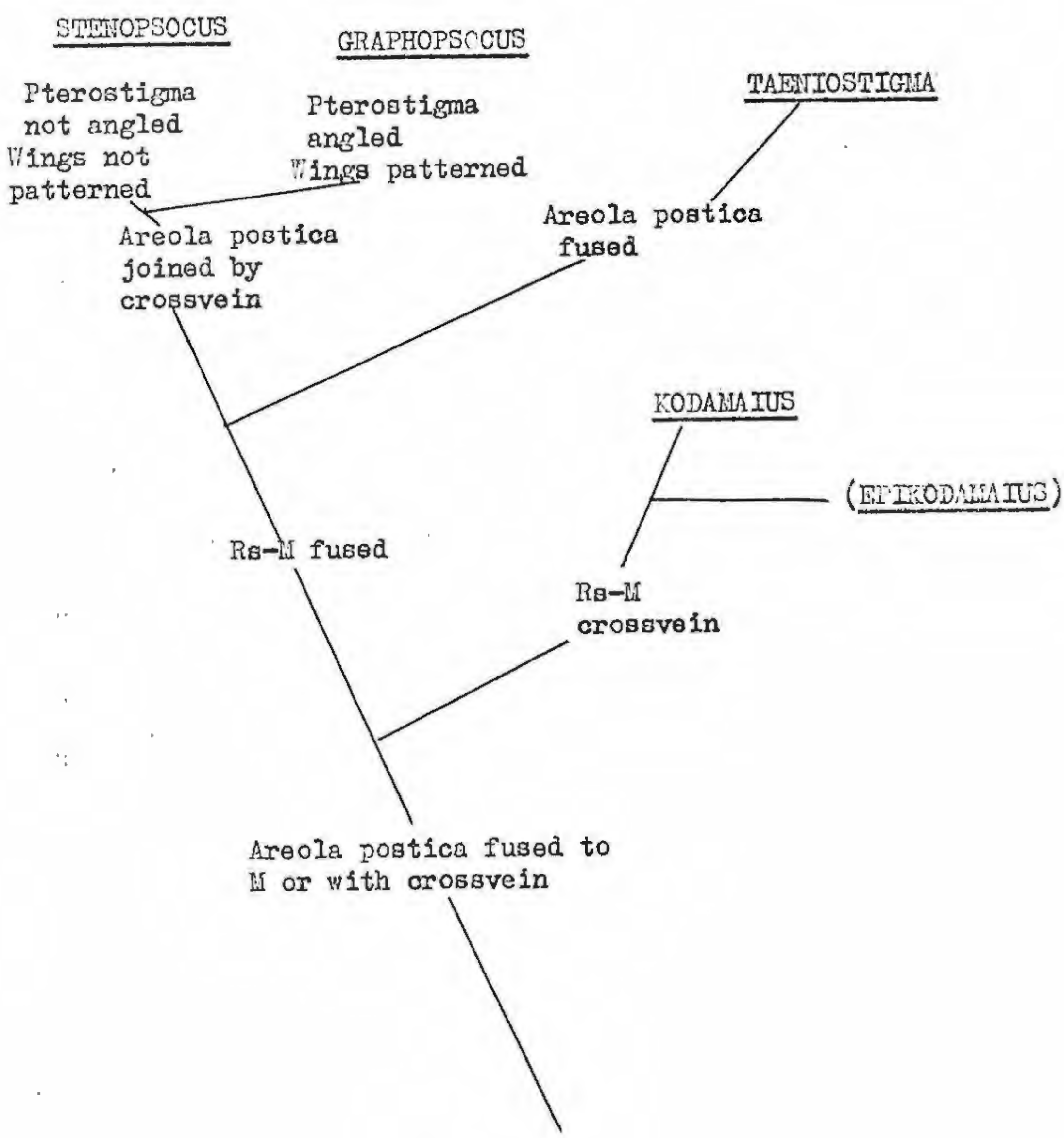
6.12 RELATIONSHIPS WITHIN THE TRICHOPSOCIDAE



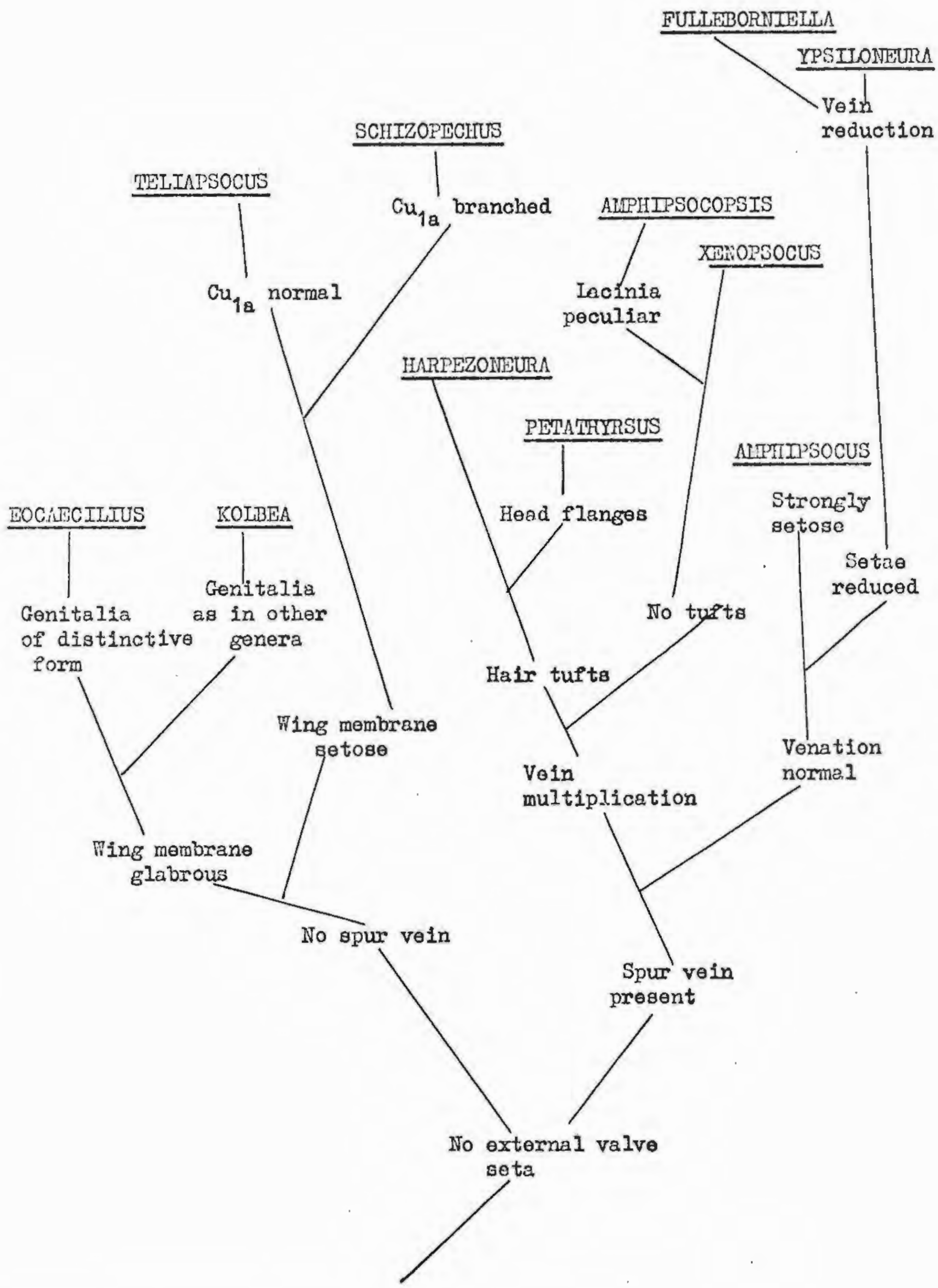
6.13 RELATIONSHIPS WITHIN THE PSEUDOCAECILIIDAE



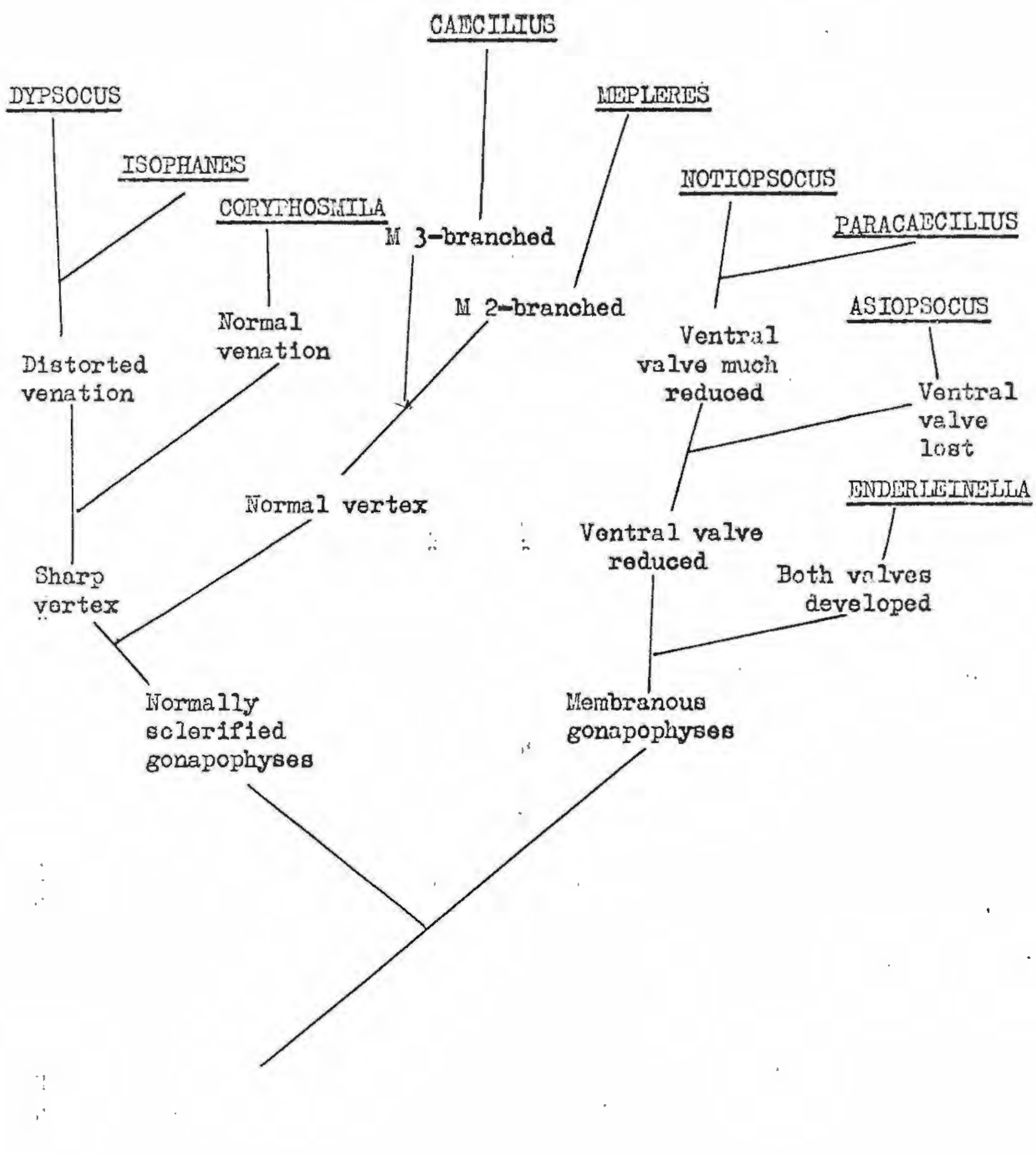
6.14 RELATIONSHIPS OF GROUPS OF CAECILIETAE



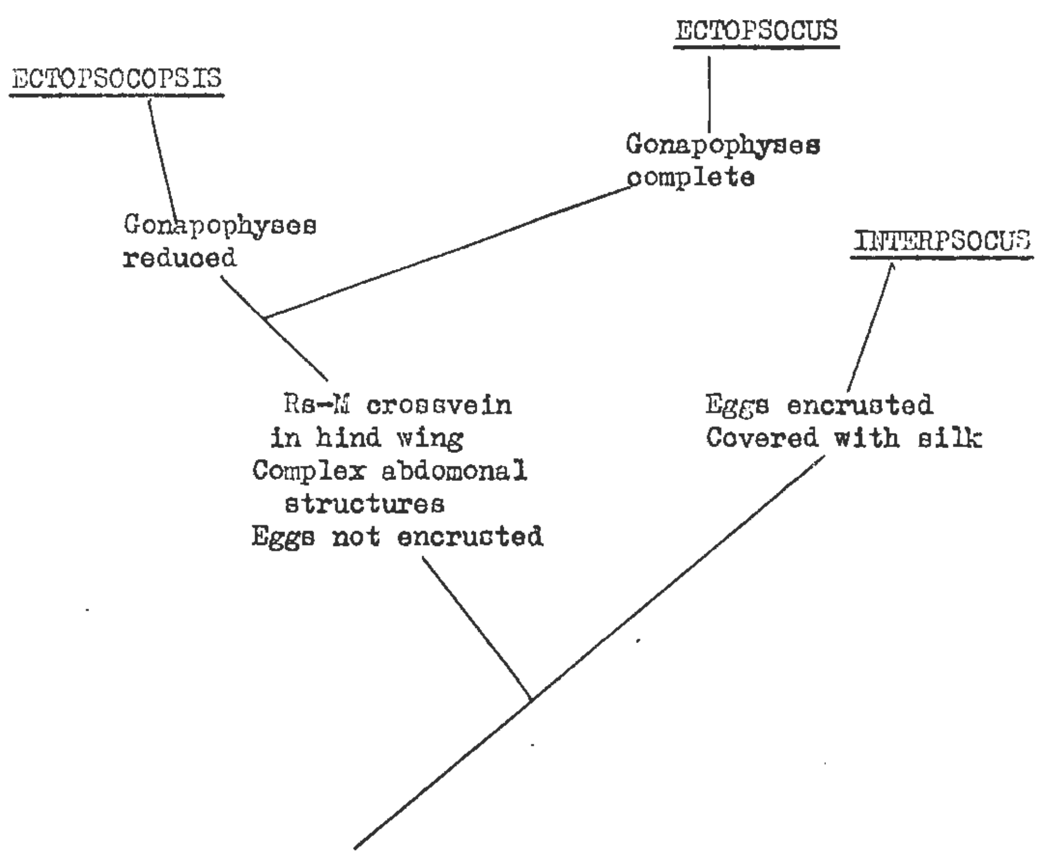
6.15 RELATIONSHIPS WITHIN CAECILIETAE GROUP I



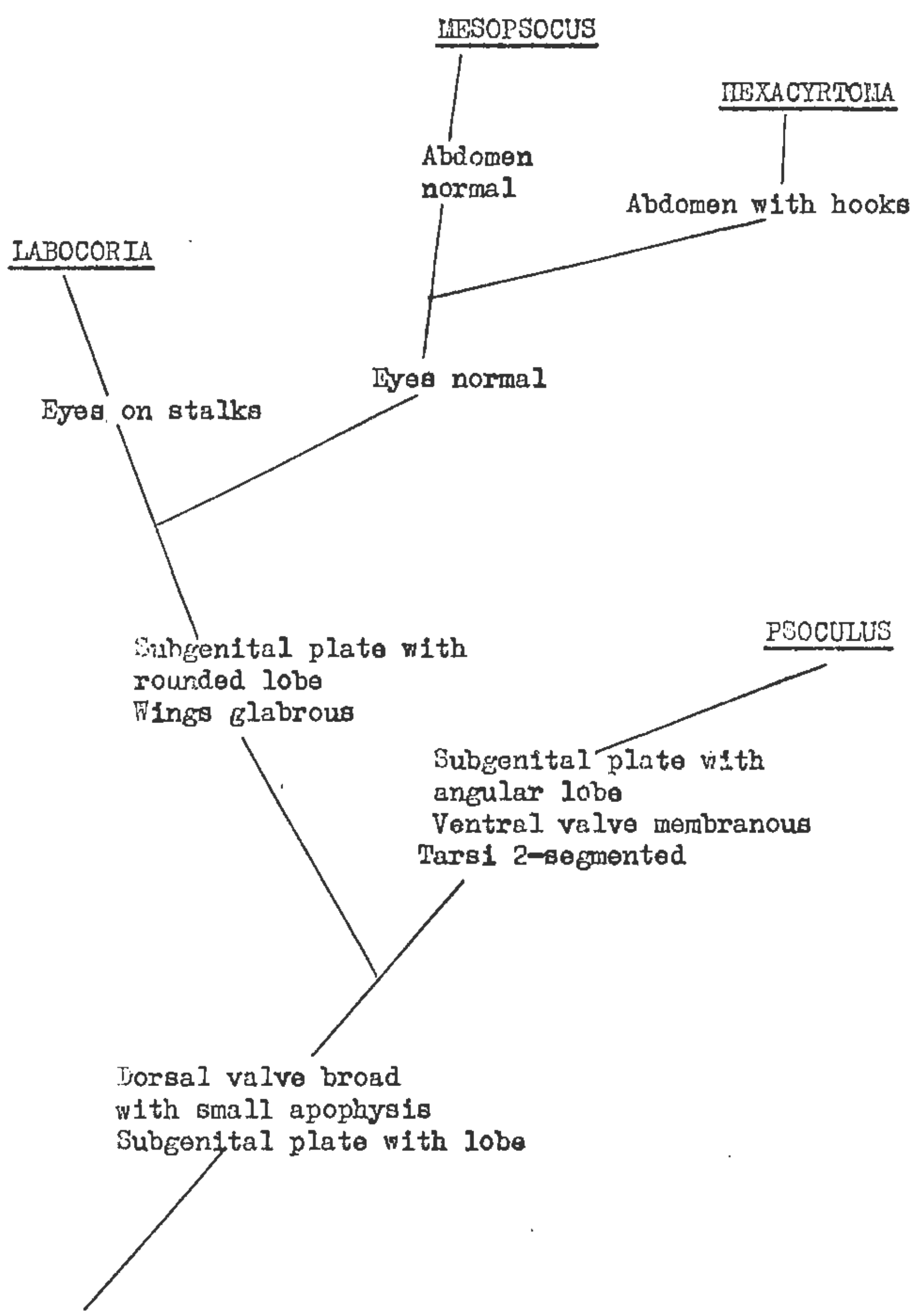
6.16 RELATIONSHIPS WITHIN CAECILIETAE GROUP II



6.17 RELATIONSHIPS WITHIN CAECILIETAE GROUP III



6.18 RELATIONSHIPS WITHIN THE ECTOPSOCINAE

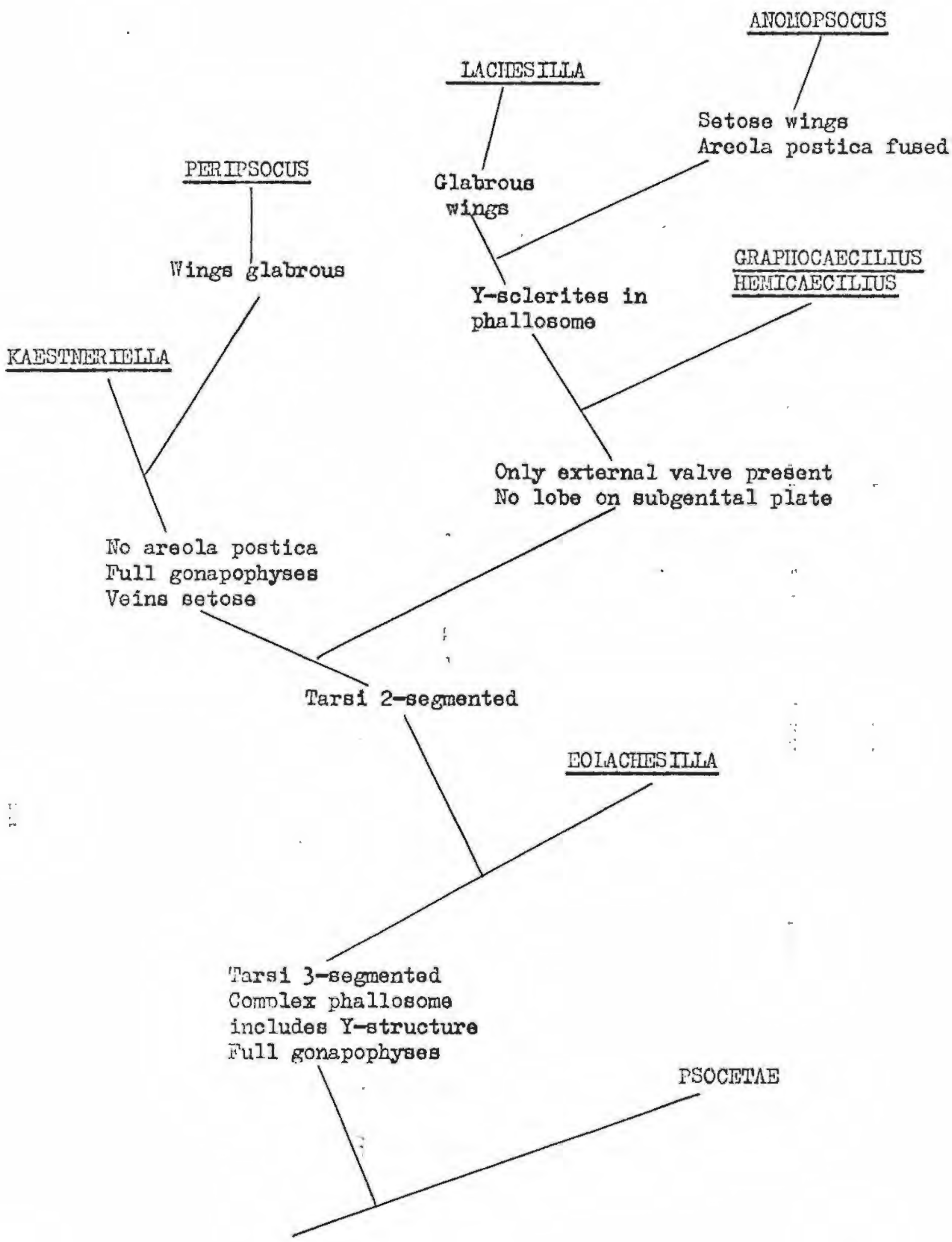


6.20 RELAIONSHIPS WITHIN THE MESOPSOCIDAE AND PSOCULIDAE

(Part of GROUP II)

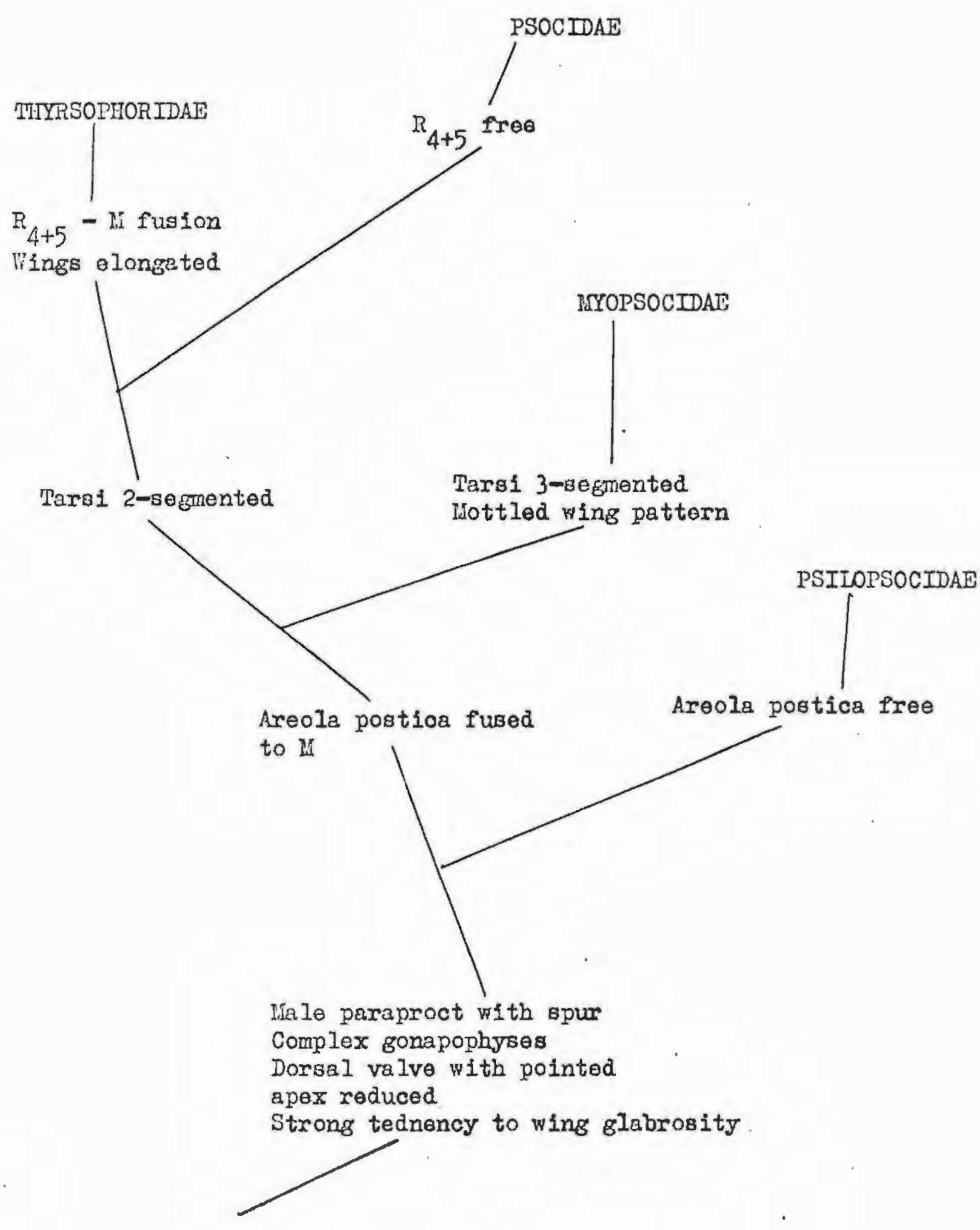
KEY TO GENERA OF THYLACELLOIDEA

Note: Only two genera are included in the Thylacelloidea. *Thylax* (from Copal) appears to be very similar to *Thylacella* (see note under generic definition).



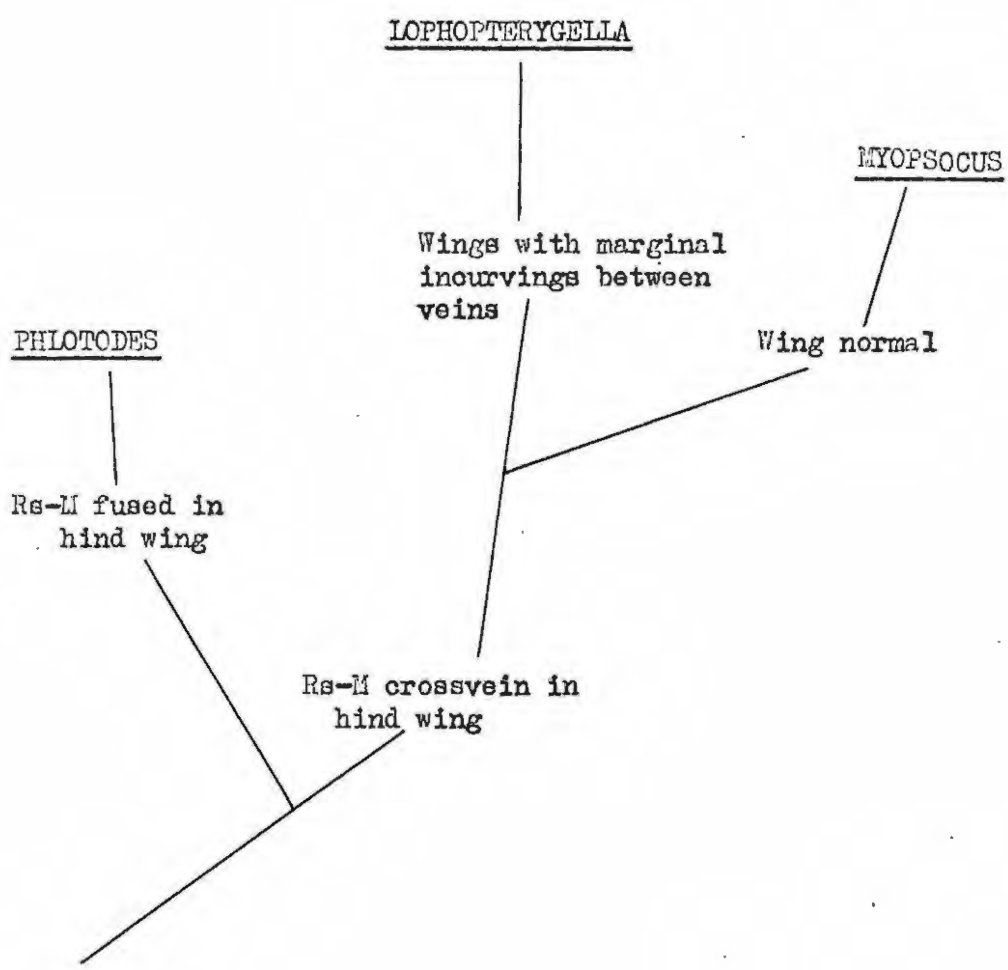
6.23 RELATIONSHIPS OF THE LACHESILLIDAE, GRAPHOCAECILIUS AND ANOMOPSOCUS AND PERIPSOCINAE

(part of GROUP III)

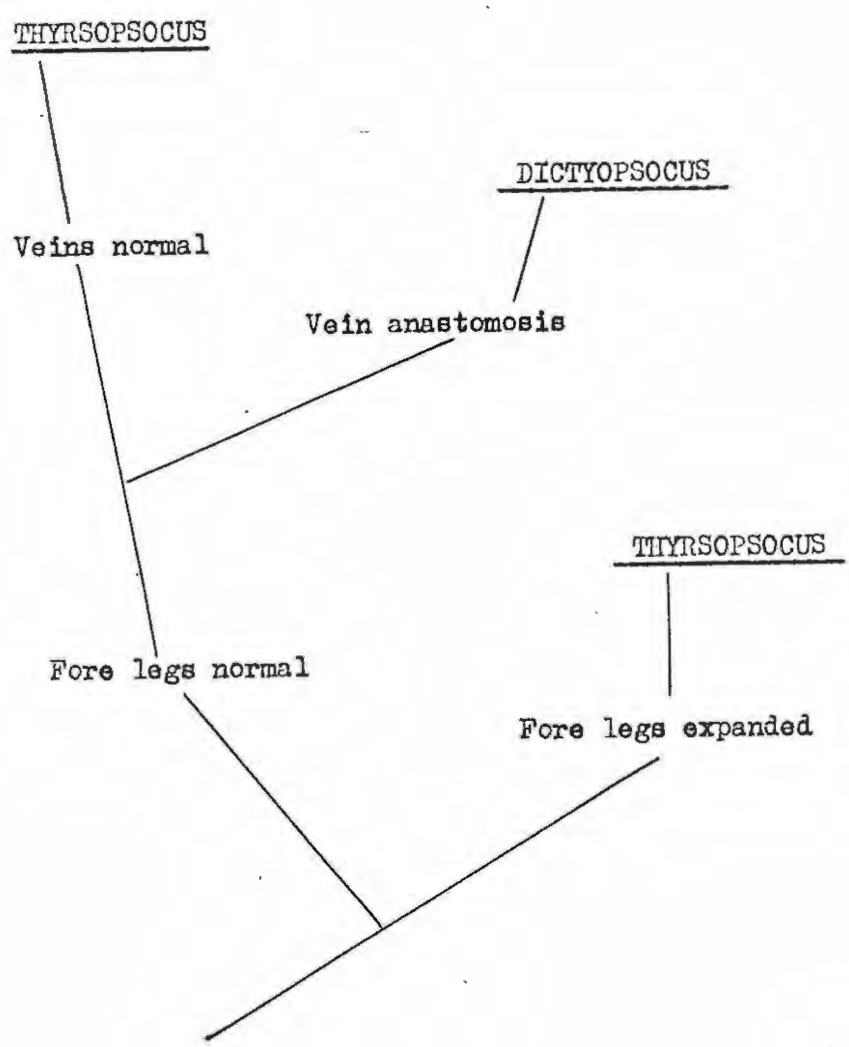


6.24 RELATIONSHIPS WITHIN THE PSOCETAE

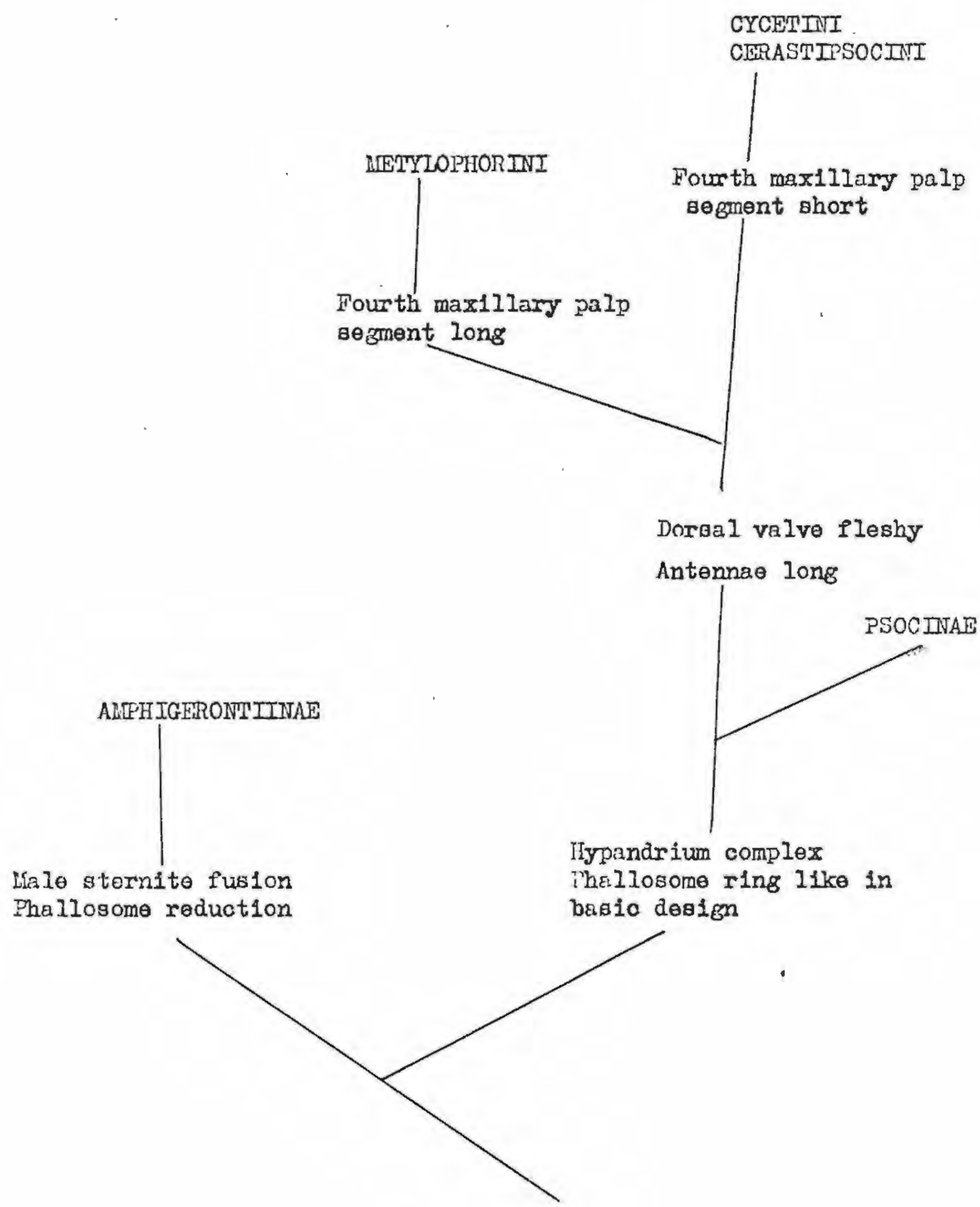
(part of GROUP III)



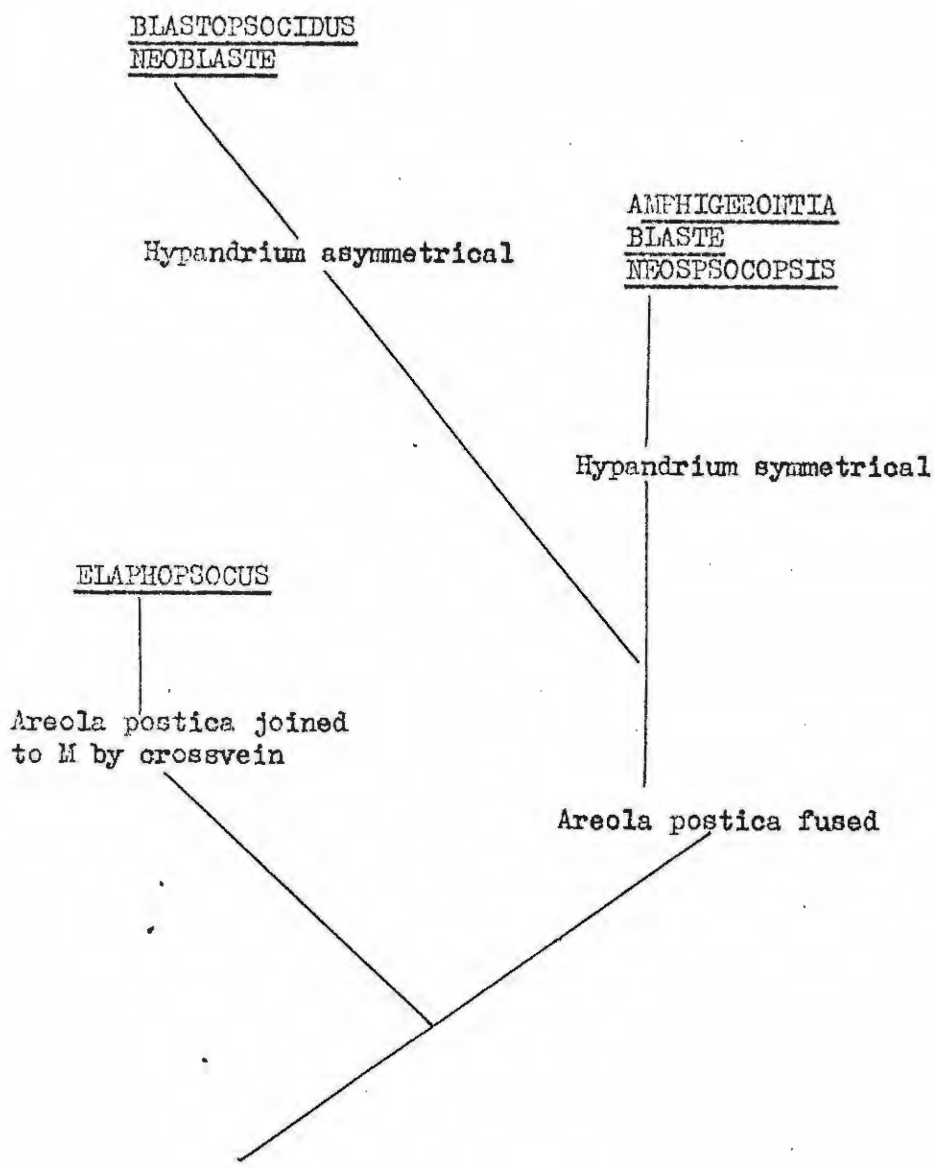
6.25 RELATIONSHIPS WITHIN THE MYOPSOCIDAE



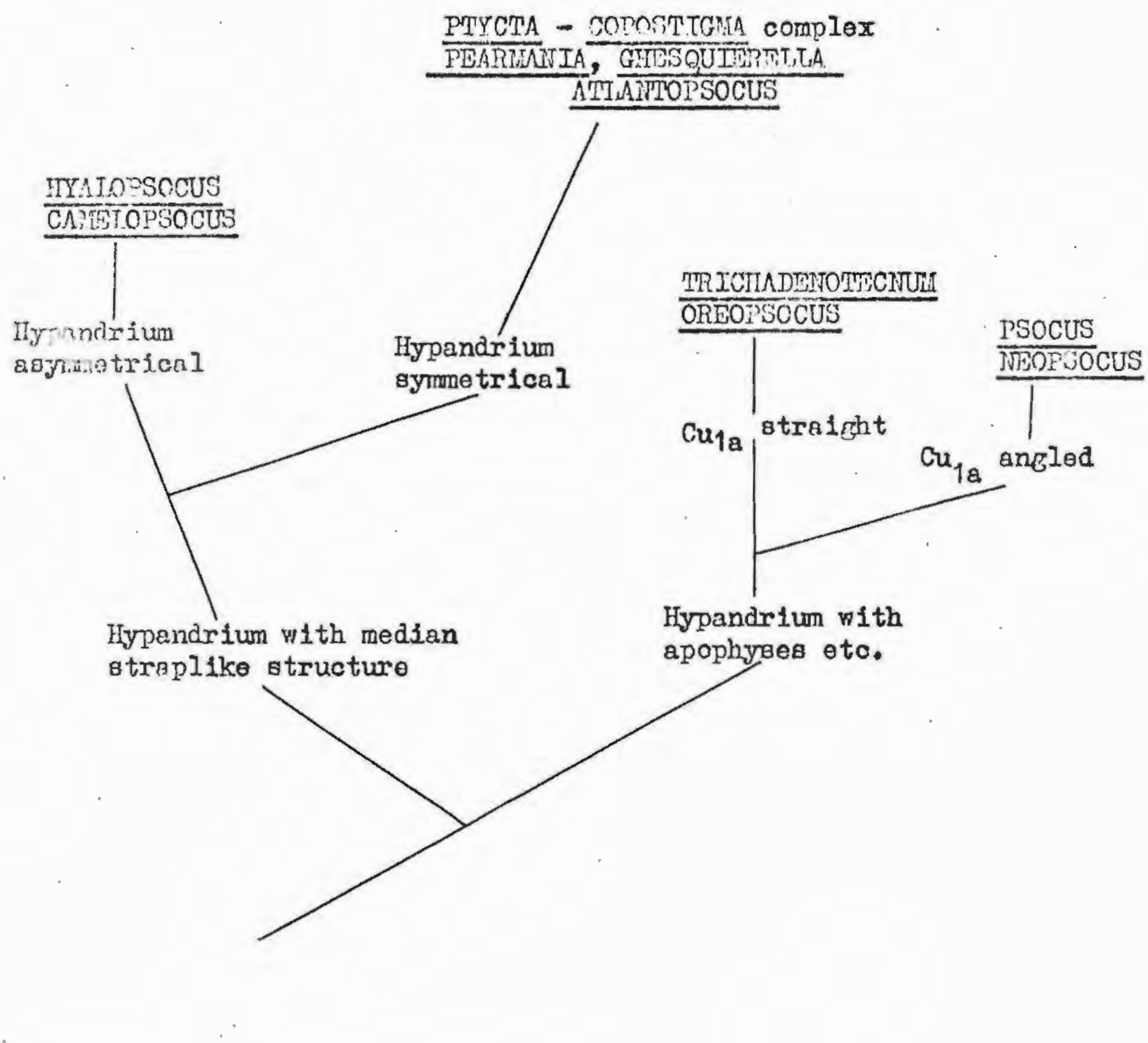
6.26 RELATIONSHIPS WITHIN THE THYRSOPHORIDAE



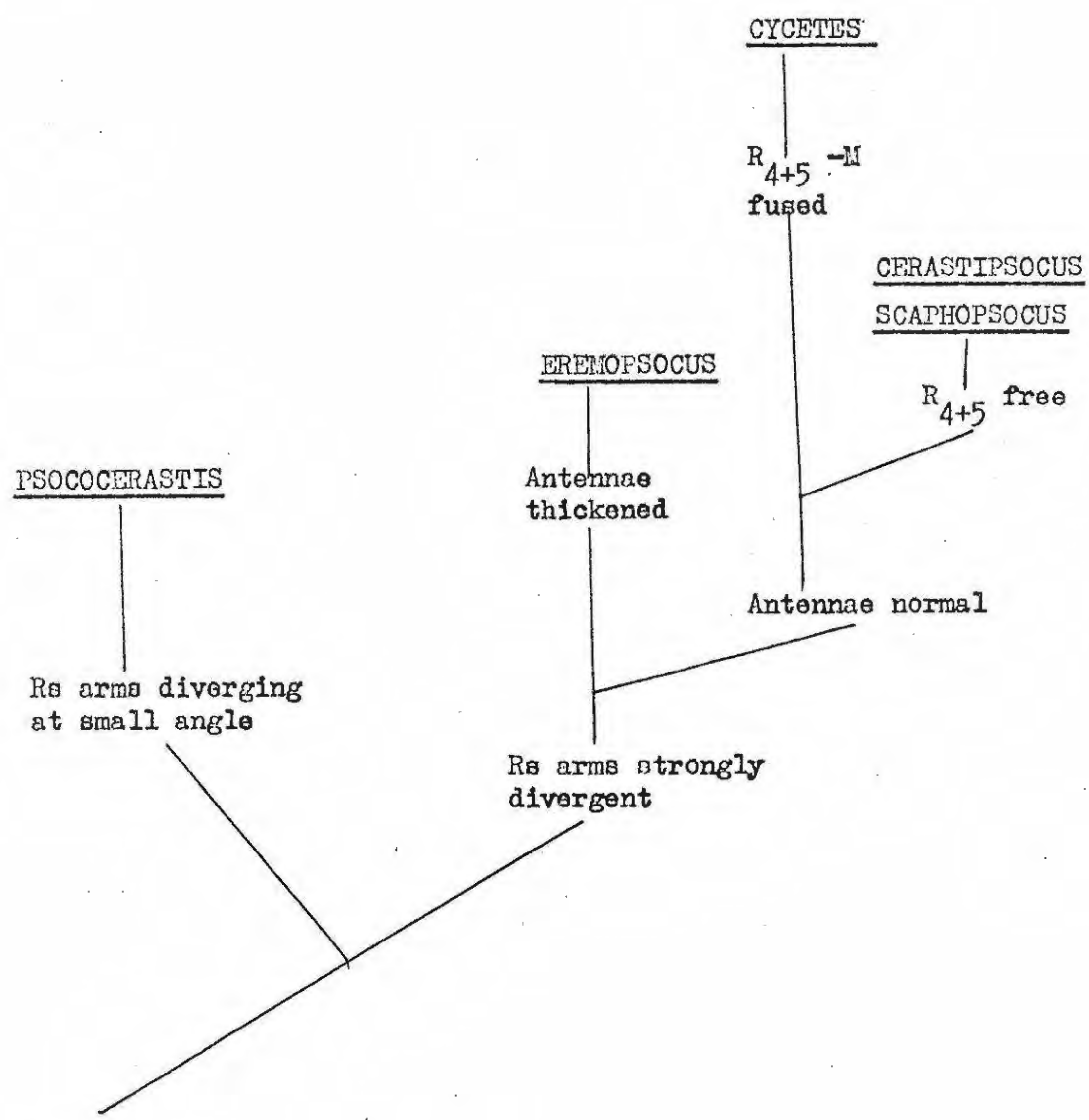
6.27 RELATIONSHIPS OF GROUPS WITHIN THE PSOCIDAE



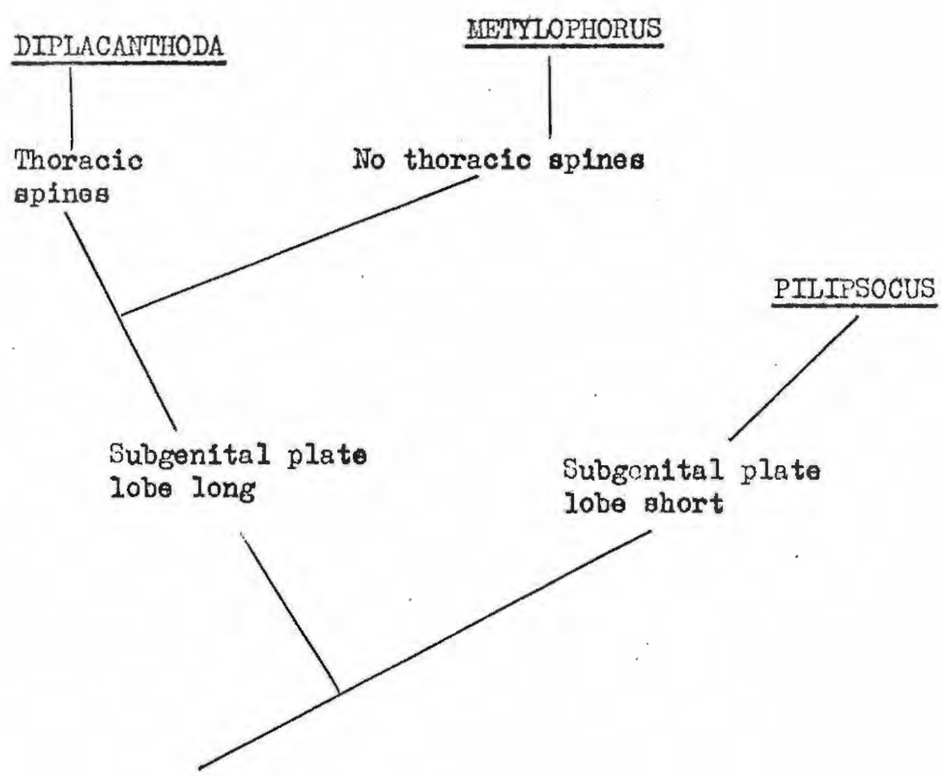
6.28 RELATIONSHIPS WITHIN THE AMPHIGERONTIINAE



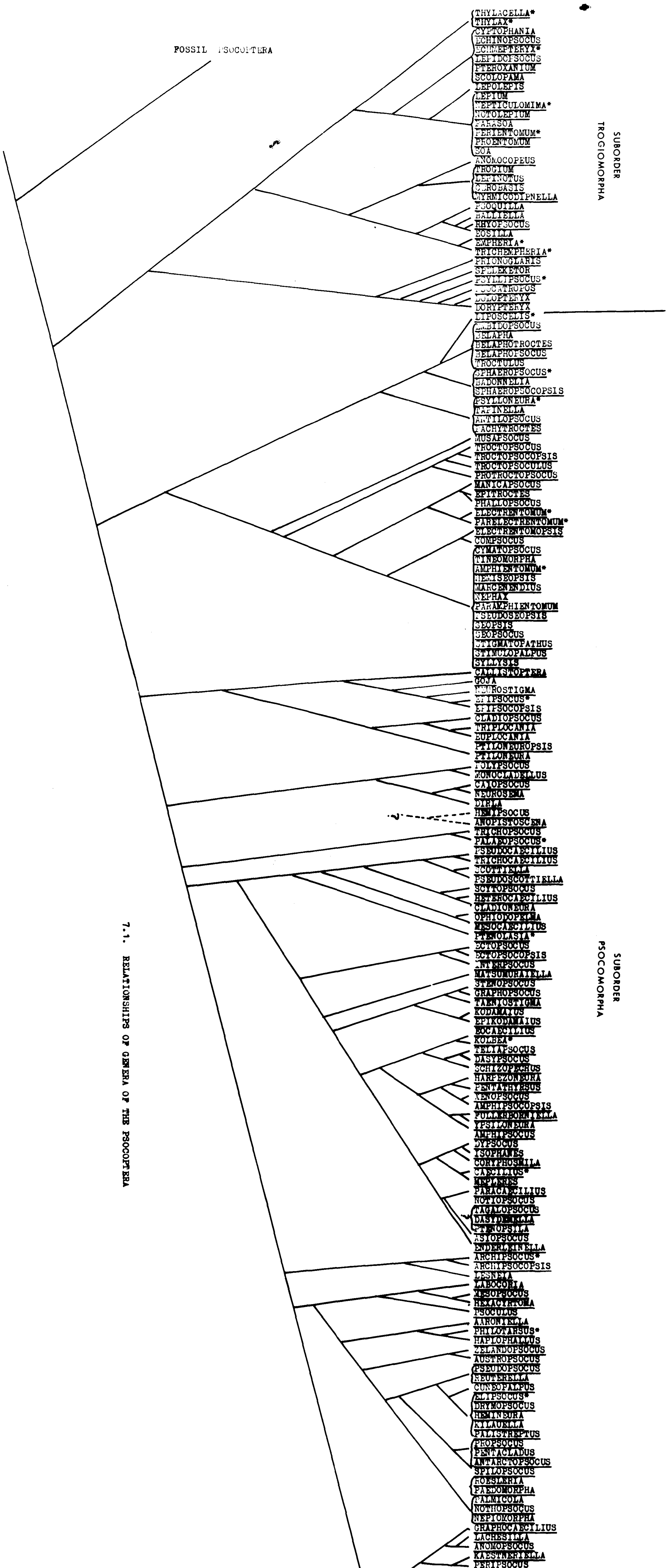
6.29 RELATIONSHIPS WITHIN THE PSOCINAE



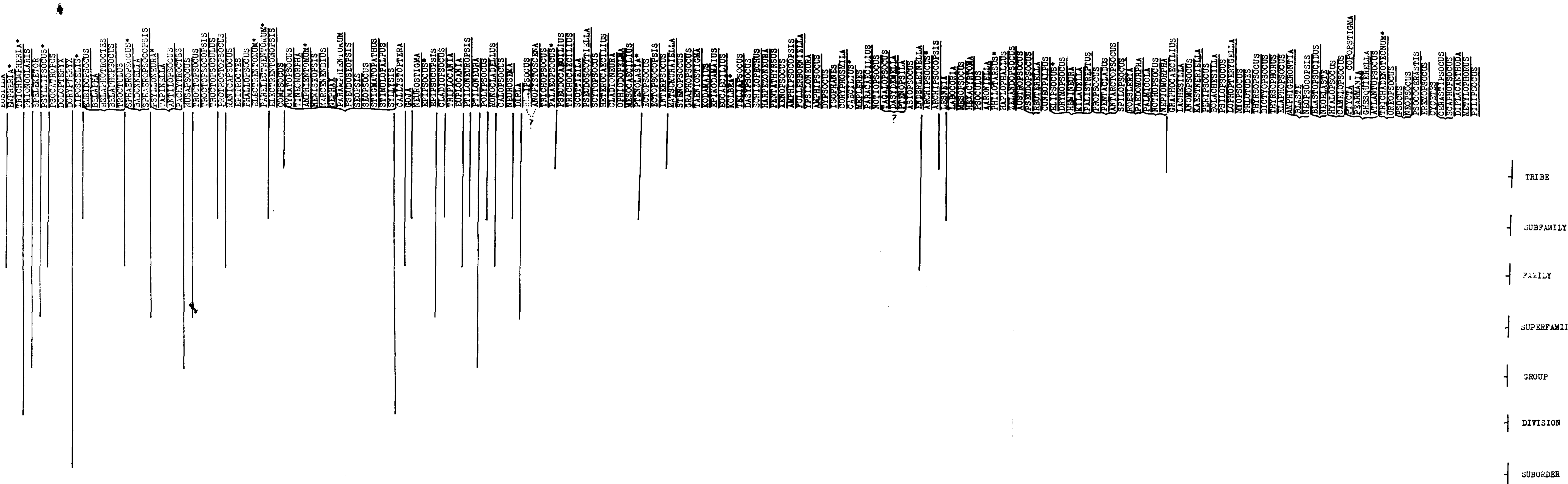
6.30 RELATIONSHIPS WITHIN THE CERASTIPSOCINI



6.31 RELATIONSHIPS WITHIN THE METYLOPHORINI



7.1. RELATIONSHIPS OF GENERA OF THE PSOCOPTERA



7.2 SUPRAGENERIC CATEGORIES OF THE PSOCOPTERA

APPENDIX

KEY TO THE GENERA OF THE PSOCOPTERA

The following key is divided into two, a key to the Superfamilies followed by a key to the genera within each Superfamily.

As the key is intended to be a practical aid to identification easily seen characters are used where possible, although these may vary a little. This problem arises particularly where convergence has taken place e.g. in a group with 13-segmented antennae there may be one or two aberrant genera with fewer segments. Where this occurs more stable, less easily seen, characters needing special preparation of specimens are also given. Males and females of some genera will be keyed out at different parts of the key and, again usually due to convergence in obvious characters, related genera may appear well separated from their nearest relatives.

This key owes much to the work of Roesler (1944) with whose key it corresponds in many groups.

Identifications should, of course, be checked against the generic definitions and figures.

KEY TO SUPERFAMILIES OF PSOCOPTERA

1. Antennae more than 20-segmented, sometimes with secondary "annulation". Tarsi 3-segmented. Pterostigma never thickened or absent. Paraprocts with strong posterior spine. (TROGIOMORPHA) 2

Antennae usually 13-segmented, if up to 17-segmented some segments are secondarily "annulated". Tarsi 2- or 3-segmented. Pterostigma thickened or not. Paraprocts without posterior spine. (PSOCOMORPHA).........8

2. Head short and broad. Inner side of second maxillary palp segment with peg-like sensillum. Fore wings with Cu_2 and IA ending separately at wing margin. Brachyptery or aptery common. Body and wings sometimes with scales. (TROGIOFORMIA) 3

Head long. Inner side of second maxillary palp segment without sensillum. Fore wings with Cu_2 and IA meeting in a point (nodulus). In brachypterous forms at least some venation evident. Never with scales on body or wings. (PSYLLIPSOCIFORMIA) 6

3. Claws with preapical tooth. Body and wings with scales except a few genera in which the fore wings are pointed. (PERIENTOMETAE).........4

Claws without preapical tooth. Body and wings without scales. Apterous or with wings broadly rounded at apex. (TROGIETAE) 5

4. Wings and body without scales. (Antennae about 40-segmented. Hind wings with R_1 arising basad of M_2. Hind wings with closed basal cell).. THYLACELLOIDEA
(*Thylax* and *Thylacella*)
(Page 7)

Wings and body scaly .... PERIENTOMOIDEA
(Page 8)

5. Fore wings present only as flap-like vestiges or absent. Hind wings absent .... TROGIOIDEA
(Page 11)

Fore wings fully developed or reduced but always with at least some recognizable veins. Hind wings often reduced .... PSOQUILLOIDEA
(Page 12)

6. Claws without preapical tooth...................7
Claws with preapical tooth. (At least a few setae on veins of fore wings)......... PSYLLIPSOCOIDEA
(Page 13)

7. Lacinia present in adults .... SPELEKETOROIDEA
(only one genus *Speleketor*)

Lacinia absent in adults .................PRIONOGLAROIDEA
(only one genus *Prionoglaris*)

8. Labial palps 1- or 2-segmented. Antennae 11- to 17-segmented, at least some flagellar segments with secondary "annulations". Pterostigma not thickened. Tarsi usually 3-segmented. Winged forms, if not bearing scales, lack ctenidiobothria. Pearman's organ, if present at all, in form of a hyaline, hemispherical capsule. Subgenital plate usually with T-shaped

sclerite. Gonopophyses complete, external valve glabrous. Second maxillary palp segment sometimes with sensillum. (AMPHIENTOMIFORMIA) ...9

Labial palps unsegmented. Antennae 13-segmented, or occasionally with fewer. Secondary "annulations" never present. Winged forms with ctenidiobothria. Pterostigma thickened. Scales never present. Tarsi 2-segmented. Pearman's organ usually present, well developed and strongly chitinized. Subgenital plate without T-shaped sclerite. Gonapophyses various, but with external valve (or its remnant) setose. Maxillary palp without sensillum. (PSOCIFORMIA)........................12

9. Antennae usually 15-segmented, at most 17-segmented, occasionally fewer than 15-segmented. Wings usually reduced or absent. IA and Cu_2 end separately at wing margin (no nodulus). Body and wings not scaly. Meso- and metanotum often fused. Claws with preapical tooth. Wings held horizontally over abdomen. Head short. No maxillary palp sensillum. (LIPOSCELETAE)...................................10

Antennae 11- to 15-segmented. Wings seldom reduced, rarely absent. IA and Cu_2 meeting wing margin together (nodulus). Body and wings frequently scaly. Meso- and metanotum not fused. Claws variously toothed. Wings usually held roof-wise over abdomen. Head long Maxillary palp sensillum often present. (AMPHIENTOMETAE)..................................11

10. Wings, when present, with incomplete venation, lacking terminal branching. (In all apterous forms meso- and metathorax fused)..........LIPOSCELOIDEA
(Page 14)

Wings, when present, with complete venation. (In both alate and apterous forms eyes situated near vertex. Meso- and metathorax distinct. Thoracic sterna narrow, without setae. Hind femora never broadened) .. ..PACHYTROCTOIDEA
(Page 16)

11. Tarsi 2-segmented ........................MUSAPSOCOIDEA
(only one genus Musapsocus)

Tarsi 3-segmented .... AMPHIENTOMOIDEA
(Page 17)

12. Labrum on inner side with two strongly chitinized ridges, often converging towards and fusing with anterior margin and showing through to outer side. Lacinia broadening towards apex which is divided into many small teeth. Outer edge of mandible bluntly angled. Claws fairly straight with preapical tooth. Head long, genae long. (EPIPSOCETAE) 13

Labrum without chitinized ridges. Lacinia equally broad in distal third or slightly narrowing, usually with apex divided into few large teeth. Outer edge of mandible smoothly curved. Head short. Claws usually curved, with or without preapical tooth. (PSOCETAE).....14

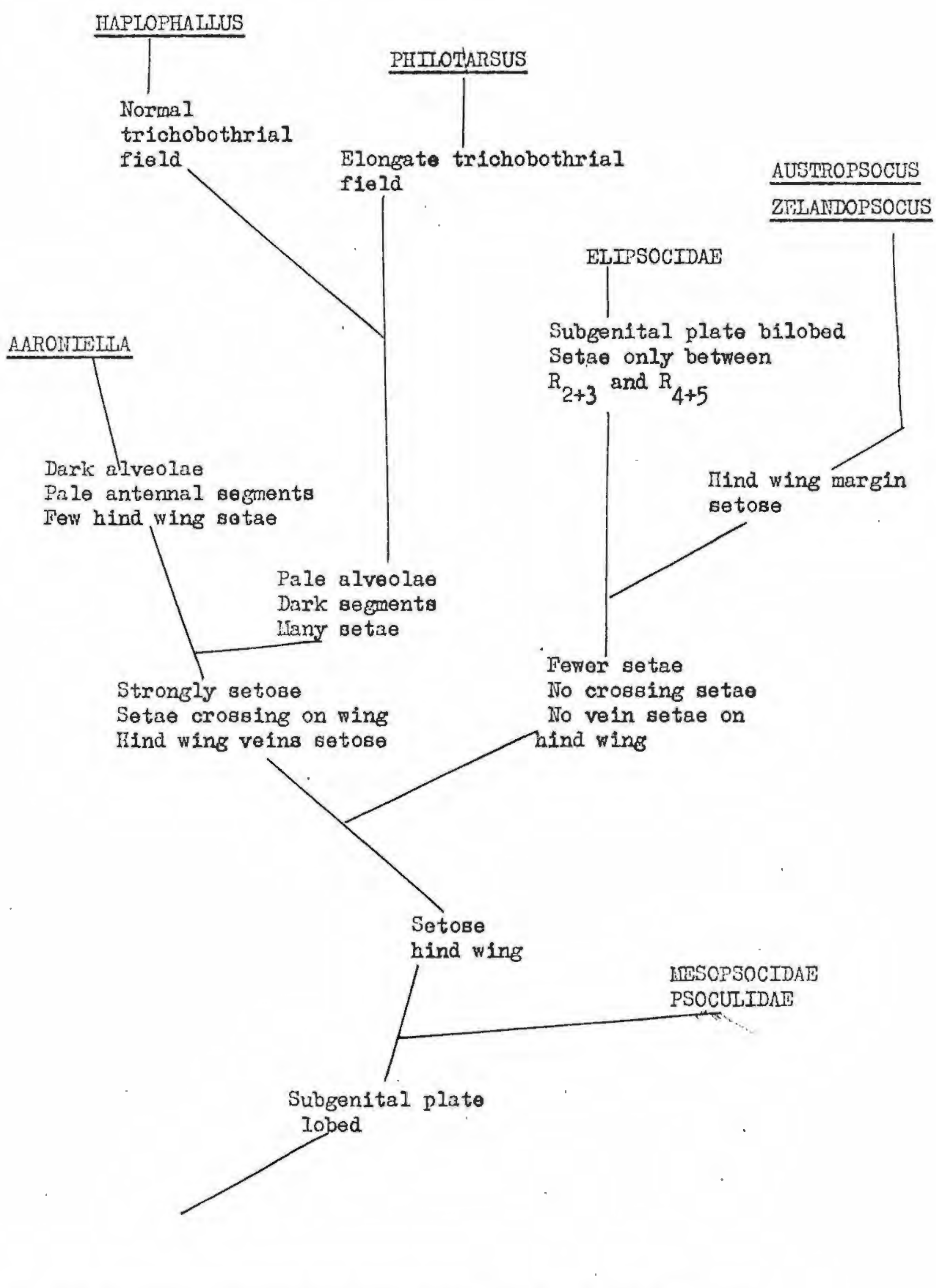
13. Tarsi 2-segmented ........................EPIPSOCOIDEA
(Page 21)

Tarsi 3-segmented .... PTILONEUROIDEA
(Page 22)

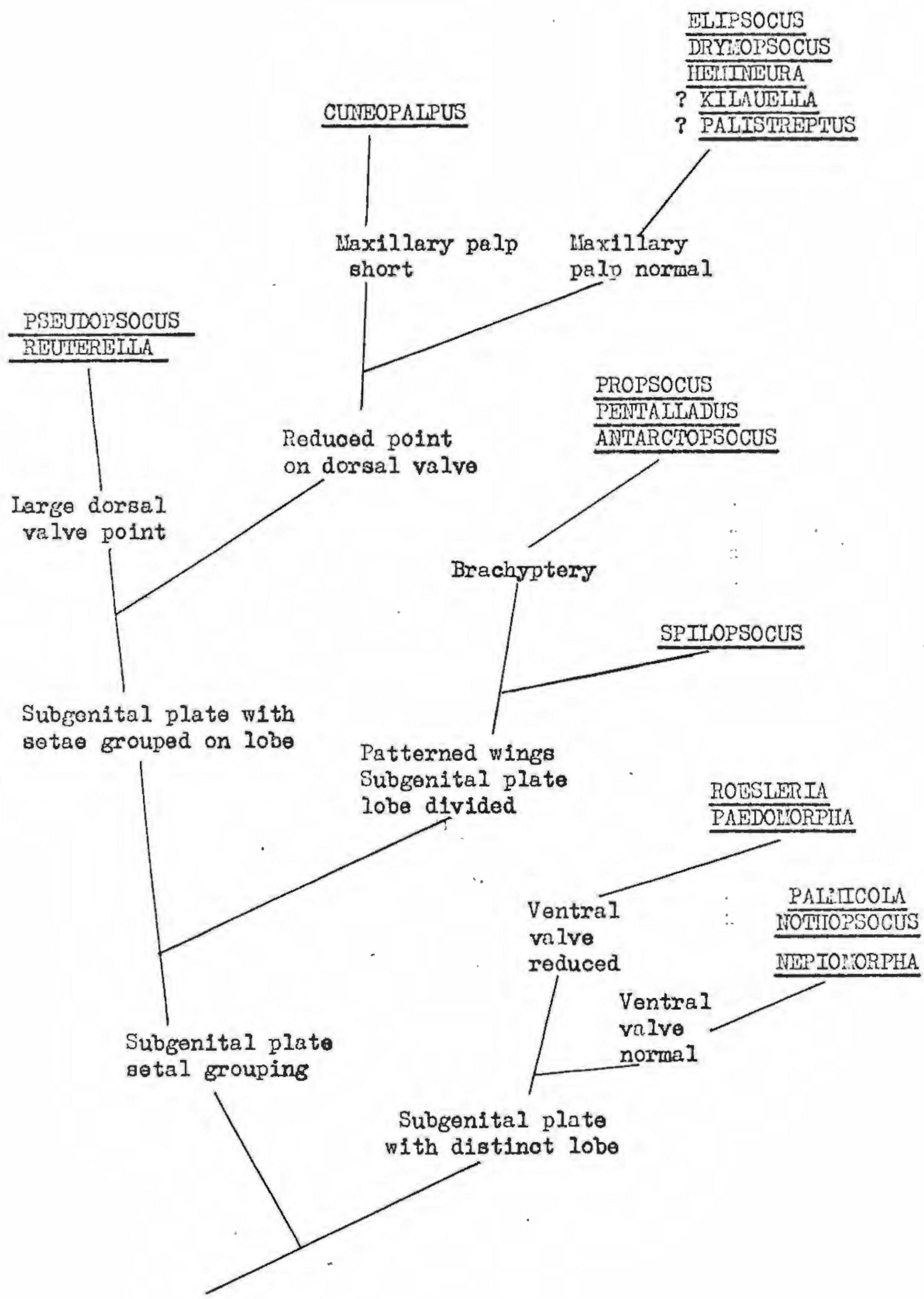
14. Fore wings with Rs and M joined by a cross-vein and either with M less than 3-branched

or with some veins anastomosing to form a more or less extensive reticulation .... CALOPSOCOIDEA (Page 23)

Fore wings with Rs and M fused. If Rs and M are joined by a crossvein then neither M less than 3-branched nor with reticulation ... PSOCOIDEA (Page 24)



6.21 RELATIONSHIPS WITHIN THE PHILOTARSIDAE (part of GROUP II)



6.22 RELATIONSHIPS WITHIN THE ELIPSOCIDAE
(part of GROUP II)

KEY TO GENERA OF PERIENTOMOIDEA

1. Antennae less than 30-segmented. Segments relatively long, about four times as long as wide. (Hind wing with closed basal cell). (PERIENTOMINAE)......... 9

   Antennae 30-segmented to 50-segmented. Segments relatively short, about twice as long as broad 2

2. Fore wings reduced, elytriform, without any obvious venation. Hind wings absent. (LEPOLEPIDINAE)..Lepolepis

   Fore wings and hind wings fully developed or reduced but with evident venation 3

3. Hind wings with closed basal cell. (LEPOLEPIDINAE) Lepolepis

   Hind wings without closed basal cell. (LEPIDOPSOCIDAE) 4

4. Fore wings with Rs branched. Hind wings usually present......... 7

   Fore wings with Rs simple. Hind wing reduced or absent 5

5. Fore wings with M 3-branched. Hind wings minute. Ocelli present .... Scolopama

   Fore wings with M 1- or 2-branched. Ocelli absent 6

6. Fore wings drawn out into a long point. Rs and M fused for a length. Basal section of Rs absent so that Rs appears to arise from M. Hind wings absent .... Echinopsocus

Fore wings almost rounded. Rs and M not meeting .... Pteroxanium

7. Fore wings with M 3-branched. Ocelli present. Hind wings developed 8

Fore wings with M 2-branched. Ocelli absent. Hind wings reduced .... Cyptophania

8. Fore wings with Rs and R_1 joined by a cross-vein, sometimes absent .... Echmepteryx

Fore wings with Rs and R_1 fused for a length. Hind wings with M_1 and M_2 separate or arising from common stem .... Lepidopsocus

9. Fore and hind wings reduced, sometimes to small vestiges .... Parasoa

Fore wings not reduced 10

10. Fore wings with Sc complete, basal section ending in R. Hind wings with R_1 arising distad of M_1 11

Fore wings with Sc incomplete. (Fore wings acuminate) 12

11. Fore wings rounded .... Soa

Fore wings accuminate.......................*Proentomum*

12. Hind wings with R_1 arising distad of M_1. (In fore wings R_1 and Rs fused for a length or meeting in a point).....................*Nepticulomima*

Hind wings with R_1 arising basad of M_1.............13

13. Hind wings with R_1 arising between M_1 and M_2 (exceptionally opposite M_1)......................14

Hind wings with R_1 arising basad of M_2. (R_1 and Rs joined by a crossvein)..............*Notolepium*

14. Fore wings with R_1 and Rs fused for a length or meeting in a point...............*Perientomum*

Fore wings with R_1 and Rs joined by a crossvein.................................... *Lepium*

KEY TO GENERA OF TROGIOIDEA

1. Fourth segment of maxillary palp more than twice as long as wide. (Mesothorax weakly developed. Hind tibiae with 2 spurs)................. Lepinotus

   Fourth segment of maxillary palp hardly twice as long as broad, hatchet-shaped 2

2. Laciniae asymmetrical, left lacinia much reduced. (Metathorax better developed than mesothorax. Males without abdominal "brush". Females not known). (ANOMOCOPEIDAE) ...... Anomocopeus

   Laciniaeequally developed. (Males with abdominal "brush". Mesothorax better developed than metathorax) 3

3. Hind tibiae with only 2 apical spurs. Fore wings reduced to scale-like remnants. (Antemnae 27- to 29-segmented) ....Trogium

   Hind tibiae with 1-3 preapical spurs in addition to 2 apical spurs.(Fore wings reduced or absent)............................4

4. Fore wings strongly reduced to scale-like flaps or small knobs. Hind tibiae with 1 or 2 preapical spurs as well as two apical spurs.................................... Cerobasis

   Fore wings absent. Hind tibiae with 3 preapical and 2 apical spurs .... Myrmecodipnella

KEY TO GENERA OF PSOQUILLOIDEA

1. Hind wings with M branched. Fore wings with M_3 arising distad of Rs bifurcation. Macropterous. (EMPHERIIDAE) 2

   Hind wings with M simple, or wings reduced. (PSOQUILLIDAE) 3

2. Most of fore wing membrane setose .... *Trichempheria*

   Most of fore wing membrane not setose ...... *Empheria*

3. Fore wing venation clear, wings not elytriform 4

   Fore wings elytriform, venation indistinct. (Hind wings lack R_1) .... *Eosilla*

4. Hind wings with R_1 present 5

   Hind wings lacking R_1 .... *Balliella*

5. Fore wings with stem of cubital fork at least as long as Cu_2 .... *Psoquilla*

   Fore wings with stem of cubital fork hardly a third as long as Cu_2 .... *Rhyopsocus*

KEY TO GENERA OF PSYLLIPSOCOIDEA

1. Margin of fore wings setose or strongly so. Fore wings often reduced. Hind wings may be absent. Brachypterous forms with fore wing margin with long setae, sometimes as long as half the width 2

   Margin of fore wings glabrous. Veins with a few small setae. Brachypterous forms have only scattered setae on reduced fore wings ...... Psyllipsocus

2. Fore wings with Rs and Cu branched 3

   Fore wings with Rs and Cu simple or absent 4

3. Margin of fore wings with strong setae in more than one row. Cu_{1a} only twice as long as Cu_{1b}. Hind wings reduced. Body and antennae strongly setose ....Psocatropos

   Margin of fore wings setose. Cu_{1a} more than five times as long as Cu_{1b}. Hind wings not reduced. Body and antennae fairly setose ..Psyllipsocus

4. Fore wings with M 2- or 3-branched. Venation variable but at least 7 veins present ......Psocatropos

   Fore wings with M not branched. (Fore wings elongate, narrow) 5

5. Only two veins (Rs, M) present ....Dorypteryx

   Only 5 unbranched veins present (R_1, Rs, M, Cu_1, Cu_2) ....Dolopteryx

KEY TO GENERA OF LIPOSCELOIDEA

1. In alate forms fore and hind wings present. Eyes near vertex, hemispherical, compound. In apterous forms eyes remote from vertex, each of two large elements alone or preceded by six or fewer ocelloids. In all forms prothorax with lobar divisions. Thoracic sterna broad basally. (LIPOSCELIDAE) 2

In alate forms only fore wings present, elytriform. In all forms eyes remote from vertex, composed of two ocelloids, none greatly enlarged. Pronotum simple. Thoracic sternites narrow, without setae. Hind femora not broadened (SPHAEROPSOCIDAE) 7

2. Tarsi 2-segmented 3

Tarsi 3-segmented 4

3. Antennae 9-segmented ....Belaphopsocus

Antennae 10-segmented ....Troctulus

4. Hind tibiae with strong apical spur. Alate forms with large, many-faceted eyes and 3 ocelli, apterous forms with eyes of few ocelloids and no ocelli. Hind femora without protuberance 5

Hind tibiae without apical spur. Apterous. Eyes of 6-8 ocelloids, no ocelli. Hind femora with protuberance at point of greatest width ....Liposcelis

5. Fourth segment of maxillary palp elongate, little thicker than third segment ....Embidopsocus

Fourth segment of maxillary palp much larger than third segment 6

6. Fourth segment of maxillary palp spherical .Belapha

Fourth segment of maxillary palp somewhat swollen ....Belaphotroctes

7. Fore wings not bent ventrally along margin. At least 4 main veins. Number of ommatidia variable. Body sculpturation strongly granulose. Fourth segment of maxillary palp fusiform 8

Fore wings bent ventrally along margin. Only 2 main veins present. 7 ommatidia. Body sculpturation finely granulose. Fourth segment of maxillary palp subcylindrical, very long ....Badonnelia

8. 5 principle veins. R_1 and Rs simple. M and Cu_1 branched. Cu_2 rudimentary ....Sphaeropsocus

4 principle veins, simple, (Cu_2 absent), confluent apically or not. (3-10 ommatidia)Sphaeropsocopsis

KEY TO GENERA OF PACHYTROCTOIDEA

1. Head with antler-like outgrowths on vertex Antilopsocus

Head without antler-like outgrowths on vertex 2

2. Ocelli present. Antennae more than 15-segmented 3

Ocelli absent. Antennae 15-segmented (Apterous)...................................... 5

3. Wings broad, glabrous ....Psylloneura

Wings narrow. Fore wings with small setae on margin 4

4. Hind wings with R_1 present. Fore wings lacking distal section of Sc ....Pachytroctes

Hind wings without R_1. Fore wings with distal section of Sc ....Tapinella

5. Eyes reaching level of vertex. Third tooth of lacinia very small, lacinia apparently with 2 teeth ....Tapinella

Eyes not reaching level of vertex. Lacinia clearly with 3 teeth.............. ....Pachytroctes

KEY TO GENERA OF AMPHIENTOMOIDEA

1. Lacinial tip with median cusp divided, lateral cusp with two or more prominent preapical denticles. (Wings and body without scales. Antennae 11-, 13-, or 15-segmented. Fore wings with 2A running a short distance along wing margin then joining IA. No scales). (TROCTOPSOCIDAE).......................2

Lateral cusp of lacinial tip curved outward, bearing low, rounded denticles (AMPHIENTOMIDAE)...5

2. Antennae 13-segmented..........................3

Antennae 11- or 15-segmented.....................4

3. Fore wing with M-Cu crossvein..............Troctopsocus

Fore wing with areola postica free.........Troctopsocopsis

4. Antennae 15-segmented.....................Protroctopsocus

Antennae 11-segmented.....................Troctopsoculus

5. Body and wings without scales...................6

Body and wings scaly. (AMPHIENTOMINI) 12

6. Antennae 13- or 14-segmented. 7

Antennae 15-segmented...........................10

7. Antennae 13-segmented 8

Antennae 14-segmented ....*Compsocus*

8. Eyes pubescent ....*Electrentomopsis*

Eyes not pubescent 9

9. Hind wings with basal section of Rs absent .*Electrentomum*

Hind wings with basal section of Rs present *Parelectrentomum*

10. Epicranial plates raised into knobs on vertex.
R_1 broadened into a flat plate at wing margin *Manicapsocus*

Epicranial plates normal. Wings reduced or
absent 11

11. Wings reduced in male, with a single vein.
Very small in female ....*Nothoentomum*

Apterous ....*Phallopsocus*

12. Media in hind wings 2-branched 13

Media in hind wings simple or hind wings reduced .. 14

13. Ocelli close to eyes. Margin of fore wings
not sinuous behind apex ....*Tineomorpha*

Ocelli removed from eyes by more than their
diameter. Margin of fore wings sinuous
behind apex ....*Cymatopsocus*

14. Three ocelli. Fore wings with 2A 15

Two or no ocelli. Fore wings without 2A 22

15. Hind wings with R_1 ending in costa 16

Hind wings with R_1 ending free in wing, basal section of Rs absent 17

16. Claws with one preapical tooth. Fore wings without distal section of Sc. ....Hemiseopsis

Claws with two preapical teeth. Fore wings with distal section of Sc..................Amphientomum

17. Claws with one preapical tooth 18

Claws with two preapical teeth 20

18. Distal section of Sc present.....................19

Distal section of Sc absent................Stimulopalpus

19. No sensillum on second maxillary palp segment ....Pseudoseopsis

Sensillum on second maxillary palp segment . Seopsis

20. Fore wings with stem of radial fork at least two thirds length of R_{2+3}. Distal section Sc absent from fore wings 21

Fore wings with stem of radial fork very short or even absent. Females brachypterous .... Seopsocus

21. Fore wing margin not sinuous...............Paramphientomum

Fore wing margin sinuous...................Syllysis

22. Ocelli absent. Macropterous. Cu_2 and nodulus present............................Stigmatopathus

Ocelli present. Fore wings strongly reduced with reduced venation. Cu_2 and nodulus absent.............................Nephax

Note: Marcenendius is probably an Amphientomid but cannot be placed owing to the poor original description.

KEY TO GENERA OF EPIPSOCOIDEA

1. Pterostigma fused with Rs for a length.
Hind wings with M 2-branched.
(CALLISTOPTERIDAE) ....Callistoptera

Perostigma without spurvein. Hind wings
with M simple or 5-branched (EPIPSOCIDAE) 2

2. Media in hind wings 5-branched ....Goja

Media in hind wings simple 3

3. Pterostigma traversed by 5-9 crossveins ....Neurostigma

Pterostigma normal 4

4. Lacinia hardly broadened apically, with
narrow internal tooth and external tooth
rounded then extended apically into a
process ....Epipsocopsis

Lacinia with narrow internal tooth and
external tooth divided into many small
teeth ....Epipsocus

KEY TO GENERA OF PTILONEUROIDEA

1. Media in hind wings 2- to 4-branched. Media in fore wing 5- to 8-branched (CLADIOPSOCIDAE)....2

   Media in hind wings simple (PTILONEURIDAE) 3

2. Apex of areola postica pointed, joined to M by crossvein. Media in fore wings 7- to 8-branched, in hind wings 4-branched.....*Ptiloneuropsis*

   Apex of areola postica rounded, free ....*Ptiloneura*

3. Media in fore wings 4-branched ....*Euplocania*

   Media in fore wings 3-branched 4

4. Fore wings without many side branches arising from veins ....*Triplocania*

   Fore wings with many small side branches arising from veins ....*Cladiopsocus*

KEY TO GENERA OF CALOPSOCOIDEA

1. Fore wings with areola postica pointed and long, Cu_{1b} only little shorter than Cu_{1a}. At least some veins in distal part of wings forming a network. M at least 3-branched. IA almost as long as Cu_2. Vertex sharp. (Female gonapophyses complete). (CALOPSOCIDAE)....3

   Fore wings with areola postica semicircular or triangular, Cu_{1b} much shorter than Cu_{1a}. No network of veins. M simple or 2-branched. (Female gonapophyses reduced). (POLYPSOCIDAE)....2

2. Fore wings with M 2-branched ....Polypsocus

   Fore wings with M simple ....Monocladellus

3. Fore wings of normal form, about three times as long as wide....................................4

   Fore wings broad, only twice as long as wideCalopsocus

4. All branches of R, M and Cu in fore wing connected by network of veins..............Neurosema

   Only branches of R connected by network of veins..................................Dirla

KEY TO GENERA OF PSOCOIDEA

1. Labial palps broadly triangular, laterally diverging; lacinia narrowing apically usually without strongly diverging teeth. (Gonapophyses of female usually reduced, the external valve being represented by a strong seta only. Claws without preapical tooth. Tarsi 2-segmented). (CAECILIINI)......................2

Labial palps short and appressed, nearly semicircular. Lacinia with apical third equally broad or broadening towards apex, usually markedly toothed. (Gonopophyses various, rarely without well developed, setose external valve)..........................33

2. Vertex sharply angled; head flattened 3

Vertex rounded 5

3. Areola postica fused to media; M 2-branched. Isophanes

Areola postica free, not fused to media; M 3-branched 4

4. Venation normal, not distorted ....Coryphosmila

Venation distorted ....Dypsocus

5. Areola postica fused to M or joined to it by a crossvein (discoidal cell closed). Apterous forms not known. Fore wings with M 3-branched....6

Areola postica free; if otherwise then apterous or the fore wing has M more than 3-branched.......11

6. Pterostigma without vein from apex to Rs..........7

Pterostigma with vein from apex to Rs. (Hind wing margin setose, mainly between R_{2+3} and R_{4+5}).10

7. Hind wing margin with setae mainly between R_{2+3} and R_{4+5} ....<u>Matsumuraiella</u>

Hind wing margin with setae along whole length....8

8. Pterostigma short and broad 9

Pterostigma very long and narrow. Areola postica fused with M for a length..........<u>Taeniostigma</u>

9. M_1 divided near wing margin . ...<u>Epikodamaius</u>

M_1 not divided ....<u>Kodamaius</u>

10. Pterostigma long and narrow. Fore wing veins and margin with strong setae..........<u>Stenopsocus</u>

Pterostigma short and broad. Fore wing veins and margin weakly setose ....<u>Graphopsocus</u>

11. Pterostigma with spurvein Brachyptery not known.......................................12

Pterostigma without spurvein or wings reduced.....18

12. Fore wings with Rs 3- to 4-branched. Veins in basal half of wings with setal tufts. Hind wings with M branched............................13

Fore wings with Rs 2-branched. No setal tufts. Hind wings with M simple 15

13. Pterostigma with complete crossvein from hind angle to Rs.........................Pentathyrsus

Pterostigma with at most a spurvein, likewise at apex of areola postica...................14

14. Fore wings with Rs and M fused for a length. M with 5 or more branches. Strongly setose.Harpezoneura

Fore wings with Rs and M meeting in a point or joined by a crossvein. M 4-branched..... Xenopsocus

15. Fore wings with M 3-branched.....................16

Fore wings with M not 3-branched.................17

16. Distal veins with one row of setae.........Fulleborniella

Distal veins with more than one row of setae Amphipsocus

17. Fore wings with M 4-branched...............Amphipsocopsis

Fore wings with M 2-branched...............Ypsiloneura

18. Forewings with Cu_1 5-branched. Macropterous. Schizopechus

Fore wings with Cu_1 2-branched (areola postica normal). Brachyptery and aptery known............19

19. Hind wing margin setose along whole length. Apterous and brachypterous forms known............20

Hind wing margin setose mainly between R_{2+3} and R_{4+5}. Apterous or brachypterous forms not known..31

20. Veins of fore wings and outer half of hind wings with more than one row of setae. Brachypterous females have strongly setose bodies.......21

Veins of fore wings with exception of R with one row of setae. Hind wing veins glabrous. Brachypterous females finely setose..............22

21. Pterostigma short and broad. Setae long....Dasypsocus

Pterostigma narrow. Setae fairly short. Females often apterous.....................Kolbea

22. Fore wings with setae on membrane in distal half of wing. Macropterous ....Ptenolasia

Fore wings without setae on membrane of distal half of wing. Females with wings sometimes reduced...23

23. Fore wings with M 3-branched. Females often with reduced wings...............................24

Fore wings with M 2-branched, macropterous..Mepleres

24. Pterostigma narrow, without distinct hind

angle. Macropterous............................25

Pterostigma with R_1 curving. Sometimes with reduced wings or apterous........................26

25. Wing apex pointed..........................Lacroixiella

Wing apex rounded..........................Tagalopsocus

26. Ventral valve of gonapophyses pointed............27

Ventral valve of gonapophyses rounded at apex.....29

27. Dorsal valve of gonapophyses pointed. (Rs at least slightly sinuous before bi-jurcation. Females sometimes apterous or brachypterous)............................Caecilius

Dorsal valve of gonapophyses rounded.............28

28. Dorsal valve as long as ventral valve. (Wing apex somewhat pointed)...............Eocaecilius

Dorsal valve short, rudimentary. (Rs almost straight before bifurcation)........Enderleinella

29. Ventral and dorsal valves distinctly separate, of greatly differing sizes.............30

Ventral and dorsal valves fused, of subequal sizes (Females apterous)..........Asiopsocus

30. Fore wings with M 2-branched ....<u>Notiopsocus</u>

Fore wings with M 3-branched. (Macropterous)
Rs almost straight before bifurcation......<u>Paracaecilius</u>

31. Fore wings with margin and veins setose...........32

Fore wings glabrous ....<u>Ptenopsila</u>

32. Fore wings with setae on veins, not on
membrane ....<u>Dasydemella</u>

Fore wings with setae on membrane and veins. <u>Teliapsocus</u>

33. Fore wings with areola postica joined to
media (discoidal cell closed). Exceptionally
females are brachypterous but these have
glandular setae on head 34

Fore wings with areola postica free or absent
(discoidal cell open). Sometimes brachyp-
terous or apterous but without glandular setae
on head 71

34. Tarsi 3-segmented.................................35

Tarsi 2-segmented................................ 39

35. Media in fore wings 5-branched (Claws
without preapical tooth)...................<u>Pentacladus</u>

Media in fore wings 3-branched....................36

36\. Fore wings with pattern made up of many irregular, confluent spots. (Claws with preapical tooth. Macropterous)..................37

Fore wings with bold pattern. (Claws with or without preapical tooth. Brachypterous forms with evident venation.)...................Propsocus

37\. Hind wings with Rs and M fused for a length. Phlotodes

Hind wings with Rs and M joined by a crossvein....38

38\. Fore wing margin straingt between veins.....Myopsocus

Fore wings with margin curving between veins. Lophopterygella

39\. Fore wings with M 2-branched. (Macropterous)......40

Fore wings with M 3-branched or wings reduced.....41

40\. Fore wings with Cu_{1a} normally developed, joined to M by a crossvein. Rs and M meeting in a point........................ Hemipsocus

Fore wings with Cu_1 fusing with M but with distal section of Cu_{1a} absent. Rs and M fused for a length........................Anopistoscena

41\. Claws with preapical tooth. Subgenital plate of female simple. Male paraproct without chitinous spurs...........................42

Claws with preapical tooth. Subgenital plate of female with median posterior lobe. Male paraproct with spurs............................43

42. Fore wings with setae on margin and veins. Setae fine and in one row on veins..........Antipsocus

Fore wings only in basal third with setae on veins. Margin glabrous. (Gonapophyses reduced to one pair)........................Anomopsocus

43. Pterostigma widest in distal half.................46

Pterostigma widest in basal half..................44

44. Fore tibiae flattened and broadened........Thyrsophorus

Fore tibiae normal, cylindrical..................45

45. Fore wings with network of veins in apical half...................................Dictyopsocus

Fore wings with normal venation, no network.Thyrsopsocus

46. Fore wings with radial fork free, not meeting media...................................47

Fore wings with R_{4+5} meeting media..........Cycetes

47. Fourth segment of maxillary palp elongate, at least about 2.5 times as long as wide. (Sometimes apterous or with reduced wings)........52

Fourth segment of maxillary palp short, less than twice as long as wide (Antennae at least double wing length or more. Dorsal valve of gonapophyses with a short apical point. Nymphs without knobbed setae, solitary, large to very large species.

Macropterous.)....................................48

48. Fore wings with R_{2+3} and R_{4+5} separating at a narrow angle, about 60°........................49

Fore wings with R_{2+3} and R_{4+5} separating at a wide angle, 90° or more........................50

49. Hypandrium asymmetrical....................<u>Pearmania</u>

Hypandrium symmetrical....................<u>Psococerastis</u> and <u>Pilipsocus</u>

50. At least first flagellar segment strongly thickened..................................<u>Eremopsocus</u>

First flagellar segment not abnormally thickened..51

51. Sc ending in costa.........................<u>Scaphopsocus</u>

Sc not ending in costa.....................<u>Cerastipsocus</u>

52. Antennae hardly longer than fore wing, often shorter. Dorsal valve of gonapophyses usually pointed. Nymphs often with knobbed, glandular setae. (Sometimes apterous or brachypterous)..................................55

Antennae at least one and a half times wing length. Dorsal valve of gonapophyses broadly rounded. Nymphs without knobbed, glandular setae. (Usually large species. Macropterous)....................................53

53. Veins and hind margin of fore wings especially

in basal half, setose. Scutellum of meso- and metathorax with strong spines..........Diplacanthoda

Fore wings glabrous. No thoracic spines..........54

54. Pterostigma with spurvein.................Brachinodiscus

Pterostigma without spurvein...............Metylophorus

55. Eighth and ninth sternites of male abdomen strongly chitinized and partly fused to form a capsular structure occupying from a quarter to a half of the abdomen. Fore wing with first section of Cu_{1a} usually shorter than second. Parameres usually separated............66

Apex of male abdomen normal. Pallosome with parameres fused to form a ring-like structure, Fore wings with first section of Cu_{1a} usually longer than second. (If brachypterous females compare couplets 59 and 64)....................56

56. Eyes on lateral extensions of head.........Steleops

Eyes normal....................................57

57. Outer margin of fore wings and apex of hind wings with fine setae. Indistinct spur- vein on pterostigma....................... Ptycta

Fore wings glabrous...........................58

58. Pterostigma concave basad of broadest point......61

Pterostigma convex basad of broadest point.......59

59. Discoidal cell strongly concave on distal margin. Females brachypterous but with abdominal segments raised into conspicuous "hump"....................................Camelopsocus

Discoidal cell normally a little concave. Abdomen normal...................................60

60. First and second sections of Cu_{1a} almost in a straight line.........................Oreopsocus

First and second sections of Cu_{1a} at an angle to one another.......................Atlantopsocus

61. Hind angle of pterostigma (broadest point) sharp usually with spurvein......................64

Hind angle of pterostigma rounded, without spurvein...62

62. First and second sections of Cu_{1a} almost in a straight line.........................Trichadenotecnum

First and second sections of Cu_{1a} at an angle to one another...........................63

63. Rs and M fused for a short length..........Psocus
Psocidus
(see text definition)

Rs and M joined by a short crossvein.......Ghesquierella

64. Adults without knobbed glandular setae. Areola postica fused with media..................65

Adults with knobbed glandular setae. Females brachypterous. Areola postica usually meeting media in a point........................Neopsocus

65. First and second sections of Cu_{1a} almost in a straight line. Rs and M meeting in a point. Rs straight before bifurcation......Hyalopsocus

First and second sections of Cu_{1a} at least at a small angle to one another. Rs and M not meeting in a point. Rs somewhat sinuous before bifurcation........................Copostigma complex

66. Areola postica joined to M by a crossvein. (Macropterous)............................Elaphopsocus

Areola postica fused to M. (If brachypterous females, these have knobbed glandular setae)......67

67. Adults with knobbed glandular setae. Females brachypterous........................Neopsocopsis

Adults without knobbed glandular setae. (Macropterous)...................................68

68. Rs and M in fore wings fused for a length.........69

Rs and M in fore wings joined by a crossvein Amphigerontia

69. Hypandrium asymmetrical ....Blastopsocidus

Hypandrium symmetrical...........................70

70. Hypandrium with sharply pointed lateral lobes....................................Blaste

Hypandrium with lateral lobes not pointed...Neoblaste

71. Tarsi 3-segmented................................72

Tarsi 2-segmented................................96

72. Fore wings short, round, elytriform, with long setae.................................Austropsocus

Macropterous or brachypterous, in latter case wings not elytriform and without excessively strong setae.........................73

73. Hind wings usually with IA less than half as long as Cu_2. Wings with some setae. In apterous females subgenital platle simple with two posterior lobes, or with two groups of marginal setae..............................74

Hind wings with IA at least half as long as Cu_2. Wings glabrous. In apterous females subgenital plate with median posterior lobe.......93

74. Hind wings without marginal setae. Fore wings setose..............................Eolachesilla

Hind wings with at least some marginal setae......75

75. Hind wings setose along most of margin. Always macropterous. Hypandrium strongly chitinized. Subgenital plate with median posterior lobe.................................76

Hind wings setose only between R_{2+3} and R_{4+5}. Females often with reduced wings or apterous. Hypandrium normal. Subgenital plate with two lobes on hind margin or with two groups of setae on margin..............................79

76. Setae on apical margin of fore wings not crossing each other......................<u>Zelandopsocus</u>

Setae on apical margin of wings crossing each other....................................77

77. External valves of gonapophyses triangular. Wing setae often arising from dark spots. (Paraproct of male normal). Hypandrium narrowing at base, emarginate................<u>Aaroniella</u>

External valves not triangular. Wing setae never on dark spots. (Paraproct of male sometimes tapering, trichobothrial field distorted). Hypandrium broad-based.................78

78. Dorsal valve of gonapophyses pointed apically. Male paraproct tapering. Trichobothrial field distorted...........................<u>Philotarsus</u>

Dorsal value of gonapophyses rectangular with a small process. Trichobothrial field normal. <u>Haplophallus</u>

79. Female without gonapophyses. Male with fore wing membrane setose.................<u>Lesneia</u>

Females with gonapophyses. Fore wings of male with glabrous membrane.....................80

80. Ventral valves of gonapophyses reduced to a small flap. Males unknown.....................81

Ventral valves not reduced......................82

81. At least some body setae with expanded tips. Paedomorpha

Body setae normal..........................Roesleria

82. Wings of both sexes much reduced.
Venation not evident..............................83

Wings absent. If reduced or developed
always with evident venation.....................84

83. Fore wing remnant elytriform...............Antarctopsocus

Fore wing remnant not elytriform (micropterous) Nothopsocus

84. Areola postica fused with media for a length
or joined to it by a crossvein, never apterous......85

Areola postica free in brachypterous or normally winged forms; apterous forms known...........87

85. Media with more than 3 branches............Pentacladus

Media with 3 branches.............................86

86. Male hypandrium bilobed; female with dorsal
valve long, apically divided...............Propsocus

Male hypandrium with inwardly curving hind
margin not distinctly laterally lobed; female with broad rectangular dorsal valve
with small preapical apopyses..............Palistreptus

87. Fourth segment of maxillary palp oval-
elongate i.e. normal..............................88

Fourth segment of maxillary palp truncate, hatchet-shaped.......................Cuneopalpus

88. Fore wing with strong colour pattern........Spilopsocus

Fore wings without strong colour pattern (or wings reduced)...............................89

89. Cu_2 in fore wing setose. Females fully winged....92

Cu_2 in fore wing without setae. Females apterous or brachypterous........................90

90. Hind wings without marginal setae between R_{2+3} and R_{4+5}. Female apterous............Hemineura

Hind wings with marginal setae between R_{2+3} and R_{4+5}. Females apterous or brachypterous.......91

91. Female apterous, without trichobothria. Antennae at most half as long as body. Setae on fore wings normal. Pulvillus fine.......Pseudopsocus

Female brachypterous, with trichobothria. Antennae at least half as long as body. Pulvillus broad. Setae on fore wings fine, sparse and short..........................Drymopsocus

92. In hind wing Cu not strongly recurved near wing margin. Fore wings with Rs and M fused for a length..............................Elipsocus

Hind wings with Cu strongly recurved near margin. Rs and M joined by a crossvein....Kilauella

93. Areola postica with Cu_{1b} long, Cu_{1a} curved so that the forking of Cu_1 is well basad of the junction of Cu_{1b} with wing margin. Fore wings darkly mottled. Always macropterous..................................Psilopsocus

Areola postica tall, Cu_{1a} arched. Brachypterous or apterous females known...............94

94. Abdomen with strong protuberances on segments 1 to 6. Apterous females only known. Hexacyrtoma

Abdomen without protuberances..................95

95. Eyes on stalks.........................Labocoria

Eyes normal............................Mesopsocus

96. Areola postica absent (Cu_1 simple). (Brachypterous females have glabrous wings and complete genitalia)........................97

Areola postica present. (Brachypterous females have setose wings or only one pair of gonapophyses. Brachypterous and apterous males known)..................................103

97. Fore wings with a few setae on membrane. Setae in two rows on veins in distal part of wing.............................. Kaestneriella

Fore wings without setae on membrane...........98

98. Fore wings with Rs and M fused for a length or meeting in a point...............................99

Fore wings with Rs and M joined by crossvein. Palmicola

99. Hind wings with Rs and M fused for a length.......100

Hind wings with Rs and M joined by a crossvein....102

100. Fore wings with Rs and M fused for a length.......101

Fore wings with Rs and M meeting in a point. Interpsocus

101. Veins setose..............................Nepiomorpha

Veins without setae........................Peripsocus

102. Subgenital plate bilobed behind, the lobes setose. Gonapophyses complete. Male without complex chitinized structure on dorsal aspect of end of abdomen....... ....Ectopsocus

Subgenital plate with lobes reduced or with small median lobe. Gonapophyses reduced to rudiment of external valve. Ninth tergite of male forming a more or less complex chitinized structure.......................Ectopsocopsis

103. Fore wings with veins and margin glabrous.........104

Fore wings with veins and margin setose. Apterous forms with antennae shorter than body..... 105

104. Hypandrium simple. Gonapophyses complete. Electropsocus

Hypandrium complex. Gonapophyses reduced to one pair..............................Lachesilla

105. Wings present or absent, setae only rarely present on membrane. Veins evident to wing margin in brachypterous forms, apterous forms with more than one pair of valves...........107

Fore wings present in females. Veins indistinct, membrane strongly setose, males brachypterous or apterous. Hypandrium and subgenital plates simple. Genitalia reduced to one pair of valves or absent..................106

106. Gonapophyses absent. Phallosome narrow, elongate, ovoid............................Archipsocopsis

One pair of gonapophyses present. Phallosome without external parameres, broad, oval, no sclerification of bulb..................Archipsocus

107. Veins in fore wings with more than one row of setae.....................................117

Veins in fore wings with a single row of setae, or wingless...............................108

108. Winged...113

Wingless.......................................109

109. Some body hairs expanded at tips or apically plumose..110

Body hairs normal 111

110. Body hairs expanded apically...............Paedomorpha

Body hairs plumose apically................Nepiomorpha

111. Ventral valve of gonapophyses pointed...........112

Ventral valve of gonapophyses broad, membranous and with small apical papilla.......Psoculus

112. Subgenital plate with posterior median lobe. Palmicola

Subgenital plate without posterior lobe.....Reuterella

113. Antennae twice as long as fore wing. Palaeopsocus

Antennae less than twice as long as fore wing 114

114. Hind wing with Rs and M fused for a length........ 115

Hind wings with Rs and M joined by a crossvein. Reuterella

115. M in fore wings 3-branched......................116

M in fore wings 2-branched.................Hemicaecilius

116. Hind wings with setae along whole margin....Trichopsocus

Hind wings with setae only between R_{2+3} and R_{4+5}..............................Graphocaecilius

117. Media in fore wings 3-branched..................119

Media in fore wings 2-branched..................118

118. Costa strongly thickened..................<u>Pseudoscottiella</u>

Costa normal.............................<u>Scottiella</u>

119. Preapical tooth on at least one claw of a pair....120

Claws without preapical tooth...................123

120. Setae of fore wing arising from veins.......<u>Mesocaecilius</u>

Setae of fore wing standing adjacent to veins and sometimes also on membrane............121

121. Setae adjacent to veins only..............<u>Cladioneura</u>

Setae on membrane..............................122

122. Fore wings with Rs and M fused for a length. <u>Trichocaecilius</u>

Fore wings with Rs and M connected by a cross-vein..................................... <u>Scytopsocus</u>

123. Fore wings with Rs straight before bifurcation. <u>Pseudocaecilius</u> <u>Heterocaecilius</u> (see comment in text)

Fore wings with Rs sinuous before bifurcation. <u>Ophiodopelma</u>