THE AMBLYCERA
(PHTHIRAPTERA : INSECTA)

BY

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SYNOPSIS

The taxonomic characters used for the separation of the families comprising the Amblycera are described and the relationships of these families discussed, with special reference to the lice of the Marsupials. A discussion on the suprageneric divisions of the Phthiraptera and a key to these are included.

INTRODUCTION

Elsewhere (Clay, 1969), a key to the genera of the Menoponidae together with an assessment of the taxonomic characters of that family has been published. Such characters have now been studied in the other families of the Amblycera with a view to finding a more reliable basis for the relationships within the superfamily. For the purpose of this review the Amblycera are divided as follows: Menoponidae;

Boopidae; Laemobothriidae; Ricinidae; Trimenoponidae; Gyropidae (Protogyropinae, Gyropinae, Gliricolinae).

CHARACTERS FOR THE SEPARATION OF FAMILIES

1. *Head Setae and Sensilla.* It has been shown (Clay, 1969) that in the Menoponidae these conform to certain patterns. Parts of the setal patterns are similar in the Boopidae and to a lesser extent in the Laemobothriidae ; usually in this latter family and in the Boopidae, with the exception of *Latumcephalum* and *Paraboopia*, the alveoli of two of the temple head setae (26 and 27 ; Clay, 1969, figs. 2–3) are contiguous as in many of the Menoponidae. In the other families the chaetotaxy is different, although some of the setae as numbered in the Menoponidae are identifiable ; in the New World mammal-infesting families the differences are largely due to the increase in the number of setae. Some of the genera of the Boopidae have the number and position of the head sensilla similar to the condition in most of the Menoponidae.

2. *Antennal Sensilla.* The antenna of the Phthiraptera never has more than five segments : the scape, pedicel and a flagellum of three segments, the last two in the Amblycera frequently being fused to form a single segment. In addition to the sensory setae, there are sense organs on the last two segments of the flagellum or, in those species in which these two segments are fused, the sense organs are found on the terminal segment only. The Menoponidae have a sensillum coeloconicum on each of the last two segments in the five-segmented antenna and two on the terminal segment in the four-segmented antenna (Clay, 1969). The Boopidae (Pl. 1, fig. 1) and the Ricinidae (Pl. 1, fig. 2) also have this arrangement of the sensilla ; the Laemobothriidae with four segments differ in having three sensilla on the terminal segment (Pl. 1, fig. 3).

Unlike these groups, the Trimenoponidae and Gyropidae show considerable superficial diversity in the form of the antennal sense organs even within genera. As the antenna is always four-segmented in these families the sense organs, also probably modified sensilla coeloconica, are on the terminal segment. Examination with the light and scanning electron microscopes[1] (SEM) shows that there are four adjacent sense pegs forming the sense organ (Pl. 3, fig. 13). Two of these pegs are conspicuous furrowed structures, visible from the surface view and two are smaller and of a different form, each arising within an inner cavity and frequently not visible from the surface. The differences between the sense organs are shown in the types of cavities in which the pegs occur, the following being examples : a. Two surface cavities, so that superficially this type appears rather similar to that of the Menoponidae, but it has four, not two, sense pegs (Pl. 1, fig. 4, *Gyropus ovalis*). b. The four pegs are in four cavities with four separate small openings on the lateral surface of the antenna (Pl. 1, fig. 5, *Macrogyropus dicotylis*). c. Four larger

[1]SEM photographs. The antenna of the Phthiraptera have presented certain problems of cleaning and coating for the SEM. It has, however, been an agreeable surprise that specimens originally treated with KOH and mounted in Canada Balsam can be removed from the slide and used ; also, after appropriate treatment, so can dried material collected from skins. This has made it possible to photograph the antennal sense organs of such South American genera as *Protogyropus*, *Harrisonia* and *Cummingsia*, which are rare in collections.

separate openings on the tip of the terminal segment, some of which may be protected by outgrowths from the margin, the two larger sense pegs are easily visible from the surface but the two cavities with the smaller pegs usually appear empty from this view (Pl. 1, fig. 6). This type is found in *Gyropus freitasi*, *G. lenti*, *Macrogyropus heteronychus* and *Protogyropus* ; in *Phtheiropoios wetmori* the cavities containing the larger pegs are wider and the inner sides are tuberculate (Pl. 2, fig. 7). d. In this there is virtually one cavity, the walls between not reaching to the surface (Pl. 2, fig. 8. *Macrogyropus amplexans*). Types a–d are found in the Gyropinae. e. A single outer cavity with the two large pegs each end and a central inner cavity divided into two with the other two sense pegs, which are sometimes visible from the surface ; the outer cavity may or may not be protected by processes from the cavity margin (Pl. 2, figs 9–11 ; Pl. 3, figs 13–14). This type is found in *Gliricola* and *Pitrufquenia* (Gliricolinae) and *Cummingsia*, *Harrisonia* and *Philandesia* (Trimenoponidae). *Trimenopon hispidum* (Trimenoponidae) has a similar organ but the base of the cavity is composed of a number of small cavities and the organ is large and may incorporate one of the antennal setae (Pl. 2, fig. 12).

In the New World Amblycera there is a tendency for a breakdown of the intervening walls of the four cavities to form one large cavity. This type of organ could have been developed only in a group with a four-segmented antenna in which the sense organs are adjacent to each other. In the Menoponidae the antenna may be four- or five-segmented and the sensilla either adjacent or on separate segments. These facts together with evidence (Symmons, 1952) suggesting that the Menoponidae are the most primitive of the Phthiraptera, make it probable that the type of antennal sense organ found in this family is the most primitive. If the characters of the antennal sense organ reflect relationships, then in the Amblycera these would suggest a relationship between the Menoponidae, Boopidae, Ricinidae and Laemobothriidae on one hand and between the Gyropidae and Trimenoponidae on the other, with perhaps a closer relationship between the Trimenoponidae and the Gliricolinae. These sense organs have been considered entirely from the point of view of their value in taxonomy ; further studies by other methods are necessary to understand their histology and physiology.

As the Ischnocera are believed to be less primitive than the Amblycera (Hopkins, 1949, Symmons, 1952) and differ from them in many features it is of interest to consider their antennal sense organs. These differ markedly from those of the Amblycera, having in addition to cavities with a sense peg, other sensory areas. These areas in *Trichodectes*, when studied by means of a stereo pair of SEM photographs, are seen to be saucer-shaped structures, each with a central raised area and a varying number of radiating ridges separated by narrow grooves (Pl. 3, fig. 18). In the Philopteridae, in which there are five antennal segments, the organ on segment V comprises two of the saucer-like sensilla and a third sensillum with a central cavity containing the sense peg ; the whole sometimes surrounded by a number of grooves. The position of these three sensilla relative to one another may prove to be of taxonomic value (Pl. 3, figs 15, 16). On segment IV there is a similar organ, but this has only one of the saucer-like sensilla. In *Trichodectes melis* (Trichodectidae), in which the terminal segments of the antenna are fused, the sensilla

are similar to those of the Philopteridae but lie adjacent to each other on the last segment (Pl. 3, fig. 17). A more detailed study of the antennal sense organs of the Ischnocera is being undertaken.

Haematomyzus (Rhynchophthirina) has antennal sense organs similar to those of the Ischnocera ; a cavity and two saucer-like areas with raised ridges on segment V (Pl. 4, figs 19, 20) and a single saucer-like area and a cavity on segment IV. The cavity on both segments differs from that found in the Ischnocera in having the sense peg surrounded by a number of protruding leaf-like filaments (Pl. 4, fig. 21). In at least some of the Anoplura (e.g. *Haematopinus tuberculatus*), the sense organ on segment V is similar to that found in the Ischnocera in having a cavity and two saucer-like areas with internal ridges, each area and the whole group being surrounded by a number of grooves.

The similarity of these antennal sense organs in the Ischnocera, Rhynchopthirina and Anoplura and their differences from those of the Amblycera, is further support for the taxonomic division between the Amblycera and the former three groups.

3. *Mouthparts.* These are fundamentally the same in all the Amblycera, with the exception of some of the Ricinidae (Clay, 1949). The mandibles of the Menoponidae, Laemobothriidae and Philopteridae (Ischnocera) have a conspicuous bunch of filaments attached posteriorly, which are here considered to be the prostheca ; some at least of the Trichodectidae (Ischnocera) also have this but the filaments are shorter and less conspicuous. A prostheca of this form has not been seen in the examination of whole mounts and dissections of specimens belonging to the Ricinidae, Boopidae, Trimenoponidae and Gyropidae, in which it is perhaps secondarily lost. This form of filamentous prostheca is found in at least some of the Psocoptera. The number of segments forming the maxillary palpus is rarely five (*Trimenopon*), commonly four and frequently less in the New World mammal-infesting forms. Apart from the majority of the Menoponidae, only the Boopidae and Laemobothriidae have the pair of subterminal setae, one of which is peglike, on the terminal segment of the maxillary palpus (Clay, 1968, Pl. 1, figs 6–7). The labial palpi are present in all the families with the exception of the Ricinidae. In all the Menoponidae there are five terminal setae on this palp, four or five in the Boopidae and the Gyropinae, four in the Trimenoponidae and not more than three in the Gliricolinae. The hypopharynx shows so much variation in reduction and modification of its parts between and within generic and suprageneric taxa that its form is of doubtful use in the consideration of relationships.

4. *Tentorium.* Symmons (1952) placed the tentorium of the Amblycera in five groups based on the amount of reduction in its sclerotization. She showed that there was no obvious correlation between the form of the tentorium and of the mouth parts or with the degree of sclerotization of the head and suggested that its form, therefore, might be of phylogenetic significance. However, Symmons herself (1952 : 388) showed that there was some parallel reduction in the amount of sclerotization, citing the non-sclerotization of the posterior part of the anterior arms in *Trinoton* and *Piagetiella* (Menoponidae), *Heterodoxus* (Boopidae), *Gyropus* (Gyropidae) and the non-sclerotization of the bridge in *Piagetiella, Heterodoxus, Gyropus, Gliricola, Trimenopon Laemobothrion* and *Ricinus;* this may also be the case

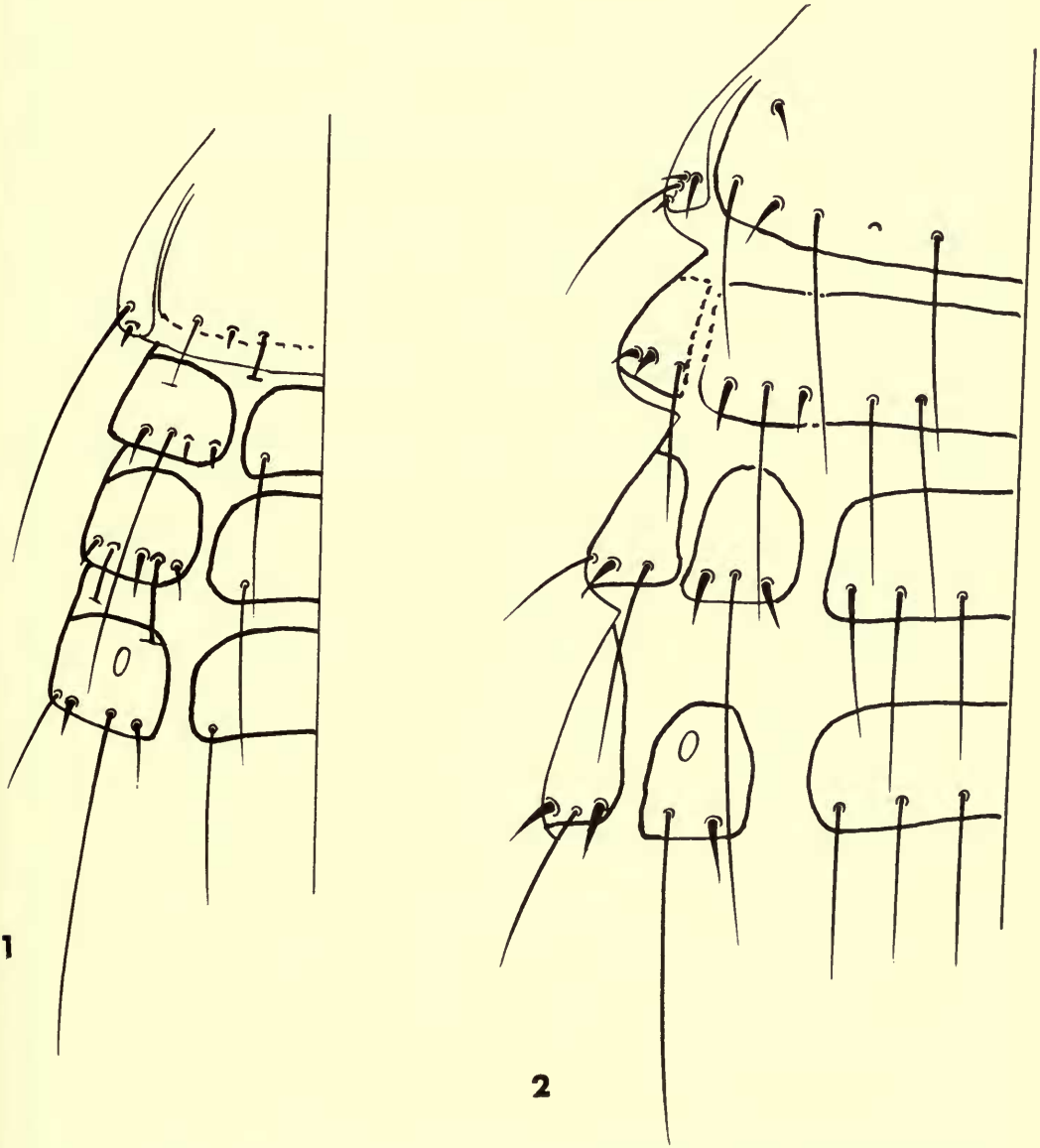
in *Pacifimenopon* (Menoponidae). Thus, although there is a reduction in the tentorial sclerotization in the mammal-infesting Amblycera, there is a similar though lesser reduction in some of the Menoponidae, so that this does not necessarily denote relationship in all cases. There is variation within the Menoponidae of the position of the base of the antenna relative to the posterior articulation of the mandible and also of the position of the ommatidia, or the ocular seta where the former are not apparent, in relation to the posterior end of the antennal fossa. This variation is presumably due to the shortening or lengthening of different areas of the head, which also effects the position of the tentorial pits. One of the features, according to Symmons, showing the similarity between *Ricinus* and *Laemobothrion* is the position of the posterior tentorial pits near the occipital foramen. *Ricinus* and *Laemobothrion* have a superficial resemblance due to the elongation of the head in an antero-posterior direction and to the posterior elongation of the parietal areas (temples). In fact, the heads in the two families are rather different. In the Ricinidae the elongation of the head has taken place in the clypeal area in front of the anterior tentorial pits, which thus appear to lie rather more posteriorly than in other genera. The antennae and ommatidia are in a posterior position on the head and in *Trochiloecetes*, in which there is no posterior lengthening of the parietal area, the posterior point of the antennal fossa is almost on the postero-lateral corner of the head. In *Laemobothrion*, although the antennal base and the ommatidia are rather far removed from the posterior mandibular articulation, they are approximately in the middle of the head and the anterior tentorial pits in their most common position, that is at the level of the posterior mandibular articulation. Symmons showed that *Ricinus* and *Laemobothrion* have a fine ligament in place of the usual sclerotized bridge, although in *L. opisthocomi* (not seen by Symmons) the bridge is as broad as in some of the Menoponidae. Symmons (: 379) has shown that *Laemobothrion* differs from *Ricinus* in the absence of the ventral prothoracic muscles, there being no trace of their apodemes from the bridge in the former genus. Symmons placed *Ricinus* and *Laemobothrion* together in one of her phylogenetic groups, but perhaps there is no reason to consider the Ricinidae to be nearer related to the Laemobothriidae than either are to the Menoponidae. This is further discussed below.

5. *Legs*. These show considerable diversity even within families and between genera parasitic on the same host species, where the same adaptive forces might be presumed to operate. There is variation in the length of the tarsal segments, the angle at which the second tarsal segment joins the first and the presence or absence of a well-developed first euplantula, apart from the extreme modifications of the tarsus and tarsal claws found in the Gyropidae. Even if the first euplantula is well developed in the Boopidae, Trimenoponidae and Gyropidae it does not have the typical striated or banded appearance found in most of the Menoponidae (Clay, 1969 : 14), although in species of the former families it may be tuberculate. Many of the Boopidae have processes (Pl. 5, fig. 25) on the second tarsal segment similar to the condition in *Pseudomenopon* (Clay, 1969) and believed by Kéler to represent the second euplantula. All the Amblycera have two tarsal claws, with the exception of the Gyropidae, which never have more than one claw on the second and third

legs. There is some controversy about the presence or absence of claws in the Gliricolinae (Kéler, 1955 ; Mayer, 1954). Kéler's interpretation of the *Gliricola* leg is followed here, that is a two-segmented tarsus, the second bearing a narrow seta-like claw and a large euplantula. The majority of the Menoponidae have either ctenidia or brushes of setae on the venter of the third femur ; one genus (*Microctenia*) has comb-like projections in this position (Clay, 1969, Pl. 6, fig. 32) ; the Laemobothriidae also have comb-like projections (Pl. 4, fig. 22), but quite dissimilar from those of *Microctenia*. All the remaining families, as in some of the Menoponidae, have no definite ctenidia or brushes. The Gyropidae with the exception of *Protogyropus* have at least one pair of legs modified for clasping the hair of the host as described by Ewing, 1924. An important feature of the leg separating the Boopidae and avian-infesting Amblycera from the New World mammal-infesting families is the form of the first coxa. It has been described in *Myrsidea* (Menoponidae) by Mayer (1954 : 100) as an elongate bladder lying flat on the body with its caudal end on the sternum in the form of a closed sac and its cranial end joined to the first pleural ridge by a single condylar joint ; this makes the first coxa a characteristic feature of the Boopidae and avian-infesting Amblycera.

6. *Thorax and Abdomen.* These two parts of the body are considered together as in many Amblycera there is a close association between the thorax and the first abdominal segment. In the mammal-infesting Amblycera there is a tendency towards the reduction of the anterior segmentation by various degrees of fusion of the thoracic segments, reduction of the first abdominal segment and its fusion with the metathorax. In the Boopidae the mesonotum is distinct but there has been some confusion about the metanotum and its relation to tergum I. Tergum II, identified by being next to the first spiracle-bearing segment which is always III, is fully developed and it seems probable that the plate immediately anterior to this is the fused metanotum and tergum I. Each side of a typical Menoponid metanotum (Text-fig. 3) is a narrow suture separating off the metapleurite, the inner dorsal seta (d) of which is frequently spine-like ; the outermost posterior marginal seta (o) of the metanotum is usually long. In the Boopidae it is possible to make out a similar pattern : immediately posterior to the mesonotum (Text-figs 4, 5) is a plate separated or partly separated each side by a suture from a lateral sclerite bearing spiniform setae at two levels. The central plate is transversely divided by an indistinct suture, anterior to which is a line of setae, the outermost one being long and here identified as the outer metanotal seta ; lateral to this seta is a spiniform seta, presumably homologous with the metapleural seta of the Menoponidae. Near the posterior margin of the central plate are other setae, presumed to be those of tergum I ; at this level laterally is a spiniform seta, presumed to be that of pleurite I. The SEM picture on Pl. 5, fig. 26 shows the dual nature of the central plate. Further evidence is seen in the species of *Paraheterodoxus* (Text-fig. 5) in which there is a pair of strongly spiniform setae in the posterior row of the central plate similar in form and position to the pair found on each of terga II-VIII. There seems little doubt therefore that in the Boopidae tergum I is present but fused to the metanotum. In the Trimenoponidae, according to Kéler (in press), the fusion of the thoracic segments shows much variation : the meso- and metanotum may be

fused (*Harrisonia*), the meso- and pronotum fused (*Trimenopon* and *Cummingsia*) or the mesonotum free (*Philandesia*). Tergum I in all the Trimenoponidae is reduced to a greater or lesser extent, but is free. The Gyropidae also show considerable variation in the amount of fusion of the thoracic segments, and the fusion and reduction of tergum I. All three thoracic nota may be fused (*Monothoracius*),



FIGS 1–2. *Eidmanniella* sp. Dorsal view of part of metathorax and anterior abdominal segments, somewhat diagramatic. 1, Second nymphal instar. 2, Third instar.

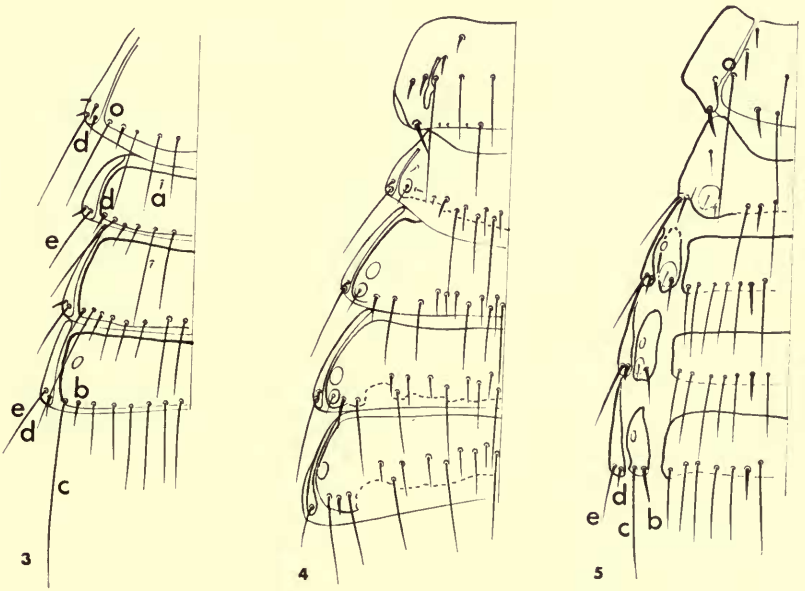
or the meso- and metanotum fused or all may be separate (*Macrogyropus dicotylis*). Tergum I may be free and well developed (*Pitrufquenia*) or considerably reduced in size but free or fused to the metanotum (*Protogryropus*). In *Protogyropus* the meso- and metanotum and tergum I are all fused together. The mesonotum is free in the Menoponidae and Boopidae but fused with the metanotum in the Laemobothriidae and the Ricinidae. Tergum I and II are fully developed in the Menoponidae and Laemobothriidae, except in some female Menoponidae in which the anterior segments of the abdomen are modified ; in the Ricinidae tergum I is fused with the pteronotum as in *Protogyropus*. This variation in the fusion of the thoracic and abdominal segments and the similarity of the condition in unrelated groups and the differences within related groups indicates that these modifications must have taken place independently on many occasions ; they are probably of little value in considering relationships.

The oblong heavily sclerotized postnotum as found in the majority of the Menoponidae is present in the Boopidae, together with the cluster of four anterior (medio-anterior) mesonotal setae, also characteristic of most of the Menoponidae. A postnotum of this type is present in some species of the Gyropidae and Trimenoponidae but the associated cluster of small setae has not been seen in these forms.

There are certain setae and groups of setae on the abdomen remaining constant in number and in position relative to each other within the higher taxonomic categories ; these may form useful landmarks in the study of homologies. In previous papers (Clay, 1962, 1966) these setae, such as those of the post-spiracular complex, have been omitted from the tergal counts which are given to show variation and should not preferably include non-variable setae. In all the Menoponidae and Laemobothriidae there is a small to minute seta (Text-fig. 3, a) each end of the anterior region of tergites I or II or both, perhaps having a proprioceptive function for the movements of the thorax and anterior segments. In the Boopidae this seta is present on tergum II in *Heterodoxus*, in which the post-spiracular seta is on the tergite. In *Boopia*, with the post-spiracular seta on the lateral plate, there is no seta a on tergite II but a small anterior seta on the lateral plate (absent in *Heterodoxus*) probably represents a. The most important group of setae are those associated with the spiracle and discussed below in section 7.

7. *The Abdominal Sclerites and the Spiracles.* For the purpose of the following discussion an abdominal segment is considered to have basically three sclerotized plates : a tergal (tergite), a sternal (sternite) and a lateral. All the Amblycera have one pair of thoracic spiracles and six pairs of abdominal ones opening on segments III-VIII, with the exception of the Trimenoponidae and the Gliricolinae which have five pairs on segments III-VII. The apparent position of the spiracles on the segment varies in different families and in one case within a family, but before discussing the significance of this it is necessary to consider the post-spiracular complex of setae. In the Menoponidae this complex comprises four setae as follows : the post-spiracular seta, marginal or submarginal each end of tergites I-VIII, usually long and stout on at least some segments (Text-fig. 3, c) ; two minute setae closely associated with the alveolus of the post-spiracular seta on segments II-VIII

(Pl. 5, fig. 28) and usually the lateral seta (b). This last seta, short and frequently spiniform, is found on segments II-VIII lying on the mediad side of the post-spiracular seta ; it is often close to the alveolus of this latter seta and with it sub-marginal to the marginal row of tergal setae. In some species or on some segments it may appear as part of the tergal row except for being shorter and may not be readily distinguishable ; in other species it may become confused with the anterior tergal setae. However, when the post-spiracular seta appears to change its position this associated lateral seta changes with it, suggesting that it has some developmental and functional connection. The two minute associated setae are useful in identifying the post-spiracular seta ; thus their presence within the alveolus of the trichobothria (Pl. 5, fig. 29), found on segments II-IV (Text-fig. 4) in most genera of the Boopidae, shows that these are modified post-spiracular setae. The only Amblycera in which these two minute setae appear to be absent are in some species of *Gliricola*, being replaced by a single circular, presumably sensory, area without a seta. This is similar in appearance to the circular sensillum associated with the post-spiracular seta in many Philopteridae (Clay, 1954). In *Haematomyzus* the sensillum is not associated with a seta but is in the form of a papilla-like structure lying immediately below the spiracle (Pl. 5, fig. 30). In the majority of the Menoponid genera the post-spiracular seta is the outermost seta each end of the tergite, but sometimes on one or more segments there is a small seta (d) laterad to the post-spiracular seta, its presence being constant and serving as a useful generic



FIGS 3–5. Dorsal view of part of metathorax and anterior abdominal segments, somewhat diagramatic. 3, *Eidmanniella* sp. 4, *Heterodoxus* sp. 5, *Paraheterodoxus* sp. a, anterior tergal seta ; b, lateral seta associated with post-spiracular seta ; c, post-spiracular seta ; d & e, ' pleural ' setae ; o, outermost metanotal seta.

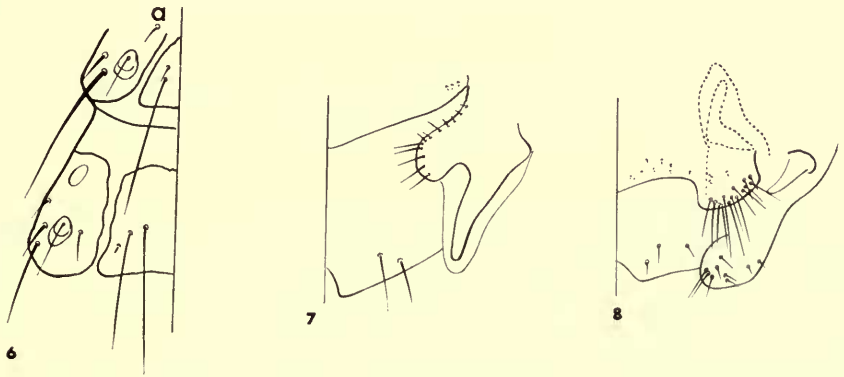
character (Clay, 1969). However, this is not a new seta but is one usually found on the lateral plate, which in some segments of some species is on the tergite. In *Eidmanniella* (Text-fig. 3), for instance, on the metapleurite there is a short spiniform seta with a longer one on its outer side ; on segments I and II there is a spiniform seta laterad to the post-spiracular seta on the tergite and the inner seta (e) on the lateral plate is no longer spiniform but is similar to the longer seta on the metapleurite ; on segment III the spiniform seta is once more on the lateral plate. In other genera the spiniform seta may disappear and not be found on the lateral plates of the posterior segments. The explanation of the differing position of this seta will be discussed below.

There are no spiracles on segments I–II in any of the Phthiraptera, but in the Menoponidae there is a seta, usually elongate each end of tergites I–II, that on II having the two minute associated setae, suggesting that functional spiracles were at one time associated with these setae. The spiracles may open on the tergites (most of the Menoponidae, *Heterodoxus*), or the lateral plates (*Boopia*, Trimenoponidae and Gyropidae) or on the mediad part of a partially divided lateral plate (*Paraheterodoxus*). In the *Colpocephalum* species parasitic on the Phoenicopteridae, as shown by Price (1965 : 128), and in some species of *Myrsidea* the spiracles of the female open on the lateral plates ; while those of the male open on the tergite, the usual position in the Menoponidae. In both sexes the post-spiracular setal complex is on the tergite. In species belonging to the Boopidae, Trimenoponidae and Gyropidae the post-spiracular complex follows the spiracles, both occuring on the same abdominal plate. It is interesting from the taxonomic point of view to consider the significance of the apparent change of position of the spiracles. In a typical Menoponid the metanotum is separated each side by a narrow suture from the pleural epimeron (Mayer, 1954), the suture being apparent from the dorsal surface owing to the flattened nature of the body. The first abdominal segment shows a similar condition, with the chaetotaxy of the lateral edge of the tergal plate and that of the lateral plate being similar to that of the metanotum and metapleurite ; this suggests that the lateral plate of segment I in the Menoponidae is also pleural. Segments II–VIII are similar in this respect, with the spiracles (on III–VIII) and post-spiracular setal complex lying near the lateral edge of the tergite. However, an examination of the nymphs shows that the arrangement of the abdominal plates during development is different.

In *Eidmanniella* sp. n. (Ryan & Price, in press) of which all three nymphal stages are available, the different instars, in addition to size differences, can be recognized as follows : first instar, tergite VIII with four setae and sternites II–VIII each with four setae ; second instar, tergite VIII with six setae and sternites II–VIII with full rows of setae ; third instar, tergite VIII with 11–12 setae and sternites with full rows of setae and incipient lateral brushes on some sternites. It is not possible to identify the abdominal plates in the available material of the first instar. In the second instar each segment has a central tergal plate separated at each end by an unhardened area from a lateral plate (Text-fig. 1) ; this latter plate bears the post-spiracular complex together with the usual marginal setae found on the lateral (or pleural) plate and the spiracles on segments III–VIII. In the third instar (Text-fig.

2) the lateral plate is divided or partly divided into two by a vertical suture which separates the post-spiracular complex, and the spiracle if present, from the rest of the lateral setae. In some specimens of second instar nymphs there is an indication of a narrow suture where the wider gap is found in the third instar. In those species in which the adult has a seta laterad to the post-spiracular seta on some segments, differentiation of the suture takes place either on one side of this seta so that it lies on the same plate as the post-spiracular seta, or on the other side so that it is with the rest of the lateral seta (Text-fig. 2). When in the adult this small plate bearing the post-spiracular complex merges with the central tergal plate by the hardening of the intervening area, only a lateral plate, appearing similar in position and chaetotaxy to the metapleurite, and perhaps also pleural, is left.

Within the family Boopidae there is variation in the adult arrangement of the abdominal sclerites. The setae which are useful landmarks are the same as those found in the Menoponidae, comprising the post-spiracular complex, seta b, and the lateral setae d and e. Seta d usually lies somewhat anterior to the longer seta e and as in the Menoponidae may be absent on the posterior segments. In adults of the species of *Boopia* and in those nymphs available for study, there is a single lateral plate on each segment bearing the post-spiracular complex, the spiracles when present, the two lateral setae d and e and sometimes other setae usually designated as pleural. This lateral plate is similar to that found in second instar Menoponidae. Third instar nymphs and adults of *Paraheterodoxus* resemble third instar Menoponidae in having a partially subdivided lateral plate. In both *Paraheterodoxus* and some Menoponid nymphs the apparent division of the lateral plate is conspicuous by transmitted light, but the SEM shows it to be a complete plate with only a line of slight unevenness (Pl. 5, figs 27, 28). This lack of surface differentiation probably means that the outer region of the cuticle is almost, if not completely, uniformly sclerotized ; the suture shown with transmitted light is probably due to lack of sclerotization in the lower regions of the cuticle. Dr B. K. Tandan has suggested that a small portion of the cuticle thus becomes less rigid than the adjoining areas and is capable of folding or distortion ; it is probably this



FIGS 6–8. 6, *Boopia* sp. Dorsal view of abdominal segments II and III. 7–8. Female terminalia. 7, *Damalinia ovis*. 8, *Goniodes assimilis*.

distortion which has made the surface of the plate slightly but definitely uneven. In the adult Menoponid the suture becomes complete, dividing the lateral plate in two, one half of which merges with the central tergal plate, while in *Paraheterodoxus* the nymphal stage persists. Nymphs and adults of *Heterodoxus* resemble those of the Menoponidae. Thus, within the family Boopidae there are three arrangements of the lateral and tergal plates all of which are found during the ontogeny of the Menoponidae. A study of the available material shows that third instar nymphs and adults of *Trimenopon* and adults of other Trimenoponidae and the Gyropidae resemble second instar Menoponid nymphs in having the single lateral plate bearing the spiracles, the post-spiracular complex and other setae usually considered pleural. In *Boopia* and the Trimenoponidae the lateral plates lie dorsal, in the Gyropinae dorsal, lateral or ventral and in the Gliricolinae ventral.

It is apparent from the foregoing that there are not only differences in the arrangement of the abdominal sclerites between nymphs and adults of the same species but also between families and within one family, between genera. Further, although the position of the spiracles and post-spiracular complex appears to differ, they are morphologically in the same position ; the apparent differences being due to where the differentiation of the suture takes place and whether the unhardened area between laterotergite and tergite becomes hardened or that between laterotergite and ' pleurite '. These processes are perhaps not very fundamental or phylogenetically permanent. *Boopia* (*Phacogalia*) *brevispinosus*, for instance, shows further divisions of the tergal plate so that the adult has segments with six abdominal plates : three tergal, two lateral and one sternal.

It is difficult to give a satisfactory name to the lateral plate which may have some pleural elements but as it bears the spiracles, either in the nymph or adult, must also have tergal elements. As Snodgrass (1935 : 71) has said ' sclerites do not define anatomical areas ' and the flattened condition of the Mallophaga make it difficult to identify the dorso-pleural and pleuro-ventral lines. It is possible that the true pleuron is largely represented by the unhardened area usually present between the sternite and lateral plate and that the lateral plate is either entirely tergal or has a pleural sclerite which is sometimes free and sometimes fused with a laterotergite ; Mayer, 1954 has shown that part of the pleuron of the prothorax in the Menoponidae is incorporated in the pronotum. Taking all these points into consideration the name *lateral plate* is perhaps the most satisfactory for a plate which may perhaps sometimes be pleural (e.g. Menoponid adults), tergopleural (e.g. Menoponid nymphs, *Boopia* adults) or entirely laterotergal, if it is believed that it contains no pleural elements.

8. *Female Gonapophyses*. This name has been used for various structures found in some of the Phthirapterous groups, but it is doubtful whether they are homologous throughout the order. Kéler (in press) describing the gonapophyses of the Boopidae as sickle-shaped bluntly or sharply pointed appendages, shows that the anal margin extends into the inner wall of these structures. It seems therefore that the setae-bearing appendage each side of the anus in *Chapinia* (Menoponidae) may be homologous with the gonapophyses of the Boopidae. In the Trichodectidae, according to Kéler (1938), the structures referred to as gonapophyses are of a different origin

and were named by him ' copulatory valves ', He shows that their margins merge directly with the wall of the genital chamber (Text-fig. 7). The structures in the Anoplura called ' gonapophyses ' by Ferris (1951) are the same, being continuous with the vulval margin. Ferris (1951 : 30) considered that the tufts of setae or lobes each side of segment IX in the Anoplura represented the gonapophyses of that segment. It seems probable that the setiferous lobes continuous with the lateral margins of the vulva (Text-fig. 8) in some species of *Goniodes* (Philopteridae) are homologous with the copulatory valves of Trichodectidae. The various lobes and processes on the venter of the posterior segments in the Philopterid genera *Goniodes, Rallicola, Wilsoniella* and *Osculotes* may be vestiges of gonapophyses as described by Ferris for the Anoplura. The structures in *Haematomyzus* called ' gonapophyses ' (Ferris, 1931 : 124) are rather difficult to interpret, but also appear to be the copulatory valves of Kéler as found in the Anoplura and Trichodectidae. There seems to be a tendency in the lice parasitic on mammals to retain gonapophyses or to develop gonapophyses-like structures ; these possibly being used in attaching the egg to a hair. Murray (1967 : 21) found that *Damalinia* utilized the copulatory valves during egg-laying. If this view of the different origin of the ' gonapophyses ' in the Amblycera on one side and in the Anoplura and Ischnocera on the other is correct, it supports other evidence used for dividing the Phthiraptera taxonomically into these two groups.

9. *Tracheal System.* A posterior commissure joining the two main abdominal trunks, believed to be a primitive character, has been demonstrated in the Anoplura, *Haematomyzus*, Boopidae, *Trimenopon*, some of the Trichodectidae and in *Nesiotinus* (Philopteridae) by Harrison, 1915 and Ferris, 1931.

Piagetiella (Menoponidae) has a transverse commissure in the fourth abdominal segment ; a character, according to Harrison (1915), probably directly associated with its habitat in the gular pouch of the host. The form of the tracheal system may therefore be partly ecological and partly phylogenetic. Harrison, 1915 demonstrated two head commissures in *Gyropus ovalis* and *Gliricola porcelli*. However, apart from the number and position of the spiracles already discussed, too little is known concerning the respiratory system of most forms to make any use of it in taxonomy.

DEFINITION OF AMBLYCERA AND INCLUDED FAMILIES

AMBLYCERA

Antenna four- or five-segmented, third segment pedunculate ; total of two to four sensilla coeloconica on fourth and fifth segments. Mandibles with articulations dorsal and ventral : filiform maxillary palpus. Tentorium complete with exception of dorsal arms ; presence of a muscle homologous with ligament of Denis in those forms examined by Symmons, 1952 : 373. At least one pair of post-spiracular setae with two minute adjacent setae, rarely absent and replaced by a single circular sensillum. Crop a simple enlargement between oesophagus and midgut, with crop teeth at its posterior end ; the figures of the crop of *Trinoton* in Blagoveshtschensky

(1949, pl. 1, figs 1–3) however suggest that there may be a small diverticulum at each end of the crop. The testis of the Amblycera usually consists of three follicles but Blagoveshtschensky (1956) found only two in the three species of *Myrsidea* he examined ; this is also the case in *Myrsidea* sp. from *Gymnorhina dorsalis*.

MENOPONIDAE Mjöberg, 1910

1. Antenna four- or five-segmented. 2. Two sensilla coeloconica : one on each of segments four and five in the five-segmented antenna and both on the last segment in the four-segmented antenna. 3. Labial palpi present. 4. Five distal setae on labial palpus. 5. Maxillary palpus four-segmented. 6. Head chaetotaxy conforms to certain patterns (Clay, 1969). 7. Pro-, meso- and metanotum separate. 8. Coxa I elongated antero-posteriorly. 9. Legs II and III with two tarsal claws. 10. Tergum I not fused with metanotum and normally developed, at least in males. 11. Six pairs of spiracles, present on abdominal segments III-VIII. 12. Post-spiracular setal complex each end of central tergites.

In addition the following are characteristic of most of the Menoponidae, although not present in all genera : a. Two subterminal setae on last segment of maxillary palpus, one of which is usually peg-like. b. Two of the dorsal submarginal setae (26 and 27) on temples with the alveoli contiguous. c. Subocular comb row. d. Transverse prontotal carina. e. Typical oblong well-sclerotized postnotum. f. Females with typical anal corona of setae.

BOOPIDAE Mjöberg, 1910

The Boopidae agree with the Menoponidae in characters 1, 2, 3, 6–9, 11. There may be four or five distal setae on the labial palpus (4) ; the number of segments in the maxillary palpus is usually four but may be reduced to two or three (5) ; the spiracles and the post-spiracular complex may be on the central tergites or the lateral plates (12). Tergum I is always fused with the metanotum (10). Members of this family also agree with the Menoponidae in characters a, d, e and sometimes c, and except for the genera *Paraboopia* and *Latumcephalum*, all agree with b. One character common to all the Boopidae and apparently not found elsewhere in the Amblycera is the presence of a seta, usually spiniform, borne on a protuberance each side of the mesonotum (Pl. 5, fig. 26, s). This character together with the fusion of tergum I with the metanotum and the presence of gonapophyses of a distinctive form separates the members of the Boopidae from the Menoponidae. As shown above Harrison demonstrated in some species of the Boopidae a posterior abdominal tracheal commissure not found as yet in any of the Menoponidae. Symmons (1952) showed that *Heterodoxus* differed from the majority of the Menoponidae in the non-sclerotization of the posterior part of the anterior arms and by the reduction of the bridge to a ligament. Harrison & Johnston (1916 : 339) considered that the main characters separating the Boopidae from all other known Mallophaga was the ' large accessory sac associated with the male genitalia '. However, Kéler (in press) has shown that this is the spermatophore, a structure also found in some of the Menoponidae (Clay, 1968).

Paraboopia and *Latumcephalum* resemble each other and differ from the rest of the Boopidae in having a reduction in the number of segments of the maxillary palpus, a somewhat atypical pattern of head setae and with setae 26 and 27 not contiguous ; post-spiracular setae of segments II-IV not modified as trichobothria and a reduction in the length of the tarsus in *Latumcephalum.* Kéler (in press) considered this last character to be transitional between the condition in the Boopidae and the Trimenoponidae. In both genera the last segment of the antenna is greatly reduced but the line of division between four and five can be seen and the two sensilla coeloconica lie one each side of this line. As in *Boopia* the spiracles open on the lateral plates. Although some of these characters are also found in the New World mammal-infesting Amblycera it does not follow that the two genera are intermediate between these New World groups and the rest of the Boopidae. The characters are not of the kind which necessarily denote relationships (see discussion below) and some of them are also found in the Menoponidae. Further, *Paraboopia* and *Latumcephalum* have the majority of the characters listed above for the Boopidae and in addition the male genitalia, gonapophyses and the presence of spermatophores are all typical of that family.

LAEMOBOTHRIIDAE Mjöberg, 1910

The Laemobothriidae agree with the Menoponidae in characters 1, 2 (except that there are three not two sensilla coeloconica), 3–5 and 8–12. The head chaetotaxy (6) is not quite typical and the meso- and metanotum are fused (7). Characters a, d and usually b as in the Menoponidae ; the typical oblong postnotum (e) is absent and there is no typical anal corona (f).

Members of this family have the following characters in common not known elsewhere in the Amblycera : an area of sculpturing on the temples (Pl. 4, fig. 23) with outer rows of peg-like projections (Nelson & Price, 1965) ; venter of third femur and some sternites with patches of microtrichia of characteristic form (Pl. 4, fig. 22) ; tibiae II and III distally with terminal dorsal patch of microtrichia (Pl. 4, fig. 24) and an anterior patch of smaller microtrichia ; the mentum (*sensu* Symmons, 1952, fig. 18) with bladder-like lobe, conspicuous in untreated specimens.

RICINIDAE Neumann, 1890

The Ricinidae agree with the Menoponidae in characters 1, 2, 5, 8, 9, 11 and 12. There are no labial palpi (3, 4) ; the head chaetotaxy is atypical (6) and tergum I is fused with the pteronotum. The family has none of the characters a–f. They are distinguished from all other Amblycera by the absence of labial palpi ; presence of a conspicuous flap-like protrusion (pulvinus) attached each side to two horizontal sclerites of the labrum ; and in having the meso- and metanotum and the first abdominal tergum fused together with a continuous lateral buttress of internal tergal thickening each side. They also show reduction and modification of the mouthparts (Clay, 1949).

In published descriptions and keys the Ricinidae and Laemobothriidae have been separated from the Menoponidae by the position of the antennal fossae which are

said to be ventral on the head, not lateral. In fact, a number of the Menoponidae genera have the antennal fossae located entirely on the ventral surface of the head. There is a superficial resemblance in the shape of head, thorax and abdomen in some of the Ricinidae and the Laemobothriidae that has suggested a relationship between the two families (Hopkins, 1942 : 105). However, there is considerable difference in head and body shape within the Ricinidae, for instance between *Ricinus* and *Trochiloectes*. Symmons (1952) considered that the form of the tentorium suggested a relationship between the two families, but it has been shown (under tentorium above) that this is not necessarily so. Perhaps the greatest point of similarity is the form of the lateral margins of the abdomen and the elongated internal buttresses of tergal thickening in the Laemobothriidae and some of the Ricinidae. This may be, however, a method of solving the problem of strengthening the elongated abdomen ; an internal thickened buttress is also present in some of the elongated Philopteridae (Ischnocera) parasitic on the Procellariiformes.

TRIMENOPONIDAE Harrison, 1915

The Trimenoponidae agree with the Menoponidae only in characters 1, 3, 9 and usually 5. The four sensilla (2) open to the exterior in a single cavity on the terminal segment of the four segmented antenna ; the labial palpus has 4 distal setae (4) ; the maxillary palpus is four to five-segmented (5). The fusion of the thoracic nota varies (7), tergum I is always reduced both antero-posteriorly and from side to side (10) and there are five pairs of abdominal spiracles (11) which open on lateral plates III–VII (12). Characters 2, 4, 6, 8, 11, 12, a, b, c and f are not as found in the Menoponidae ; d and e may be present or absent.

The Trimenoponidae (*sensu* Hopkins & Clay, 1952 : 12 and including *Chinchillophaga* Emerson, 1964 and *Hoplomyophilus* Mendez, 1967) contains a number of genera with rather diverse characters especially in the degree of fusion of the thoracic segments and the features of the head. The distinctive features of the Trimenoponidae are the character of tergum I and the reduction or absence of pleurite I. These characters, together with the presence of the two-clawed tarsus and the five pairs of abdominal spiracles, separate the members of this family from the rest of the Amblycera. They resemble the rest of the New World mammal-infesting Amblycera in having the abdominal spiracles and the post-spiracular setae on the lateral plates and in the form of the antennal sense organ.

GYROPIDAE Kellogg, 1896

The Gyropidae as a whole agree with the Menoponidae only in characters 1 and 3, although some of the Menoponid characters are found in certain of the genera. The family comprises three main groups which resemble each other in the general characters of the mouthparts ; general chaetotaxy of the head and abdomen ; the antenna and the antennal sensilla ; reduction of the sclerotization of the tentorium ; two head commissures in the tracheal system (based on two species only) ; spiracles and post-spiracular setal complex on the lateral plates ; legs II and III with a single tarsal claw and in all but one genus, extreme modification of

at least one pair of legs to form an organ for clasping the hair. This modification of the leg has been achieved on quite different lines in the two main groups of the Gyropidae and has probably developed independently ; the two groups also differ in the number of abdominal spiracles, one resembling the Trimenoponidae in having none on segment VIII. Although it is possible that the Gyropidae are polyphyletic, for the present they are best kept in one family using Ewing's subfamilies to show the differences.

Protogyropinae Ewing, 1924. This subfamily, represented by a single genus, agrees with the Menoponidae in characters 1, 3, 11 and d. The antennal sense organ is type c (2) ; labial palpus with four distal setae (4) ; maxillary palpus three-segmented (5) ; meso- and metanotum fused (7) ; all legs with one simple claw (9) ; tergum I fused with pteronotum (10).

Gyropinae Ewing, 1924. This subfamily agrees with the Menoponidae in characters 1, 3, 11 and d ,and also with 4, 5, 7, 10, and e in some species. The antennal sense organ varies as described above (2) ; the labial palpus has four or five distal setae (4) ; fusion of meso- and metanotum varies (7) ; development and fusion of tergum I varies (10) ; the spiracles and post-spiracular setal complex on the lateral plates. Although Werneck (1936 : 419) in his diagnosis of *Gyropus* states that the maxillary palpus (5) has four segments, *Gyropus ovalis* has only three.

Gliricolinae Ewing, 1924. This subfamily is the most unlike the Menoponidae, resembling them only in characters 1, 3, d, and sometimes 5 and e. Labial palpus with not more than three distal setae (4) ; maxillary palpus two- or four-segmented (5) ; legs II–III with single modified tarsal claw (9) ; five pairs of abdominal spiracles (11) opening on lateral plates III–VII (12).

THE SUPRAGENERIC CLASSIFICATION OF THE AMBLYCERA

There is no agreed suprageneric classification within the Amblycera ; it varies with different workers. Harrison (1915 : 124) considered that the Trimenoponidae and the Boopidae showed only a superficial resemblance to each other and believed (1922 : 154, repeated in 1926 : 1585) that the Boopidae were most nearly related to the Gyropidae, but no reasons were given. In his description of a new genus (*Acanthomenopon* = *Cummingsia*), Harrison (1922 : 154) stated that it must be placed in the Trimenoponidae, but it showed some marked features of resemblance to the Boopidae, and some points of contact with the Gyropidae ; these features were not enumerated. Harrison believed that all the mammal Amblycera were monophyletic and originated on the marsupials. Ewing (1929 : 96) considered that the boopids were near the menoponids, recognizing the Boopinae and the Menoponinae as two subfamilies of the Menoponidae. Werneck (1948 : 5–6, as quoted by Vanzolini & Guimarães, 1955 : 23–24) considered, apart from the Gyropidae, that the division of the Amblycera should be : i) trimenoponids ; ii) menoponids and boopids ; iii) ricinids. Hopkins (1947 : 537) considered that the Trimenoponidae showed no evidence of any close relationship with the Gyropidae, but were quite closely related to the Boopidae ; he gave no reason for this.

In considering the relationships neither the retention of a primitive character nor the complete loss of a character necessarily denotes relationship, as in either case this can happen independantly. However, the presence of an identical derived character does suggest a common ancestor for the forms which show it. A character, if complex, once lost is probably not developed again in the same form so that a species with such a character is probably not descended from a stock which has lost it. A character which shows much variation within related groups of species cannot generally be used to infer relationships between less similar groups ; in the Amblycera such characters are the degree of development of the hypopharynx, development of the ommatidia, the fusion of the thoracic segments and the arrangement of the abdominal sclerites. Using these criteria the possible relationships within the Amblycera are discussed.

It is unlikely that the pedunculate third antennal segment, similar throughout the Amblycera, was developed more than once. If so it was present in the ancestral form and is evidence that the Amblycera are monophyletic. Other characters (Table I A, a) probably found in the proto-amblyceran were : a five-segmented antenna with a sensillum coeloconicum on segments four and five ; labial palpi ; a four-segmented maxillary palpus ; an eye formed of two ommatidia ; a tentorium, fully developed except for the dorsal arms ; a thorax with three separate segments ; abdominal segment I fully developed and free ; two tarsal claws ; a transverse pronotal carina ; an oblong strongly sclerotized postnotum ; six pairs of abdominal spiracles opening on segments III–VIII ; at least one pair of gonapophyses and a testis formed of three follicles. It is difficult to conjecture the form of the lateral plates in the ancestral amblyceran as there are differences between adults and between adults and nymphs of the same species. In Table I only the condition found in adult Menoponidae is used ; this is considered as a proto-menoponid character as it is found in those families most similar to the Menoponidae.

The loss or modification of some of these characters can be used to differentiate the families, but sometimes they are also variable within families. Table 1 shows that the Menoponidae (8A + 3a) and the Boopidae (8A + 2a) have retained more of these proto-amblyceran characters (the A-group) than the other families. By the arguments already used the retention of supposedly ancestral characters does not necessarily denote a relationship between the two families. However, they both possess certain derived characters (Mm) possibly already present in the proto-menoponid ; this together with the fact that there are no distinctive derived characters separating the two groups, indicates that they may be relatively closely related. The position is perhaps best represented by Ewing (1929 : 26) who divided the Menoponidae into the Boopinae and Menoponinae. This change is not adopted here as it would be better considered as part of a revision of the family-group classification of the Amblycera as a whole. A resemblance between certain characters found in *Paraboopia* and *Latumcephalum* (Boopidae) and those of some of the New World mammal-infesting Amblycera has been discussed under the diagnoses of the families. As the two genera are fundamentally boopid in character it would seem that any resemblance to the S. American mammal-infesting forms is likely to be the result of convergent adaptation of an avian-infesting menoponid stock to a

mammalian environment; while many of their other features are directly derived from that ancestral stock.

The Laemobothriidae (8A) and the Ricinidae (5A) differ from the Menoponidae not only in the loss and modification of some of the A-group characters, but in the development of further differentiating characters as given in the diagnoses of the families. However, as shown by the M-group characters, the difference especially in the Laemobothriidae, are not very marked and there is little doubt that both families have arisen from a protomenoponid stock.

The remaining families and subfamilies, all parasitic on New World mammals, have fewer of the A-group characters. All have one derived character in common, the presence of four sensilla coeloconica, usually opening to the surface by a single cavity or four wide-mouthed cavities. The Gliricolinae differ most markedly from the Menoponidae in the absence or modification of the A-group characters. In addition to the form of the antennal sense organ, they have a derived character, that of the highly modified leg, as a differentiating feature. The Gyropinae are less modified than the Gliricolinae and again have characters of the leg which separate them from the Menoponidae. The presence, loss or modification of most of the A-group characters in the Trimenoponidae is similar to those in the less modified members of the Gyropidae, this not necessarily denoting relationship. However, the form of the antennal sense organ in the Trimenoponidae is so similar to that of the Gliricolinae that a relationship between them can be presumed. The loss of the spiracles on segment VIII in both Trimenoponidae and the Gliricolinae may have happened independently. The Trimenoponidae differ from the Gliricolinae in having two tarsal claws, but again this character is of doubtful use in considering relationships. There is much variation within the Gyropidae : leg I may have two tarsal claws and legs II and III one (*Macrogyropus*), all legs may have a single unmodified claw (*Protogyropus*) or at least one pair of legs may be highly modified for clasping (*Gyropus, Gliricola*). This clasping modification is so different in the Gyropinae and Gliricolinae that each type could have developed independently from the normal tarsus. The presence of one claw, as Hopkins (1949 : 391) has pointed out, is a characteristic feature of the lice of mammals, as it is of the Hippoboscidae parasitic on mammals, and does not necessarily indicate relationship.

Hopkins (1949) considered that the evidence from the present distribution of the Boopidae showed their occurrence on the Australian marsupials to be primary. Since then considerably more species of Boopidae have become known : Kéler (in press) recognizes 35 species belonging to seven genera taken from 38 species belonging to four families of marsupials. No species have been collected from the Notoryctidae (Dasyuroidea) or the Phalangeridae (Phalangeroidea), but whether this is due to absence of parasites or to lack of collecting is not at present known. The marsupials of Australasia are divided by Simpson (1945) into three superfamilies (Dasyuroidea, Perameloidea and Phalangeroidea) containing a total of six families. However, Ride (1964 : 98) has re-emphasized the inconsistency in the classification of the marsupials and the Eutheria, the former being considered as a single order although containing many forms as diverse as those comprising the Eutheria ; the latter are now subdivided into 26 orders. In spite of the Boopidae being contained

in seven genera they do not, with the exception of *Latumcephalum* and *Paraboopia*, differ greatly from each other (see key below). All three groups of marsupials contain members parasitized by species of Boopidae but there is no genus, except for the doubtfully distinct *Phacogalia*, restricted to the first two superfamilies. Three genera of the Dasyuroidea (*Dasyurops*, *Dasyurinus* and *Satanellus*) are parasitized by the same species of *Boopia* (*uncinata*) and two other genera (*Phascogale* and *Antechinus*) of this superfamily each have a species (*spinosa* and *brevispinosa*) of *Phacogalia* (? = *Boopia*). Two genera (*Perameles* and *Isoodon*) of the Perameloidea are parasitized by one species of *Boopia* (*bettongia*) while the Phalangeroidea have eight species of *Boopia* and all the remaining genera and species of the Boopidae.

If a primary infestation is postulated then all the present Boopidae would be descended from a common ancestor parasitic on the ancestral stock giving rise to the three superfamilies of marsupials (X in Text-fig. 9). According to Ride (1964) these superfamilies have been separated from each other since at least early Eocene ; if this is so it would be expected that the present Boopidae would show greater diversity and that each superfamily of the marsupials would have a specific genus or genera of parasite.

If the suggestion (Hopkins, 1949) that the Trimenoponidae, parasitic on the New World marsupials and probably secondarily on New World rodents, are more closely related to the Boopidae than to any other of the Amblycera, then a common ancestor for these two would have existed in the Cretaceous. However, the morphological similarity between the Boopidae and the Menoponidae and the disimilarity between the former and the Trimenoponidae makes this theory rather unlikely. The hypothesis which seems to fit the known facts most satisfactorily is that the infestation

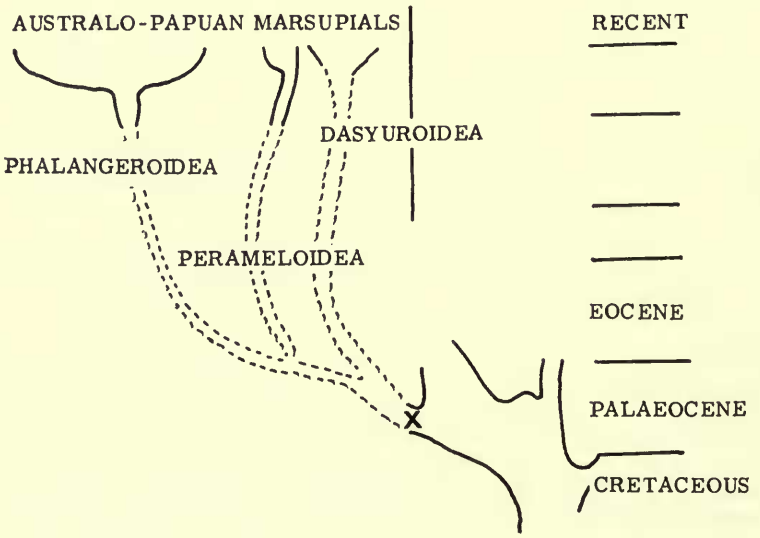


FIG. 9. A family tree of marsupials. Adapted from Ride, 1964. To agree with the text Simpson's superfamilies have been used for Ride's orders : Dasyuroidea for Marsupicarnivora ; Perameloidea for Peramelina ; Phalangeroidea for Diprotodonta.

of the Australian marsupials was comparatively late and that it arose from an avian menoponid stock, as suggested without elaboration by Ewing, 1929. This stock might have become established on an ancestral stock of Phalangeroidea, on which superfamily the diversity took place ; the parasites now found on the other two superfamilies being due to secondary infestations. The ancestral stock giving rise to the Boopidae would have had the M-group characters (Table 1) and probably most of the A-group characters now found in the Menoponidae and Boopidae. Waterhouse (1953 : 266) has shown that in *Heterodoxus* species (Boopidae) there is re-gurgitation of fluid from the midgut to the crop, a characteristic feature of the digestion of the feather-eating Menoponidae and Philopteridae, but absent in *Gliricola* and *Damalinia*, perhaps suggesting a not too distant feather-eating ancestor for *Heterodoxus*.

	V			V	V		V		V	V	V	V				V	V	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
MENOPONIDAE	d	A	A	A	A	M	A	M	A	A	A	M	M	m	m	a	a	a
BOOPIDAE	A	A	A	a-d	a	M	A	M	A	D	A	m-+	M	m	l-m	A	A	D
LAEMOBOTHRIIDAE	D	A	A	A	A	m	D	M	A	A	A	M	M	m	L	A	L	D
RICINIDAE	A	A	L	L	A	+	D	M	A	D	A	M	M	+	L	L	L	D
TRIMENOPONIDAE	D	D	A	D	a	+	a-d	+	A	A	D	+	+	+	L	a-1	a-1	D
PROTOGYROPINAE	D	D	A	D	D	+	D	+	D	D	A	+	+	+	L	A	L	D
GYROPINAE	D	D	A	a-d	a	+	a-d	+	D	a-d	A	+	+	+	L	A	a-1	D
GLIRICOLINAE	D	D	A	D	a-d	+	D	+	D	D	D	+	+	+	L	A	a-1	D

TABLE 1. Characters of the Amblyceran Families. A, Probable proto-amblyceran character in all species ; a, in most species. M, Probable proto-menoponid character (derived) in all species ; m, in most species. D, Derived character in all species ; d, in most species. L, Character absent. T, Character different. V (at top of column), Character although derived may have been acquired independently in the different groups.

1, Antenna, A, 5-segmented. 2, Sensilla coeloconica, A, 2–3 with separate surface openings; D, 4 with 1, 2 or 4 surface openings. 3, Labial palpi, A, present. 4, Labial palpus with 5 terminal setae, A. 5, Maxillary palpus, A, 4-segmented. 6, Setal pattern of head. 7, Mesonotum, A, independent. 8, Coxa I, M, antero-posteriorly extended. 9, Tarsal claws, A, 2 on legs II & III. 10, Tergum I, A, independent. 11, Abdominal spiracles, A, six pairs. 12, Position of post-spiracular setal complex, M, on central tergites. 13, Pair of subterminal setae on maxillary palp. 14, Temple setae 26 & 27 with alveoli contiguous. 15, Subocular comb-row, M, present. 16, Transverse pronotal carina, A, present. 17, Typical oblong postnotum, A, present. 18, Tentorial bridge, A, fully sclerotized.

The Trimenoponidae and Gyropidae might have been descended from a common amblyceran stock, probably avian-infesting, which became established first on the S. American marsupials giving rise to the Trimenoponidae. Perhaps part of this stock, before great divergence had taken place, became established on the New World Hystricomorph rodents, giving the Gyropidae ; secondary infestation by Trimenoponidae on this group of rodents would also have taken place. It can be postulated that the Hystricomorphs arrived in S. America without any Amblyceran parasites. This hypothesis would explain the presence of both Trimenoponidae and Gyropidae on the New World Hystricomorphs and the absence of members of both families on any of the Old World Mammals. The Gyropidae were also able to establish themselves on other mammals which entered S. America at a later date. Vanzolini and Guimarães (1955) have given a full account and discussion of the distribution of the lice of South American mammals.

Key to the Genera of the BOOPIDAE[2]

1		Post-spiracular setae on segments II-IV modified as trichobothria ; maxillary palpus 4-segmented	2
–		Post-spiracular setae on segments II-IV unmodified ; maxillary palpus 2- or 3-segmented.	6
2	(1)	Spinous process arising near base of each maxillary palpus ; spiracles on central tergal plates (Text-fig. 4)	3
–		Head without such spinous processes ; spiracles not on central tergal plates .	4
3	(2)	Abdominal lateral plates of VII & VIII broad and darkly pigmented	***MACROPOPHILA***
–		Abdominal lateral plates of VII & VIII not as above . .	***HETERODOXUS***
4	(2)	Pair of short, stout spiniform gular setae ; segments I-VIII each with pair of stout spiniform setae on tergites (Text-fig. 5) and sternites ; abdominal lateral plates partly divided by suture (Text-fig. 5) .	***PARAHETERODOXUS***
–		Without such gular setae ; segments I-VIII without such spiniform setae ; lateral plates not so divided	5
5	(4)	Head with sinus occipitalis (*sensu* Kéler in press) forming dorsal horizontal line across head immediately caudad to occipital setae (21–23) ; plantar pulvillus of tarsal claws with freely projecting point. .	***PHACOGALIA***
–		Head without sinus occipitalis ; plantar pulvillus without projecting point	***BOOPIA***
6	(1)	Maxillary palpus 2-segmented ; ocular seta on process.	***LATUMCEPHALUM***
–		Maxillary palpus 3-segmented ; ocular seta not on process .	***PARABOOPIA***

The Classification of the Phthiraptera

It is generally accepted that the Phthiraptera are derived from a Psocopteran ancestor but there is controversy on the relationships of the groups within the order. Konigsmann, 1960 has made a wide review of the literature and given a full discussion of the characters in which the Phthiraptera resemble the Psocoptera. He considers the Phthiraptera to be a monophyletic group and not descended from more than one Psocid ancestor. Further, he has considered in detail the evidence for the view expressed by various authors (Harrison, 1928 ; Webb, 1946 and Hopkins, 1949)

[2]This is a simplified key including some of the characters used by Kéler (in press) ; this author has been followed in recognizing *Macrophila* and *Phacogalia* as genera, although it is perhaps doubtful whether this serves any useful purpose.

that the Anoplura are more nearly related to the Ischnocera than either is to the Amblycera. Konigsmann considers that the evidence supports this view and that the Phthiraptera can be divided into two main groups : the Amblycera on one side and a group A on the other ; this latter group comprises the Ischnocera, Rhynchophthirina and the Anoplura. Additional evidence strengthening this view which has emerged from the present study is the similarity of the antennal sense organs in the species belonging to group A and their difference from those of the Amblycera and the different origins of the ' gonapophyses ' in the two groups.

It seems probable that the Mallophaga (Amblycera and Ischnocera) are not monophyletic and the present nomenclature of the groups within the Phthiraptera does not therefore reflect the true state of the relationships. The most satisfactory way of amending this would be to drop the name ' Mallophaga ' and have four suborders within the Phthiraptera as follows : Amblycera, Ischnocera, Rhynchophthirina and Anoplura.

Key to Groupings in the PHTHIRAPTERA

1		Third antennal segment pedunculate ; maxillary palpus present. Post-spiracular seta of at least one abdominal segment with 2 minute associated setae or rarely with single minute circular sensillum only, in which case only one tarsal claw on legs II and III . . . **Amblycera** 2
–		Third antennal segment not pedunculate ; maxillary palpus absent. Post-spiracular setae without 2 minute associated setae 9
2	(1)	Spiracles absent on segment VIII (5 pairs) 3
–		Spiracles present on segment VIII (6 pairs) 4
3	(2)	Two tarsal claws on legs II & III . . . . . ***TRIMENOPONIDAE***
–		One tarsal claw on legs II & III . . . . . ***GLIRICOLINAE***
4	(2)	One tarsal claw on legs II & III 5
–		Two tarsal claws on legs II & III 6
5	(4)	At least one pair of legs strongly modified for clasping hair . ***GYROPINAE***
–		Legs not modified for clasping hair (single unmodified claw on each leg) ***PROTOGYROPINAE***
6	(4)	Labial palpi undeveloped ; labrum with hyaline extension each side (pulvinus) ; meso- and metanotum and tergum I fused together . . ***RICINIDAE***
–		Labial palpi at least one-segmented ; no pulvinus ; meso- and metanotum and tergum I not all fused together 7
7	(6)	Temples with area of sculpturing with outer rows of peg-like projections (Pl. 4, fig. 23) ; venter of 3rd femur and some sternites with patches of microtrichia of characteristic form (Pl. 4, fig. 22) ; meso- and metanotum fused ***LAEMOBOTHRIIDAE***
–		Temples without such sculpturing ; venter of 3rd femur and sternites without such patches of microtricha ; meso- and metanotum not fused . . . 8
8	(7)	Mesonotum with pair of seta-bearing protruberances ; tergum I fused to metanotum . . . . . ***BOOPIDAE***
–		Mesonotum without pair of seta-bearing protuberances ; tergum I not fused to metanotum . . . . . ***MENOPONIDAE***
9	(1)	Piercing mouthparts (sac containing 3 stylets) ; pronotum not apparent **Anoplura**
–		Manibulate mouthparts ; pronotum reduced or fully developed . . . 10
10	(9)	Mandibles borne at end of long proboscis . . . **Rhynchophthirina**
–		Mandibles not borne at end of long proboscis . . . . **Ischnocera**

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PLATE 1

FIG. 1. *Heterodoxus longitarsus*. Terminal segments of antenna, × 980. S, sensillum coeloconicum on 2nd segment.

FIG. 2. *Ricinus elongatus*. Terminal segments of antenna, × 933.

FIG. 3. *Laemobothrion* (*L.*) *vulturis*. Terminal segments of antenna, × 620.

FIG. 4. *Gryopus ovalis*. Antennal sense organ, × 3870.

FIG. 5. *Macrogyropus dicotylis*. Terminal antennal segment, × 734.

FIG. 6. *Gyropus* sp. from *Cercomys canicularis*. Terminal antennal segment, × 8400.

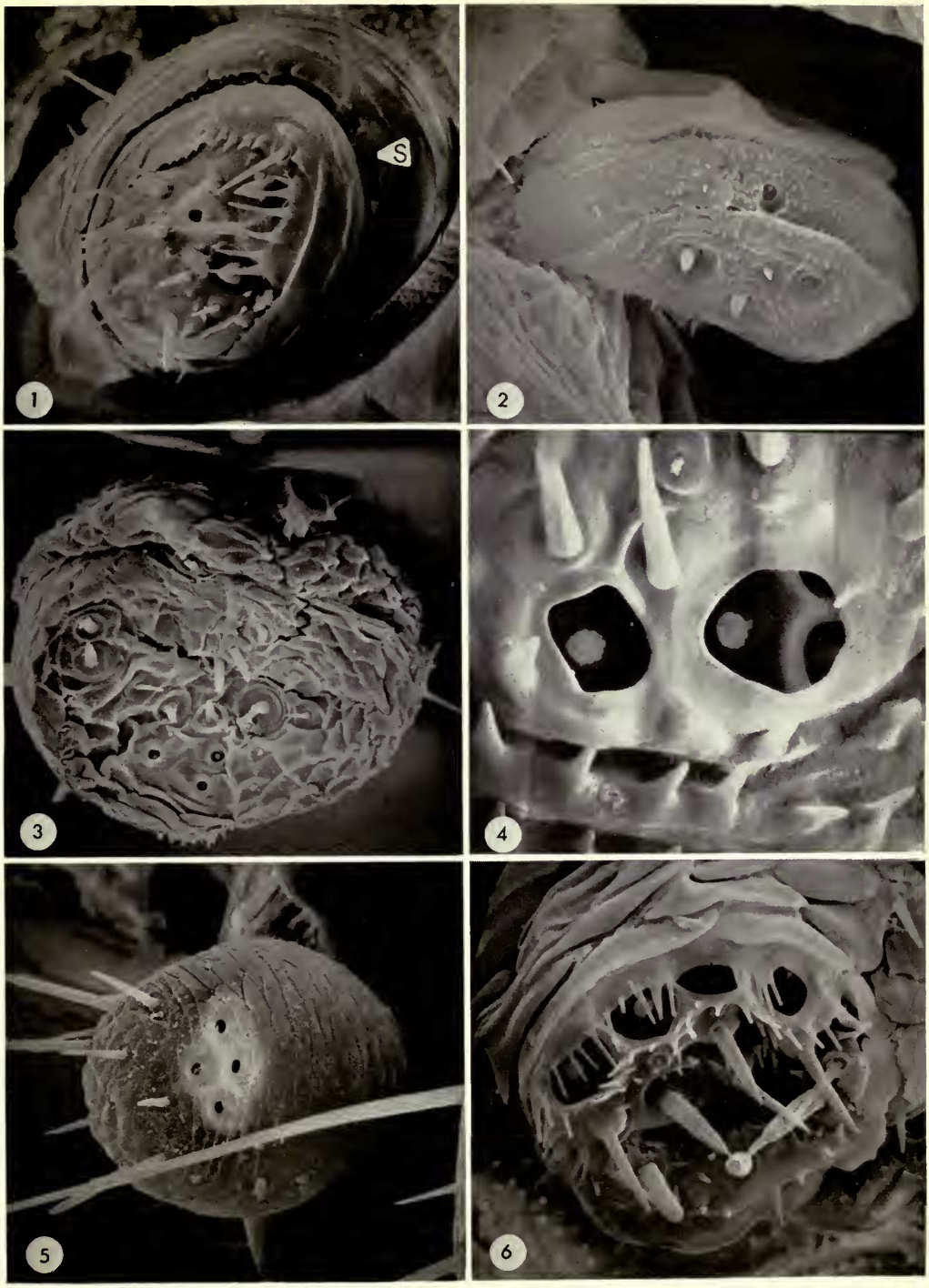
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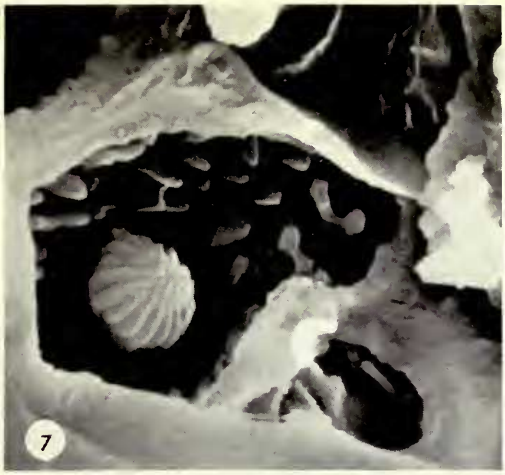
PLATE 2

FIG. 7. *Phtheiropoios wetmori*. Part of antennal sense organ, × 8334.
FIG. 8. *Macrogyropus amplexans*. Terminal segment of antenna, × 1200.
FIG. 9. *Gliricola porcelli*. Antennal sense organ, × 4934.
FIG. 10. *Cummingsia* sp. Antennal sense organ, × 3334.
FIG. 11. *Trimenopon* (*Philandesia*) *chinchillae*. Antennal sense organ, × 7334.
FIG. 12. *Trimenopon* (*T.*) *hispidum*. Antennal sense organ, × 1600.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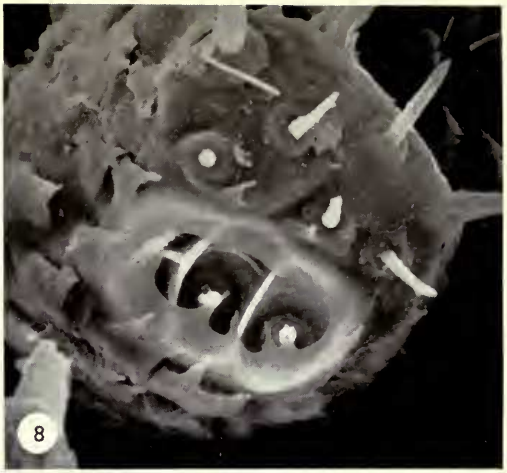
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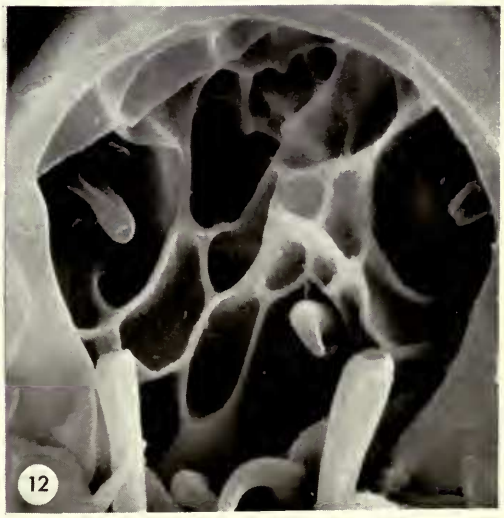
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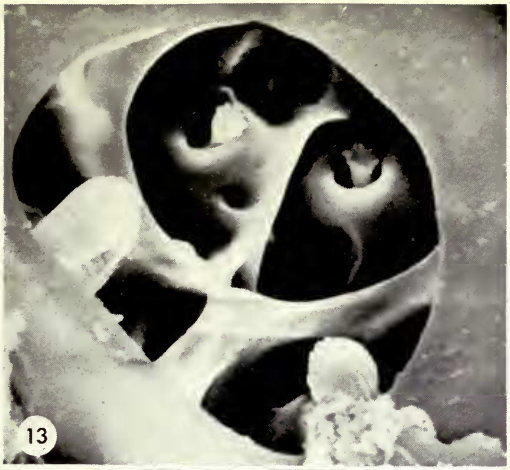
PLATE 3

FIG. 13. *Pitrufquenia coypus*. Antennal sense organ, × 5067.
FIG. 14. *Harrisonia* sp. Antennal sense organ, × 5373.
FIG. 15. *Goniodes lagopi*. 4th and 5th antennal segments, × 667.
FIG. 16. *Naubates prioni*. 4th and 5th antennal segments, × 1400.
FIG. 17. *Trichodectes melis*. Antennal sense organ on terminal segment, × 1300.
FIG. 18. *Trichodectes melis*. One of the circular areas shown in fig. 17, × 10,334.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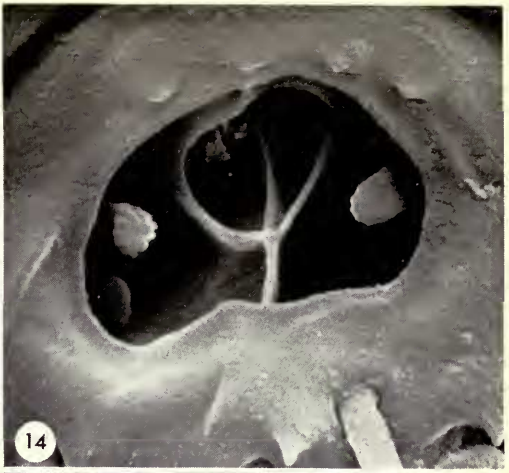
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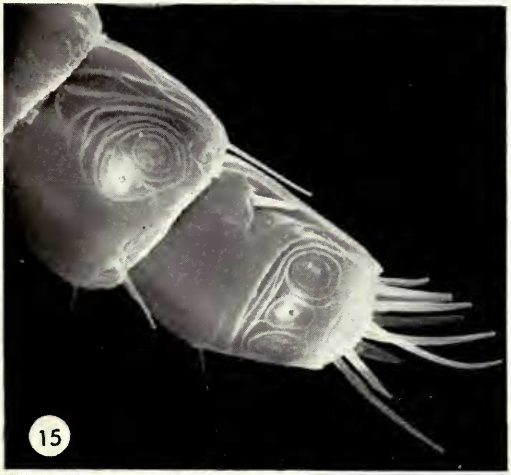
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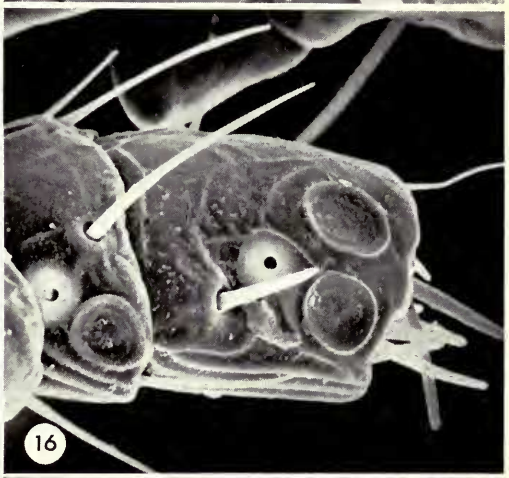
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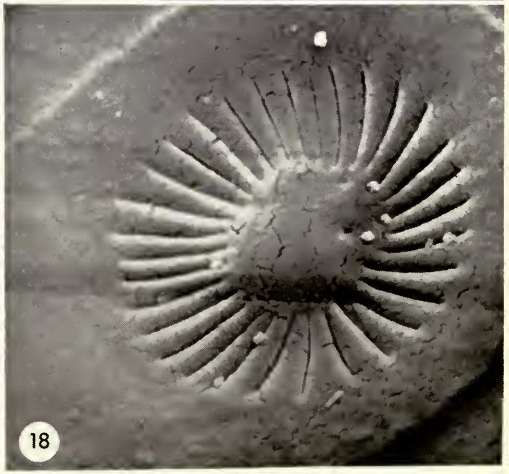
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PLATE 4

FIG. 19. *Haematomyzus elephantis*. Sense organ of 5th antennal segment, × 4667.
FIG. 20. *Haematomyzus elephantis*. Upper circular sense organ of fig. 19, × 9333.
FIG. 21. *Haematomyzus elephantis*. Sense peg and surrounding filaments from terminal antennal segment, × 15,334.
FIG. 22. *Laemobothrion* (*L.*) *vulturis*. Combs from abdominal sternites, × 867.
FIG. 23. *Laemobothrion* (*Eulaemobothrion*) *chloropodis*. Edge of temple, × 886.
FIG. 24. *Laemobothrion* (*L.*) *vulturis*. Distal end of tibia, × 400.

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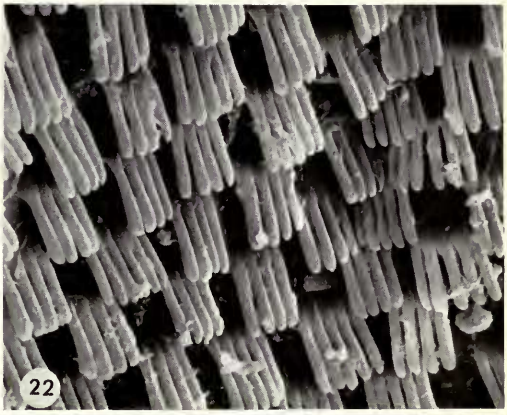
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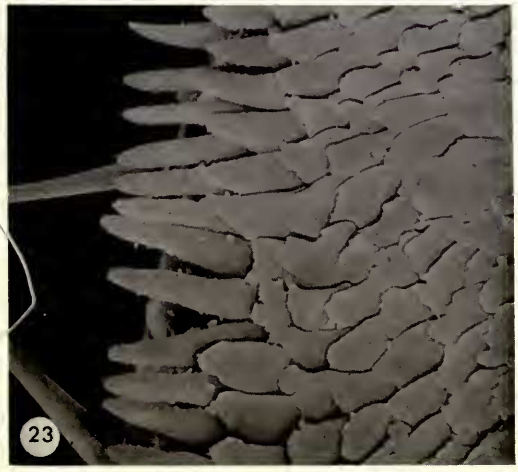
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PLATE 5

FIG. 25. *Boopia grandis*. Second tarsus of second leg, × 440.

FIG. 26. *Heterodoxus longitarus*. Meso- and metanotum and terga I and II, × 140. s, mesonotal protuberance with spiniform seta ; m, metanotum ; t, tergum I.

FIG. 27. *Paraheterodoxus insignis*. Parts of lateral plates and tergites of segments III, IV and V, × 161.

FIG. 28. *Trinoton* sp. Lateral plate of nymph, × 440 ; c, post-spiracular seta.

FIG. 29. *Heterodoxus longitarsus*. Trichobothrium of segment II showing the two minute associated setae, × 7000.

FIG. 30. *Haematomyzus elephantis*. Sense organ associated with spiracle, × 7667.

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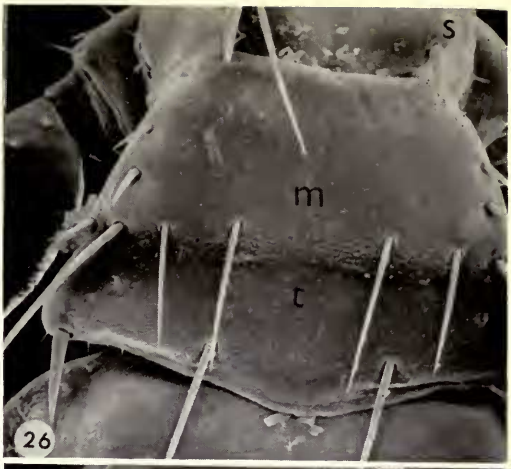
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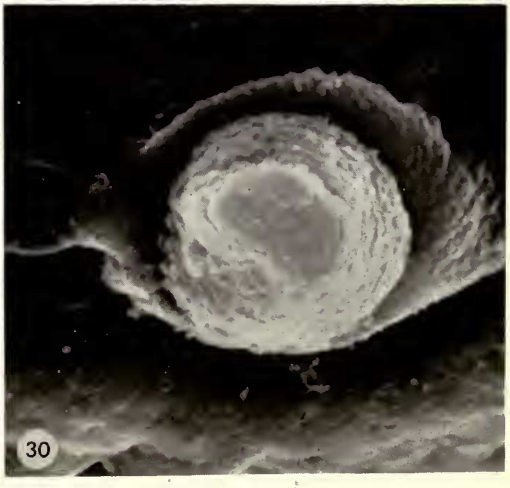
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