PROTHORACIC REGION OF ACALYPTERATE DIPTERA:

a) MORPHOLOGY, b) TAXONOMIC SIGNIFICANCE.

A Thesis submitted in part fulfilment of the requirements for the Degree of Doctor of Philosophy in the University of London.

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ABSTRACT.

The prothoracic morphology of a wide range of Acalypterates has been examined, and is described in some detail. Conflicting terminologies for the various sclerites are discussed and a comprehensive system of nomenclature is proposed for them.

The possible uses of prothoracic sclerites in Acalypterate systematics has been surveyed, leading to a detailed study of the probasisternum (or prosternum).

The variability of the prosternum has been analysed, in an attempt to arrive at an understanding of the evolution of its shape and the relation between this and the evolution of Acalypterates. The methods by which it has been attempted to derive such information from modern forms are presented in full.

The status and probable relationships of 23 Acalypterate families are discussed, comparing deductions made using prosternal shape with deductions based upon other characters. In conclusion it is suggested that variation in prosternal shape provides a reasonably reliable guide to Acalypterate inter-relationships, and could be especially useful in unravelling relations between families.

Attention is drawn to the possible applications of methods used here in other studies, and to the differing information content of dimorphic and polymorphic taxonomic characters.

CONTENTS.

SECTION 1: INTRODUCTION

According to Oldroyd (1964), about 80,000 species of Diptera are known to science. One of the largest sub-groups within the Order is the Acalypterae (or Acalypteratae), a section of the Sub-order Cyclorrhapha, with perhaps 20,000 species. The vast number of species involved, coupled with the fact that many are of small size, not superficially very attractive, but fragile and difficult to handle, has resulted in this being one of the least understood of insect groups. In this respect the Acalypterates occupy a position similar to that of the Parasitica within the Hymenoptera, or the Staphylinoidea among Coleoptera.

There have been few morphological studies of the Dipteran thorax. Except in the case of Crampton's work (1942), these usually occur as part of a description of the general morphology of single species. Discussion of comparative anatomy is then unavoidably based upon the work of a number of different authors and a variety of interpretations (Braula provides an extreme case: see under Braulidae).

Interest in the modifications undergone by the pterothorax to accommodate specialised flight musculature, has produced detailed discussion of its structure, at the expense of discussion of the prothorax. The attitude of most authors is summed up by Ferris (1950), who dismisses the prothorax with the remark "Serving merely as a support for the prothoracic legs". Prothoracic morphology of Acalypterates has been mentioned by Ferris (1950), Hassanein and Abd-el-Salam (1962), Nayar (1962), and Pandey and Agrawal (1962). Apart from Nayar (Dacus and Sphyracephala), each of these authors has examined only a single species.

Prothoracic structures have also been referred to by taxonomists. This has resulted in the development of a system of terminology independent of that used by morphologists, but which incorporates terms that have morphological connotations. A number of names are now available for most sclerites, causing confusion.

Through the combined effects of these various factors, Acalypterate taxonomy continues to be a very great problem to systematists. In order to grapple with the group at all, most authors have specialised in the study of individual families, and even then only ten authors (Aczel, Frey, Hendel, Hennig, Keiser, Melander, Morge, Shewell, Steyskal and Tonnoir) have published papers that deal with any family on a World basis. So far, little work has been done on the ways in which relationships between families can be elucidated, with consequent confusion over family definitions. As Sabrosky (1960) says, "Family classification in the Acalypterates will be one of the areas of ferment in the years ahead". As yet only six people have tried to discuss the major classification of Acalypterates to any extent. Not suprisingly, each attempt has produced very different results.

A final complicating factor in the study of Acalypterates results from their greater abundance outside the Holarctic region than within it. Of the sixty-two families currently recognised, twelve are completely absent from the Holarctic. Conversely, of important authors at present working on Acalypterates, some twenty are based in the

Holarctic, four in the Ethiopian, three in the Australasian and one each in both the Oriental and Neotropic regions. Because of this, Acalypterate family definitions are based principally on European faunas. As tropical and southern Acalypterates become better known, family definitions are constantly having to be reviewed, producing great instability in the literature. Five new family names have been introduced by reputable workers during the past ten years.

Despite the more restricted fauna of the Holarctic, it is still inadequately known. Britain, with some 1,000 species in 44 families, has never had any comprehensive account, in English, of half of them.

There is an obvious need for more work on Acalypterates, embracing all aspects of their study. The account of prothoracic morphology presented here is directed at establishing the part which prothoracic sclerites can play in unravelling some of the current problems of Acalypterate systematics. It should also provide indications of other potentially useful lines of investigation. During the course of this work, some 2,150 species from all over the World, belonging to 800 genera and between them representing 59 families, have been examined. This is in the region of a 10% sample of all known species and involves a much higher proportion of known genera.

The family names used here are those of Hennig (1958), since his is the most recent comprehensive account of Acalypterate classification. In addition, the family names Somatiidae and Pseudopomyzidae have been incorporated, as being names introduced since 1958, by authors with knowledge of Hennig's work.

It has not been possible to check the validity of all the generic names used in the text. They refer to the species at present found under those names in the British Museum (Natural History) at South Kensington. When apparent anomalies have been encountered, the taxonomic position of the specimens involved has been checked. A list of all the genera examined appears in the appendix.

SECTION 2: MORPHOLOGY OF THE PROTHORACIC REGION

2a) INTRODUCTION

In the following account each of the prothoracic sclerites is considered in turn. Those of the prosternal region are treated in the most detail, because they come in for further discussion in subsequent sections. Special attention has also been given to the cervical organ, since it has been ignored by morphologists previously, and also because of its apparent association with prosternal sclerites. Prothoracic musculature, apart from that associated with the probasisternum, is not considered.

2b) PREPARATION OF MATERIAL

Apparent sutures in dry specimens are not always what they seem, and may also be camouflaged by confusing pigmentation of the cuticle. For these reasons, and also to make illumination easier, the thoracic content of the specimens used for morphological work was removed, and the cuticle itself then bleached and stained.

Some of the material for this work came from spirit collections (in this case 50-70% ethanol with a little glycerine added), but by far the greater proportion was acquired dry. The preparative methods used proved equally successful for specimens from either source.

2c) PREPARATION TECHNIQUE

(1) To facilitate removal of muscles and other internal structures, specimens were left in hot 10% potassium hydroxide solution for about two hours. To aid penetration of the Potash into the thorax, the head and abdomen of each specimen was removed. The head of a dry specimen

had to be removed with care, so that the cervical sclerites were not pulled away from the thorax at the same time.

(2) After treatment in potash, specimens were transferred to water. Here the disc of the thorax was cut away, so that the remains of its soft parts could be extracted.

(3) Bleaching: Specimens were left in tubes of diaphanol out of contact with light, for about twelve hours. This was usually sufficient to render the cuticle thoroughly transparent.

(4) Staining: Three alternative cuticle stains were employed, as follows:-

a. Acid fuschin - This compound was used as a 15% solution in 90% alcohol. Bleached specimens were transferred up through the alcohols to be left in the stain for about an hour. The acidity they had acquired through contact with diaphanol allowed them to take up the stain without prior treatment in acid alcohol. Overstaining was easily corrected by leaving specimens in 70% alcohol for a short time.

Although a range of storage media was tried, none was found in which specimens stained with acid fuschin retained the stain satisfactorily. This was a serious disadvantage to its use. This stain also proved unreliable in other ways, not being very sensitive to lesser degrees of scleriotisation and sometimes violently staining areas of obvious membrane.

b. Mercurochrome - A 1% aqueous solution of mercurochrome was used. Acidity resulting from bleaching a specimen had to be removed from the cuticle before this stain could act, since it was otherwise precipitated, forming a crust over the specimen. Washing in a number of changes of distilled water was normally effective, or, with care, a dilute solution of alkali could be used. Unless sufficiently dilute (one drop of 10% potassium hydroxide in a watch-glass of water), the alkali reacted violently with the acidic cuticle, causing deformity or even disintegration.

Best results were achieved if specimens were left in this stain for two hours or more. Overstaining can be countered by leaving specimens in distilled water, when the stain slowly leaches out.

Mercurochrome proved a very sensitive stain, differentiating successfully between areas of different degrees of sclerotisation. In this work it proved less satisfactory for general usage, because specimens treated with it remained very transparent. At lower powers of magnification, this produced confusing optical effects, making it difficult to distinguish surface from sub-surface, or internal structure But under a high power objective, where differential focusing is possible and adequate lighting difficult to obtain, this high degree of transparency was very useful.

c. <u>Chlorazol Black</u> - This stain was used as a 25% aqueous solution. Ideally specimens were left in it for half an hour. No entirely successful method of removing excess stain was found, so great care had to be taken to avoid over-staining. A little pyridine in 70% alcohol will partly remove chlorazol black, but very slowly, and it has no effect on heavily overstained specimens.

This stain has the advantages of mercurochrome without possessing the attendant disadvantages of either that stain or of acid fuschin.

(5) Storage: Stained specimens were taken "up through the alcohols" to absolute alcohol, from which they were transferred to either cedarwood oil, methyl benzoate, or terpineol for storing.

Terpineol was found to be the most acceptable storage medium, since both cedarwood oil and methyl benzoate glued up the caps of the storage tubes. Further, specimens were always examined in terpineol, so that when stored in this they could be directly transferred for examination.

2d) EXAMINATION OF MATERIAL

Prepared specimens in terpineol were examined in solid watch-glasses under a binocular microscope with sub-stage illumination. Convection currents in a solid watch-glass tend to make specimens float about and this was prevented by holding them in a web of cotton wool fibres.

Graticules were used in making scale drawings.

When a higher power of magnification (x400-x1000) was required (as for detailed examination of the cervical organ), temporary mounts of the thoraces were made in cavity slides (with rings if necessary), using terpineol as mountant.

2e) THE SCLERITES OF THE PROTHORAX

(1) Pronotum. In all Diptera the pronotum is much reduced, a condition found in its extreme amongst the Schizophora. The original notum is here sub-divided into three sclerites: one ring-like, forming the dorsal anterior margin of the thorax, and bearing on its hind margin the first phragma and a pair of more posterior, lateral calli that may retain only the most tenuous connection with the rest of the pronotum. These sclerites are, respectively, the 'pronotum' and parts of the 'humeral calli' of systematists.

Some authors (Young 1921, Rees and Ferris 1939, Ferris 1950, Nayar 1962, Santokh Singh 1962, Imms 1964) consider the humeral calli to be entirely prescutal elements of the mesothorax, but there seems little justification for this view. Hammond (1881), Zalokar (1949) and Miller (1950) found muscles originating on the humeral calli with their insertions on the occiput, cervical sclerites and the trochanteral apodeme of the fore coxa. This is incompatible with a completely mesothoracic origin of the calli, which these authors believed to be prothoracic. During the course of the present work these muscles have been noted in Callistomyia (Trypetidae) and Orygma (Sepsidae). The humeral calli are also taken to be prothoracic by Snodgrass (1935), Crampton (1942), Bonhag (1949) and Pandey and Agrawal (1962).

According to Snodgrass (1935), subdivisions of the pronotum should not be given names similar to those denoting subdivisions of pterothoracic nota, since the segments of the thorax have gone such different ways in evolution.
Crampton (l.c.) named the two pronotal sclerites the antepronotum and postpronotum. Bonhag used a similar terminology. Zalokar, converse to Snodgrass's suggestion, named these sclerites the prescutum and scutum. The "prescutum" he so named since it bore the first thoracic phragma, as the phragma are always found on the prescuta of thoracic segments which bear them. The first phragma is, however, born on the hind margin of this part of the pronotum, not on its front margin, as it would have to be were this sclerite to be designated prescutal.
His assessment of the humeral calli as scutal is based on the position of muscle origins.

In the present account, Crampton's terminology of antepronotum and postpronotum is used, except where the elements of the latter sclerite are more conveniently referred to as the humeral calli.

The pronotum is best developed among Acalypterates in the two superfamilies Otitoidea and Nothyboidea, in particular in some of those Otitoid genera once grouped as Phytalmiidae and in the Nothyboid families Diopsidae and Nothybidae (see figures 2 and 4). Even here the antepron~~s~~ct~~o~~um is narrowed, by the mesonotum pushing far forward, at least in the mid-line (see figures 7 and 8). In other families, such as the Neriidae, where the prothoracic region is somewhat elongate, the antepronotum does not contribute to this expansion, remaining as a ring-like sclerite at the end of a forward extension of the mesonotum.

The antepronotum is least developed among families like those of the Drosophiloidea, where it appears as a narrow rim to the edge of the mesonotum, which has expanded to such an extent that the definitive prothorax forms but a small part of the anterior face of the thorax. This situation is typified by Ephydrids (see figure 55), and met with in an extreme form in <u>Curtonotum</u> (see figure 52). In some this pronotal collar becomes evanescent in the mid-line dorsally. It is presumably this situation which led Pandey and Agrawal (1962) to suggest that in <u>Agromyza</u> the pronotum is 'formed by the union of two sclerites in the mid-line'. In these same flies the humeral calli, originally projections at the antero-dorsal corners of the thorax, enlarge and come to lie on the front of the thorax, and are also considerably flattened out.

The humeral calli vary in size, position and shape. It is possibl that the contribution made by the pronotum and mesonotum to these projections is equally variable. Sutures certainly provide no convenient solution to this problem. In <u>Rainieria</u> (Micropezidae), each humeral callus is subdivided into two parts (see figure 7), which perhaps demonstrates how it is apportioned between pronotum and mesonotum in this genus, but this is not repeated elsewhere. Trepidaria (figure 8) shows a more frequent Micropezid condition, which corresponds well with other Acalypterates (see figures 1-9).

When the thorax is attenuated anteriorly, the humeral calli may elongate and come to occupy an entirely lateral position (see figure 2, Nothybus). They may become entirely undifferentiated, as in Micropeza (figure 9), where the position of the postpronotum cannot be determined from external features.

Hassanein and Abd-el-Salam (1962), have stated that the whole of the dorsum of the thorax in Braula is pronotal in origin. Although modified, with sutures lost and complete sclerotisation of areas membranous in other Acalypterates, the prothorax of Braula seems in fact to exhibit exactly the same plan found in other Schizophora, with the antepronotum greatly reduced and the humeral calli occupying the anterodorsal corners of the thorax (see under Braulidae). Its dorsum is then principally mesonotal.

(2) Propleuron. The propleuron is represented by an episternum and an epimeron, distinguished from one another by the line of the propleural suture marking the course of the propleural apodeme (propleural apophysis). The dorsal and posterior margins of the propleuron cannot be traced, due to loss of sutures, but since the prothoracic spiracle is intersegmental in origin, its position gives an indication of the extent of propleural elements. This is not so good a marker as in many other Diptera, however, since the membranous

area which normally surrounds it is sclerotised in Acalypterates. The resulting intersegmental sclerite may or may not be distinct, but gives every appearance of being well differentiated in *Nothybus* (see figure 2), where a triangular plate bears the spiracle. As judged by the sutures which are available, the episternum is generally well developed, but the epimeron is much reduced (see figure 12).

In many Acalypterates, propleural elements make contact with the prosternum in front of the fore coxa, producing a precoxal bridge. Projections from both sclerites can usually be seen to be involved, but the proportion of the bridge derived from each varies, and in some cases cannot be determined, because the suture has disappeared, as in Ephydridae (see figure 54).

The projection from the proepisternum which makes the pleural part of the precoxal bridge may also be present in species without a precoxal bridge, especially when these are related to bridge-bearing species. In other Diptera such a projection has been named the precoxa: Crampton (1942), Bonhag (1949). It is conceivably a remnant of a true trochantin. Rees and Ferris (1939, *Tipula*), Crampton (1942, a range of Diptera) and Ferris (1950, *Drosophila*), comment on the absence of any true prothoracic trochantin in Diptera. Crampton goes on to state that neither had he found such a structure in the related Orders of Mecoptera and Megaloptera. The findings of Ferris (1939, 1940) and Acker (1958), in papers on Mecopteran and Neuropteran morphology, contradict Crampton. The sclerite they define as the trochantin lies free in membrane.

Matsuda (1960) defined a trochantin as "A katepisternal sclerite, articulated at its ventral end to the anterior margin of the coxa;

often divided into anterior and posterior trochantins, of which the former is articulated with the coxal margin". This definition does not exclude the 'precoxa' of Acalypterates from being a remnant of a true trochantin.

There has so far been no report of a precoxa in Nematocerous Diptera. This suggests that the sclerite may be a secondary development in Acalypterates, perhaps associated with formation of a precoxal bridge (though prosternal precoxal bridges are known among Nematocera and Brachycera). It therefore seems sensible to use the name 'precoxa' or 'precoxale' for it at present, rather than to treat it as part of an original trochantin.

A sclerite which is more certainly secondary in origin is developed in the cervical membrane in Conopidae and sporadically in other families (see figure 12, 'secondary sclerite'). Here a weakly sclerotised, poorly defined but more or less lunulate plate, lies free in the membrane just antero-ventral to the coxae. There seems little justification for putting a name to this sclerotised area, since there is no readily available means of defining it, other than by its location on which basis it would qualify for consideration as trochantinal.

The coxal condyle is single-headed in all Acalypterates examined, apart from the Diopsidae, where it is two-headed. There is no trace of any ventral articulation of the coxa.

In many Acalypterates, such as Celyphids, Chloropids and Drosophilids, the propleuron maintains a greater area on the anterior face of the thorax than it does laterally. The converse is found in certain families where the anterior part of the thorax is attenuated. Here the proepisternum apparently extends onto the dorsal surface of the thorax (see figure 11), though since the sutures are obscure it would require study of the muscles to verify this. In Neriidae and Nothybidae there is great elongation of the proepisternum, the pleurosternal apophysis elongating at the same time.

(3) Sternum. In Acalypterates the prosternum is represented by three sclerites, a "presternum", which is variously developed, a basisternum, which forms the "prosternum" of systematists, and a furcasternum, always fused to mesothoracic elements. Spinasterna are absent in Diptera.

The sclerite here named the presternum lies in the cervical membrane in the mid-line, just in front of the basisternum. Anteriorly, it is in contact with parts of the cervical organ (see below). This sternite is much reduced in a number of families and in others has lost independence from the cervical organ (see figures 19-20). Only rarely, e.g. in Conopidae, Micropezidae, Sciomyzidae, it is a large plate intervening between basisternum and neck region (see figure 16). Nowhere does it bear an apodeme.

Crampton (1942) considered a primary presternum to be present in Musca, but doubted its presence in lower Diptera, where he only found an apparent presternum in Tabanus. Bonhag (1949), also working on Tabanus, designated the same plate a presternum, and at the same time suggested for it a sensory function. Where present in Acalypterates this plate is almost invariably associated with the cervical organ, frequently intimately so (see figures 16-20). This fact, as well as its variation in form (see under cervical organ), suggests that it may be a secondary structure, perhaps developed independently many times in response to demands of the cervical organ. This would account for the absence of a presternum in many lower Diptera (Crampton, 1925a, 1925b,1942, Hillyer, unpublished thesis), where the cervical organ is not so highly differentiated and can even be absent (Hillyer).

Whether or no this plate is eventually accepted as a true presternum, it is convenient at the moment to treat it as one because of its location and most probable derivation. The same plate has been called an "interclavicle" by Pandey and Agrawal (1962), on account of its position.

The main sclerite of the prosternal region is the basisternum. This plate occupies the area between the fore coxae. Posteriorly a well marked and sometimes complex suture forms its boundary with the furcasternum. Anteriorly it is surrounded by membrane of the cervix, except where it is in contact with the presternum, or when a precoxal bridge is formed with the propleura (see figures 40-56). In the latter case, the suture between sternal and pleural elements may be lacking (see figure 54). The basisternum bears a median inflection which forms internally a keel-like apodeme (see under basisternal musculature). This is registered externally as a groove, which may terminate in a pit, as in Dacus and Ochthera.

Zalokar (1947) does not differentiate between the basisternum and the third prothoracic sternite which bears the furcal arms. He referre to both as one sclerite, the "furcasternum". Ferris (1950), also writing on Drosophila, considers the probasisternum to be extensions of the proepisterna meeting mid-ventrally: Drosophila being a genus that bears a precoxal bridge. He apparently overlooked the suture between pleural and sternal elements (see figure 51). Nayar (1962) considers the basisternum to be the presternum, in Sphyracephala (Diopsidae), believing the true probasisternum to be confined to a narrow area between the furcal arms. Diopsidae have a rather exceptional form of basisternum (see below).

These various interpretations are each based on morphological investigations of only one species of fly (except in the case of Ferris, who had also examined Tipula). From the survey of Acalypterates undertaken in the present account and from the work of Snodgrass and Crampton, it seems certain that the same sclerite is being referred to throughout and that it is a true prothoracic basisternum.

The probasisternum varies greatly in shape and relative size in the different Acalypterate families. At the one extreme it is present only as a linear sclerotised strip, as in Sepsidae, Megamerinidae etc.; at the other it is fused to the propleura, forming a heavily sclerotised precoxal bridge (presternal, prosternal or prothoracic bridge of different authors), so that the only membrane remaining in the cervical region is that immediately surrounding the cervical foramen and cervical sclerites (see figures 40-56). Between these two extremes are found a range of intermediates. These include spatulate forms found in some Coelopids, cordate or shield-like forms which typify the Trypetids, and quadrate shapes seen in many Platystomatids (see figures 13-15).

A curious condition is found in the Diopsidae. Here the basisternal carina (apodeme) continues backwards between, and far posterior to, the furcal pits. The suture between basisternum and furcasternum is absent; so too is the transverse apodeme between the bases of the furcal arms and the end of the carina (see under musculature). It appears that here the basisternum has become extended backwards in the mid-line (but not laterally), so that the furcasternum has been more or less cut in two.

Nowhere among the Acalypterates is the prothoracic furcasternum an isolated sclerite, being always found fused to the external part of the mesothoracic presternum. Together these two form a triangular sclerite, (they are separated by a transverse suture in some lower Diptera, e.g. *Trichocera*, *Anisopus*, Hillyer loc.cit.) tapering posteriorly, with the pits of the furca in its anterior angles. In some flies, e.g. *Dryomyza*, this triangle is clearly marked by sutures, while in others the sutures are entirely lost (see figures 40-44).

The only prothoracic sternite which is consistently present in all Acalypterates in a recongisable form is the basisternum. The modified nature of the other sternites not only makes it frequently difficult to distinguish them, but also renders them only occasionally useful systematically. Because of this, the term 'prosternum' has been used in the following pages to denote the probasisternum, unless it is specifically stated otherwise.

(4) *Basisternal apodemes and musculature*. It is possible that variation in the shape of the basisternum in Acalypterates is correlated with differences in the associated musculature and its supporting apodemes and,therefore, with differing functions of the fore legs. Various species have been dissected during the course of this work, to investigate this possibility, and in addition the prosternal apodemes of a large number of species have been examined, using dried specimens cleared in diaphanol.

Maki (1938) found only one muscle originating on the prothoracic basisternum in Diptera, inserted on the coxal rim. He describes this muscle as the "sternal promotor of the coxa". A sternal adductor he recognises in other Orders but did not locate it in Diptera. Bonhag (1949) recognises both muscles as occuring in Tabanus, where they originate one behind the other on the basisternal carina. They are inserted on the coxal rim, the promotor antero-laterally, the adductor postero-ventrally. Miller (1950) describes these two muscles in Drosophila, but gives the name "anterior rotator" to the more anterior of the two. Here the origin of the adductor is upon the transverse ridges connecting the basisternal carina to the bases of the pleurosternal apophyses. Zalokar (1947) provides a similar interpretation of Drosophila, but does not name the muscles.

In the species examined here, the promotor of the coxa is universally present. The adductor is variously developed and sometimes appears to be lacking, for example in Sepedon (Sciomyzidae).

The promotor consistently originates along the carina of the basisternum, which can be either deep, as in Helcomyza and Coelopa (see figures 21,22,31), or shallow, as in Ephydra and Grammicomyia (Micropezidae), (see figures 23,24). In some flies, e.g. Toxopoda (Sepsidae), Calobata (Micropezidae), the basisternal keel projects posteriorly beyond the rest of the sclerite (see figures 25,26), whilst in Diopsidae the carina projects far posterior to the furcal pits (see figures 30, 36)

The promotor is inserted on the coxal rim just ventral to the condyle and may be concentrated or dispersed (see figures 31-36). In some, e.g. Rivellia, Curtonotum, the muscle seems to be differentiated into two separate strands which arise and insert one posterior to the other, distinct from the adductor (see figures 23,35). In these forms, Miller's name of anterior rotator for this muscle would seem more appropriate.

Whereas the promotor is usually a deep, fan-shaped muscle, the adductor may be reduced to a few bundles of fibres, e.g. in *Curtonatum* and the Lauxaniidae, or developed to quite a thick deltoid form as in *Orygma*. It has its origin either along the transverse apodeme between the posterior end of the basisternal carina and the arms of the pleurosternal apophysis (this apodeme is at the suture between basisternum and furcasternum), or else in the angle between these two. The insertion of this muscle is on the postero-ventral angle of the coxal rim, as in *Rivellia*, *Sphyracephala*, or more anteriorly - *Orygma* and *Sicus* (Conopidae). It passes forwards under the promotor and where their origins overlap lies beneath the other muscle. In *Orygma* a bundle of fibres lies separate from the promotor and beneath it, but dorsal to the adductor, with its insertion anterior to the latter. This would thus seem to be part of the adductor that had separated off.

A curious variation occurs in the Diopsidae where the adductor is seemingly attached to the basisternal carina, there being no transverse apodeme. In various Acalypterates this apodeme is incomplete, e.g. *Sepedon*, *Chyliza* (Psilidae), whilst in others it may bear anteriorly directed projections, e.g. in *Plagiostenopterina* (Platystomatidae) a nd *Palloptera* (Pallopteridae) - see figures 21-30. In *Rivellia* these are associated with a part of the sternal promotor which has separated from the remainder of the muscle (see figure 33).

This description demonstrates that there is little discernible correlation between variation in the form of the basisternum and variations of its associated musculature. Thus Diasemopsis and Curtonotum have externally similar basisterna, but rather different musculature and apodemes. Thus, too, Coelopa and Orygma possess similar basisterna, yet very disimilar musculature. Further,the variation that can be detected in the musculature is in no way sufficient to account for the diverse shapes exhibited by this sternite. Whatever the functional significance of the various shapes of the basisternum may be, this has to be sought elsewhere than in the requirements of differing muscle attachments. It is a moot point as to whether or no this holds true for flightless species. In the case of Sphaeroceridae, for example, where the basisternum is more or less linear, many unrelated flightless species possess slightly broader sterna than those prevalent among winged species (Richards, 1962). The converse is, however, equally true. Hackman (1962) also suggests there is some relationship between broader sterna and the apterous condition, adding that in the more strongly modified apterous Tipulid (or Limoniid) Chionea, a precoxal bridge is present.

This evidence is of doubtful value though, since a number of fully winged Tipulids also possess precoxal bridges.

(5) The Cervical Sclerites. The cervical region may be defined as that part of a fly bounded anteriorly by the head capsule and posteriorly by the sclerites of the prothorax proper. It comprises in Acalypterates three pairs of cervical sclerites and an area of flexible membrane containing them, which forms the connection between head and thorax. Also, in the mid-line, vertically between the largest pair of cervical sclerites (which lie close together here) is the cervical

organ and its associated sclerite (see below).

The cervical region has been called the cervix. It can be argued that this part of the insect is developed from at least one definite neck segment, but Snodgrass (1935) and Crampton (1942) both conclude that it originates partly from the labial segment of the head, and partly from the prothorax. A similar conclusion is derived by Henry (1958), from a study of the cervical musculature of a range of insects.

Crampton (1942), in examining a series of Diptera, identified three pairs of cervical sclerites. But Ferris and Rees (1939), and Ferris (1950), from studies of Tipula and Drosophila, respectively, make no mention of the third posterior pair. Zalokar (1947) in an independent study of Drosophila, locates only the lateral pair of cervical sclerites. Bonhag (1949) illustrates all three pairs in Tabanus.

Among Acalypterates, the anterior pair of cervical sclerites, or antero-cervicalia , are vestigial. They remain only as small strips of sclerotic material lying along the anterior extremities of the lateral cervical sclerites. They do, however, each possess a small, posteriorly directed apodeme.

The largest structures of the neck region are the lateral cervical sclerites, or latero-cervicalia . These normally lie ventro-laterally and articulate in front with the margin of the head capsule, and behind with the margin of the propleura.

The posterior pair of cervical sclerites are reduced and strap-like, articulated at their outer ends with the propleura. In surface view they are seen edge on, since each lies along the wall of a transverse dip in the cervical membrane. This dip runs along the posterior margin of the lateral cervicalia.

(6) The Cervical Organ. The structure referred to here as the "cervical organ" is essentially a pair of hair plates, arising from a sclerite which is located between the lateral cervicalia. Though apparently absent in some Diptera, this organ is to be found in all main groups of the Order and reaches its most complex form amongst the Schizophora.

The cervical organ has received scant attention from either morphologist, systematist or physiologist. Until 1962 the only published account of its structure was that of Lowne (1890) in his work on Calliphora, who described its morphology and histology. After other work on hair plates in various locations on the Insect's body surface (Mittelstaedt 1950, 1952, 1957; Pringle 1938), a further morphological account appeared (Peters 1962), again of the cervical organ of Calliphora. There the matter stands, with apparently nothing further published on the subject.

Although the prothoracic region of Diptera has been illustrated by many authors, the existence of the cervical organ is not mentioned even where it is included in an illustration; Snodgrass (1935, p.171), Hennig (1958, p.582), Hulls (1964). Even Bonhag (1949) only comments that the prothoracic presternum (closely associated with the cervical organ) has perhaps some sensory function, since it is strongly innervated from the thoracic ganglion.

In Acalypterates the sensilla of the cervical organ occur in two tight groups at the anterior angles of the cervical organ sclerite (or sella - Lowne). This degree of differentiation is not found in lower

Diptera. In Anisopus the sella bears only a few ungrouped sensilla, while in Rhagio and Volucella the sensilla form two lateral groups, which are continuous anteriorly. A deviation from the general form occurs in Leptogaster, where the sella has divided into two, each sclerite now bearing one hair plate (this information is from Hillyer, loc.cit.).

In Acalypterates the sensilla-bearing portion of the sella is deflected inwards, at a slight angle to the remainder of the sclerite, so that the hair plates occur in a depression of the cervical membrane. Most of the sensilla point slightly forwards and far outwards from the mid-line, those closer to the mid-line pointing more vertically and usually being shorter (see figures 16-20).

Arising from the sides of, and projecting over, the cavity formed by the depressed portion of the sella and the bulging lateral cervicalia, is a pair of more or less membranous flaps (see figures 18,20). These may be heavily sclerotised, as in Sicus (see figure 16). In Calliphora, where these flaps are sclerotised, Lowne gave them the name corniculae. It is towards the under-surface of the corniculae that the tips of the hair plate sensilla are orientated. In many Acalypterates a further, large, thick membranous flap projects backwards from the lip of the cervicalforamen between the lateral cervicalia, over the structures of the cervical organ pit (see figure 20). Rarely this flap may be sclerotised. It seems never to be further differentiated than this and presumably has a protective function. (In prepared specimens this flap is often seen far forwards and shrivelled, apparently unassociated with the cervical organ. Similarly, the corniculae can lose their position over the hair plates.)

The sella is sometimes only weakly sclerotised. In the majority of genera it is roughly Y shaped, e.g. in Rivellia and Sicus, but may be much attenuated as in Texara (Megamerinidae), or transverse, as in Drosophiloids. Posteriorly this plate contacts the presternum, which may be fused indistinguishably to the sella, e.g. in Dorycera (see figure 19). In Acalypterates with a precoxal bridge, the presternum is often reduced to a tiny piece connected to the sella (see figure 19) It does not contribute to the formation of the precoxal bridge. In families where the basisternum is reduced, the presternum may extend far posteriorly, as a strongly sclerotised median bar (see figure 17).

Just lateral to the hair plates in most Acalypterates small subsurface processes project inwards from the lateral cervicalia, towards the anterior angles of the sella, with which they may articulate (see figure 20). Although the hair plates themselves occur in a shallow depression, the sclerites associated with the cervical organ, and the associated membrane close to the mid-line, are all slightly raised above the more lateral cervical area. Between these two zones are a series of membranous folds like steps, running roughly longditudinally, beyond each of which, laterally, the surface is slightly lower.

Hair bearing plates located in the cervix of other Orders of insects are known to be position-indicating proprioceptive organs (Mittelstaedt 1950, 1952, 1957, Haskell 1959, Popham 1960). Lowne (1890), Hillyer (unpublished), Peters (1962) and Dethior (1963) have suggested the same function for the cervical organ of Diptera and from its structure there can be little doubt that such is its main use.

The reasons for the association of the cervical organ complex with the presternum are not so clear. This sclerite may act as no more than a support for the sella, but the presternum seems to be innervated (Bonhag 1949), and has persistently developed a pair of curious, polished, sclerotised projections at its posterior corners (see figures 17, 18, 20). The raised position of the presternum would allow these projections to contact the head ventrally. The repeated occurrence of two projections seems significant and would indicate they function individually, but are complementary to each other.

2f) CONCLUSIONS

(1) In the Acalypterates, the prothorax reaches a degree of reduction found elsewhere only in the Calypterates, and a few specialised or wingless flies. Two processes are principally responsible for this reduction:

a. The prothorax progressively loses its identity as a discrete thoracic region, by loss of sutures that delimit it posteriorly and by differential development of the remaining identifiable sclerites.

b. By incursion of the mesonotum in the mid-dorsal line, aided by general enlargement of the pterothorax and impaction of the cervical region into the thorax, the lateral and dorsal elements of the definitive prothorax come to occupy a minimal proportion of the thoracic surface. The remains of the prothorax, apart from the humeral calli, are progressively confined to the anterior face of the thorax.

(2) The structure of the prothorax is the same throughout the Acalypterates. The variation which does occur is restricted to differences in relative size and shape of the sclerites, apart from in the case of the precoxale, which may be completely absent. Only in the basisternum is variation in form both sufficiently extensive and

recognisable, to make detailed examination of its possible evolutionary significance worthwhile. This level of variation in prothoracic structur is lower than that which occurs between major groups of Diptera (see Crampton 1926, 1942 and Hillyer), a fact which does not support the contention that the Acalypterates are polyphyletic.

(3) Although it has undergone reduction and partial loss of identity, the prothorax has greater functional significance than is accredited to it by Ferris (1950), who suggests it only supports the fore legs. Cephalic muscles originate in the prothorax, which also acts via the cervical sclerites to help support the head. Further, the prothoracic region bears the cervical organ, which can only be an important sensory mechanism.

(4) Examination of a range of Acalypterate types makes it clear that, despite the general morphological uniformity, descriptions of the morphology of single species are most unreliable, almost invariably involving misinterpretations when put forward without consideration of other Acalypterates.

SECTION 3: THE PROTHORACIC BASISTERNUM AND PHYLOGENETIC SYSTEMATICS

3a) INTRODUCTION

Systematists disagree about what constitutes a taxonomic character. Mayr et al (1953) suggest a taxonomic character is "any attribute of an organism or of a group of organisms by which it differs from an organism belonging to a different taxonomic category or resembles an organism belonging to the same category". Blackwelder (1967) uses the term to mean the expression of a feature in the individual. Neither authority takes account of the fact that different taxonomic characters defined in either of these ways enjoy varying degrees of functional independence from one another, but Mayr's definition is very practical and is used here.

Three morphological features of the prothorax have so far been used as taxonomic characters in Acalypterate classification. These are the presence or absence of humeral and propleural bristles, and the presence or absence of a precoxal bridge.

All too frequently the use of a character by taxonomists develops very casually, there being no objective appraisal of its possible role in taxonomy before it is pressed into use. This is certainly true for the features mentioned above. So far as is known, no systematist has yet thoroughly surveyed the range of variation and possible functional significance of any character at present employed in Acalypterate classification. Partial surveys of the structure of the genitalia have been undertaken by Crampton (1944) and Hennig (1936-48, 1958) and of the mouthparts by Frey (1921), but these have involved too few species and have been too widely based.

Where taxonomists comment on the potential role of a character in systematics, there is rarely any mention of the criteria that they use to arrive at their conclusions. Blackwelder (1967) provides some discussion of this problem but suggests no code of practise. It is nonetheless possible to identify two principal factors which govern the usefulness of all characters for any taxonomic purpose:

1. Ease of examination and recognition of variants.
2. Distribution and abundance of variants at the various taxonomic levels.

Additional factors influence the use of a character in the exploration of phylogenetic relationships. The two primarily involved are interdependent:

3. Functions of variants.
4. Evolution of the character, and evolutionary status of the different variants.

In the following attempt to evaluate the possible role of the prosternum in taxonomy, each of these four factors is considered. Based as it is upon examinations of some 2,100 species belonging to 800 genera and representing 59 families, this is the most complete survey of any Acalypterate feature that has yet been undertaken.

It is insufficient to conclude simply that a character has both taxonomic value and phylogenetic significance. Its real usefulness, systematically, will depend upon the sort of improvements which its use can be expected to achieve, in current classificatory systems (already based on a number of characters). For this reason a comparison has been made between the prosternum and other characters as aids in the determination of Acalypterate inter-relationships. This comparison has been pitched at family level, because family inter-relationships are probably the biggest current problem in Acalypterate systematics, where the introduction of new taxonomic characters would therefore be of the most value.

This comparison has been carried out for 27 families. The other families have been omitted to avoid unnecessary repetition, since the conclusions do not depend upon examining all Acalypterates, but rather upon examination of a range of families, with differing phylogenetic status. To this end, care has been taken that among the families examined are representatives of both ends of the Acalypterate series, as well as both large and small families and ones which are currently regarded as well founded monophyletic groups and others which might be polyphyletic.

3b) THE PRACTICABILITY OF USING THE PROSTERNUM AS A TAXONOMIC CHARACTER

It is particularly important that characters used in Acalypterate classification are both readily accessible and easily interpreted, because the number of species involved is so vast that any character visible only after a laborious preparative technique is almost impossible to use even theoretically; assessment is otherwise too time consuming to allow examination in a sufficiently wide range of flies.

Apart from complications that make a specimen generally difficult to examine, such as verdigris on the pin, growth of mould, or 'loss of parts', the prosternal region may be obscured in several ways:

1. In specimens pinned through the mesonomtum, the prosternum may be fractured, making precise interpretation impossible, though it is usually possible to tell whether or not a precoxal bridge is present.

2. In specimens mounted on card points (especially tiny species), the glue used often wells up between head and thorax, obscuring the whole area.

3. In specimens where the mouthparts remain extended, part of the prosternum may be concealed.

4. In specimens that have the fore legs folded against the thorax, examination may be difficult or impossible.

5. In a few families, such as Celyphidae and Ephydridae, the head may be very closely opposed to the thorax, making the prosternal region inaccessible to view.

Apart from where they are due to the mounting method employed, these difficulties may be easily overcome by removing the heads of the specimens affected. If this is done with reasonable care, the head is not damaged and mounted on card can be put on the same pin as the rest of the specimen.

Even when the prosternal region is visible, factors can interfere with its interpretation:

1. The cervical membrane may be heavily pigmented, making it difficult to distinguish the edges of sclerites. Even so, the texture of a sclerite is normally very different from that of membrane, so that its shape can still be made out.

2. In teneral specimens the weak sclerotisation of plates again makes them difficult to distinguish from the surrounding membrane, which is itself much pleated in such circumstances, further aggravating the situation.

3. In a few families the prosternum is generally poorly sclerotised, with results similar to those described above.

4. In some families where the presternum is closely associated with the anterior margin of the basisternum, the two plates can look like one.

Only when the prosternum is weakly sclerotised is interpretation ever really difficult. This is rare however, and characteristic only of the Psilidae and certain Micropezids. Even here, species cleared and stained show that interpretation of dry specimens is only slightly at variance with that of prepared material.

In all, less than 5% of the species examined proved impossible to assess because of difficulties of examination and interpretation. A further 5% were very difficult to assess.

Interpretation of the prosternal region in dried material is not therefore much of an obstacle to its use in taxonomy. Only when it is necessary to interpret single specimens do difficulties assume much significance, and even then they are usually surmountable. Nonetheless, these difficulties do impose limitations on the degree of precision with which characteristics of the prosternum may be recognised. Thus it is impossible to use measurement of dimensions for interpretation, since the prosternum cannot be examined in plan in a high proportion of species: shape can then only be assessed by looking at the plate from a number of angles.

3c) CLASSIFYING VARIATION IN PROSTERNAL SHAPE

In one of a number of forms the prothoracic basisternum occurs in all Acalypterates. Although each species possesses a basisternum of a characteristic shape (see next section), the various shapes possessed by different species cannot be recognised as belonging to a restricted number of discontinuous types. Some discrete types certainly occur, but other shapes grade into one another with varying degrees of completeness. In order to examine distribution patterns of individual parts of this complex, a way of sub-dividing it into definable sections has to be devised. To this end, prosternal shapes which are recognisably different from each other have been segregated and each given a code symbol for reference. Intermediates have been partitioned between these segregates using specific characteristics of proportion and extent. In this way the range of forms has been cut up into a set of recognisable variants (figs: 13-15).

Quite soon now it will probably become possible to quantify shape differences in two-dimensional, bilaterally symmetrical objects, using topological techniques like that proposed by Meltzer et al (1967). However, the mathematics involved is at present very laborious and this type of approach has not been attempted here because it would have so drastically cut down the number of species that could have been examined.

The precise delimitation of each variant recognised here is obviously partly arbitrary and the resultant classification system therefore artificial. This brings attendant limitations. Firstly, both the number of variants recognised and the range of variation they each accommodate, must, at least in part, be a function of the individual constructing the classificatory system. Different authors might wish to recognise either more or fewer variants. Some variants might well be more broadly based than others. Secondly, there is no assurance that such a classificatory system would correspond with one drawn up to reflect either differences in the functions of the sclerite, or its evolutionary history. These factors are discussed in succeeding sections.

It is only possible to define the different segregates satisfactorily after the full range of variation is known. In the meantime, it is necessary to record the form taken by the prosternum in all species examined. This has been accomplished by drawing the different shapes of prosterna found in each family as they are encountered, and at the same time providing each of them with a code symbol. The prosternal shape of succeeding species in the same family can then be referred to by a symbol. This system simultaneously builds up a collection of drawings of posterna which depicts the complete range of sternal shapes found among Acalypterates.

3d) THE PROBABLE FUNCTIONS OF THE BASISTERNUM

So far as is known, the prosternum is found in one form or another in Diptera and indubitally serves as a site for muscle attachment so there can be little doubt that is has some functional significance. Some characteristics of the sclerite must inevitably be dictated by present functions, so it is necessary to establish how the plate is likely to be influenced by these, since they could throw some light on its evolutionary history.

One obvious function of the prosternum is that it provides the site for attachment of muscles of the basal segment of the fore legs, but so far there is no evidence that this association exerts any direct control over the shape of the prosternum. In all cases examined the muscles are attached exclusively to the prosternal carina and not to any other part of the plate. Also, the relative size of this apodeme varies greatly, but there is no visible correlation between its size and the size or shape of the external part of the plate.

With the forelegs used for a variety of purposes (walking, holding prey, courtship display), it is inconceivable that both the degree and direction of coxal mobility do not vary to an appreciable extent between species. Even so, this cannot be detected in arrangements of the musculature as they have been investigated here. This factor might well influence the course taken by the lateral margins of the prosternum. If indeed the lateral edges of the prosternum are shaped to accommodate different movements of the coxae, the distribution of some prosternal variants could well reflect the evolutionary history of behaviour patterns dictating the movements performed by the fore legs.

The basisternum is in some way associated with the cervical organ but it is difficult to see how this could greatly affect the shape of the sclerite. The evidence for this association is that in nearly all Acalypterates, whatever the condition of the basisternum, a more or less rigid line is maintained, mid-ventrally, between it and the cervical organ, via the presternum. This can involve a median extension of the prosternum anteriorly, irrespective of the forward extent of its apodeme, but so far as can be seen does not influence the sclerite in any other way. Since the cervial organ is universally present among Acalypterates and there is no reason to suppose its function varies very much, neither is there any reason to suppose that its demands upon the prosternal region vary significantly, in which case its effects on prosternal shape should be the same throughout the Acalypterates.

Apart from in the mid-line, the only control over extension of the prosternum anteriorly that may be surmised, is the necessity for mobility of the head. In any event, the margin of the prosternum never intrudes into the cervical region beyond the level of the posterior cervical sclerites, anterior to which the whole area is membranous up to the cervical cavity, apart from the cervical sclerites themselves. Braula is the only exception to this rule. Here there is no forward extension of the prosternum, but the cervical membrane itself is toughened. It is not possible to suggest ways in which the head might control the shape of the prosternum, other than by dictating its maximum forward extension. Where the prosternum does not reach forwards so far as the posterior cervical sclerites, the course taken by its anterior margin is presumably dictated by other factors.

In Acalypterates such as Ephydrids, the precoxal bridge constructed by contact between the prosternum and propleura must act as a supporting and strengthening element in the anterior region of the thorax. Conversely, the linear strip to which the prosternum is reduced in flies like the Sphaerocerids, can have no such skeletal significance. In fact, it is exceedingly unlikely that all of the various sternal shapes can have any specific skeletal function in common, beyond the general one of contributing to the solution of stress/strain demands in the anterior region of the thorax. The part played here by an individual sclerite must depend upon the construction of the thorax as a whole and it could well be this fact which has controlled the evolution of prosternal shape. Skeletal characteristics of the prosternal shape do suggest that they can be divided into three major categories:

1. Reduced shapes (A,B,I,J,S): where the sclerite occupies a negligible proportion of the area both between and anterior to the coxae, which is then membranous. It is difficult to see how this type of variant can either protect tissues beneath it or strengthen the front of the thorax.

2. Basiliform shapes (the remaining variants, other than the precoxal bridges): where the area between the coxae is mostly sclerotised, but where the plate lies free is the cervical membrane anteriorly. This type of sclerite must inevitably provide protection and some support for underlying tissues.

3. Precoxal bridges: where not only is the area between the coxae normally almost completely occupied by the prosternum, but the plate extends anteriorly and laterally to join the propleura. In addition to any protective functions, this type of variant is also well suited to act as a thoracic strut, in a way reminiscent of the vertebrate clavicle.

Conclusions based on this discussion of prosternal functions are of limited value since they are so dependent upon indirect evidence. Three general conclusions can none the less be made. First, the universal presence of a probasisternum in Acalypterates, whatever its shape, is presumably due to its function as the site for attachment of leg musculature. Secondly, the major characteristics of prosternal shape appear to depend primarily upon the role of the prosternum in strengthening and supporting the anterior part of the thorax. Thirdly, minor characteristics of shape can be dictated by a number of factors, such as the mobility of the coxae.

It seems certain that no single factor controls the entire character of this sclerite.

3e) VARIABILITY OF THE BASISTERNUM

1. Within the Species

It would have been impossible to investigate intra-specific variation in all the species examined. Instead, series of individuals from representative species belonging to most families have been taken.

In all cases the variation which occurs is trivial, and in fact hardly discernable. The special case provided by various mutants of *Drosophila melanogaster* has also been examined: a precoxal bridge is present unchanged in all, including apterous specimens.

Richards (1965), comments that in certain Sphaerocerids the prosternum of the male differs from that of the female of the same species. So far as can be seen this does not occur elsewhere among Acalypterates.

From the fact that it is extremely stable intra-specifically, it can be concluded that the shape of the basisternum is under strict genetic control. It follows that differences in shape between the prosterna of different species can be investigated using even single individuals to represent each species, since the shape of the prosternum in each specimen can be regarded as characteristic of its species.

2. Within the Genus

Where possible more than one species has been examined in each genus, and in larger genera upwards of ten species have been examined from each, representing as wide a geographic range as possible. The largest number of species examined in one genus was 80, in Dacus, which was made a test case.

In genera where a greater range of sternal variability became apparent, proportionally more species have been examined than in more homogeneous genera.

In 60% 75% of the genera for which two or more species have been examined, there is no more variation than found within species. Elsewhere more than one sternal variant occurs in each genus (see histograms, fig. 38) and in one case five different variants were encountered in the same genus. Under these circumstances one of them is normally dominant (i.e. occurs in a majority of species). Occasionally two variants are codominant.

This means that as a rule, inter-specific variation in prosternal shape is insufficient to be useful in characterising the different species of a genus. In fact its stability is sufficient for the shape of the prosternum to be of some use both in locating mis-placed species within a genus and in defining genera. This level of stability is in fact sufficient for the sternal variation of all genera to be compared on an equal basis, independent of the number of species each contains.

3. Within the Family.

The means at present available for grouping Acalypterate genera into families are unsatisfactory and inadequate, but unfortunately, in order to establish what degree of variation in shape of the prosternum can be expected within an Acalypterate family, families as defined at present have to be used. This difficulty can be partly overcome by dividing the families into two groups based upon current opinion of their phylogenetic status. It is then possible to compare the range of variation found in probably monophyletic families with that found in the doubtful groups. Since, as has been demonstrated, it is unusual to find more than one sternal variant in one genus, it is necessary to exclude families containing only one or two genera from discussion: they would otherwise suggest an artificially low figure for the number of variants to be expected in individual families.

Considering only the families for which five or more genera have been examined, the number of sternal variants present in the well-established monophyletic groups varies from two to eight, with the average at four. By comparison the doubtfully monophyletic families have between four and fifteen prosternal variants each, and average eight per family (see fig. 39).

Whichever category of families is selected for discussion, it can be seen that there is a greater range of variation in the shape of the prosternum within an Acalypterate family than within a genus. No family with more than five genera possesses less than two prosternal variants.

At least among the more satisfactorily established families, there appears to be a finite range of variation which characterises the family as a taxonomic unit, independent of the number of genera involved. This is not so true for the less well established families where the number of variants which occurs seems to be more dependent on the size of the family (see fig. 39).

Within each family, the frequency of occurrence of the different variants is very uneven, one variant normally occurring in far greater numbers than any of the others. The prosternal variant which occurs in both more than half the species of more than 50% of the genera examined, and also in more than 50% of the total number of species examined in a family, can be regarded as an overall dominant. Again ignoring the small families, where the concept of dominant variants becomes meaningless, overall dominants occur in thirteen out of twenty two families. In addition, secondary dominants (variants found in more than half the species of at least 25% of the genera examined) occur in more than half of the remainder.

It seems then, that a narrow range of prosternal variation can be regarded as characteristic of the Acalypterate family. It follows that the sheer number of variants present in a family can be regarded as some indication of its taxonomic validity: a conclusion reinforced by the fact that the more doubtful families contain the greater numbers of sternal variants.

The existence of dominant variants is also valuable. Through them the actual variability of the prosternum is restricted within a family to a far greater extent than it appears to be if the number of variants in a family is the only fact considered. For these reasons the shape of the prosternum can help to identify anomalous genera within a family undergoing revision: these being most likely to occur among those bearing sternal variants other than that dominant for the family.

4. Within the Superfamily

None of the Acalypterate superfamilies currently recognised is well established as a monophyletic group and the status of most of them is a matter for controversy. There is thus little to be gained from discussing prosternal variation within superfamilies, since it cannot be said which of those at present recognised constitutes a valid group.

3f) THE EVOLUTION OF BASISTERNAL SHAPE IN ACALYPTERATES

Without access to fossil record, attempts to understand the evolution of any characteric must inevitably depend upon circumstantial evidence provided by modern faunas. The fossil history of Acalypterates is virtually unknown, though Hennig (1965b) has recently described some species from Baltic amber.

Very little discussion is available, on ways in which the evolution of structural characteristics can be deduced from the structure of living forms. Blackwelder (1967) dismisses the subject by commenting that phylogenetic systematics has no sound theoretical basis. Hennig repeatedly states that it is necessary to distinguish between the plesiomorphic and apomorphic variants of a character before using it sytematically, but he offers little guidance on how this should be done, and what he does suggest is exceedingly problematic. He says (1958) that it is normally easy to resolve the question and that where one variant of a character is apomorphic in some groups but plesiomorphic in others, its evolutionary status in a particular group can be successfully interpreted by simultaneous examination of the condition of other characters in the same flies. It is difficult to understand this statement, unless it is a suggestion that an animal apomorphic in some characters is likely to be apomorphic in others. Hennig certainly seems to use this argument in discussing the condition of Ephydrid post-vertical bristles (see under Ephydridae).

If the evolutionary relationships between forms without a fossil record is ever to be in any way understood, it is obviously necessary to develop further the ways of using living forms as indicators of their own phylogeny. For this reason, methods used here to argue the evolution of the prosternum are presented in detail.

Previous attempts to divine the evolution of the prosternum in Diptera have been confined to comments upon the probable relationship between the precoxal bridge and other types of sterna. Hardy (1928-48), Clements (1951) and Hull (1962) assume that in Asilids the precoxal bridge represents a plesiomorphic condition, but without stating their reasoning. J.F. McAlpine (1963) does the same, in discussing Lauxanioidea. The opposite view is held by Hendel (1937) and Hennig (1958), both working with Acalypterates. Once again no reasoning is presented.

The problem of the evolution of the basisternum falls into three parts:

1. The inter-relationships between the various sternal shapes.
2. The directions in which evolutionary processes have proceeded.
3. The number of times these trends have been independently developed.

Assuming that the Acalypterates are a monophyletic group, their prosterna must be more closely related to one another than to sternal types occurring elsewhere. Previous discussion has demonstrated that the <u>shape</u> of the basisternum is under genetic control and that changes in shape are most likely to occur by a series of small stages. It follows that the <u>degree</u> of similarity between sternal shapes should therefore provide a measure of the closeness of their phylogenetic relationship. This hypothesis can be tested in part by examining the prosternal shapes which occur in groups of closely related species.

It is first necessary to arrive at some arrangement of sternal shapes that will represent their typological inter-relationships.

The range of sternal variations is shown in figures 13 - 15. It is obvious that each sternal variant is more similar in shape to certain others than it is to the remainder. However, selection of one shape as being that most similar to any other particular variant, is in many cases almost impossible. This difficulty can be overcome by using a two dimensional model: an approach which has been developed in the production of the 'polar diagram' (fig. 62). Here the degree of physical similarity between variants is, as far as possible, reflected in their spatial relationship on the diagram. This representation is still imperfect, a three dimensional model really being required.

If, as proposed earlier, the degree of similarity between sternal shapes is a guide to their degree of phylogenetic association, then the polar diagram must provide some reflection of the evolutionary history of the prosternum within the Acalypterates.

The acceptability of the polar diagram as a guide to prosternal evolution can be tested by comparing the apparent relationships between sternal shapes found there, with actual genetic relationships demonstrated in groups of closely related species, for example, individual genera. In order to avoid including results based on misplaced species, the only combinations which have been included in this analysis are:

1. Those where each stenal variant is found in at least <u>two</u> species of a genus.
2. Those which occur in <u>two</u> or more genera.

The second category of combinations has been extracted from genera that could not be used in the first way, because at least one variant was found in only <u>one</u> species. In this manner two sets of combinations have been produced, based on different genera.

The set based on combinations in which each variant occurs in more than one species in its genus is shown in figure 37a, the other set in figure 37b. For simplicity of presentation each set has been divided into groups which are only inter-connected by sternal variant H.

A number of points of interest emerge from comparing these sets with each other and also with the polar diagram:

1. There is great similarity between the two sets which is sufficient to allow the production of the combined set, shown in figure 37c.

2. The groups within the combined set are very similar in content to different segments of the polar diagram.

3. The precise relationships between variants is often different in the two sets and in the polar diagram.

4. Some variants do not occur in combination with others.

5. Sternal variant H is the link between all groups of shapes, however devised.

The first two of these points quite strongly support the idea that the degree of visual similarity between prosternal shapes is an indication of their evolutionary inter-relationships. However, the placing of five of the variants (E,Q/T, T, W, Z) argues against this general hypothesis, or at least against the ability of the polar diagram to express it. Shapes that are similar as a result of convergent evolution (symplesiomorphy), might well be wrongly placed in the polar diagram and these five variants could be evidence of convergence. It is also possible that the procedures adopted for excluding from consideration genera containing wrongly placed species, have not been sufficiently rigorous. This could be argued further if it seemed likely that the connecting links between all shapes, phylogenetically, were to be found somewhere among the Acalypterates. However, some variants do not occur in combination with others in any genus.

The third and fourth points can be considered together. The precise relation between shapes arrived at in the groups of combinations, has been achieved by taking account of the number of times that each combination occurs. Since some variants do not occur in combination with any others it seems certain that some of the phylogenetic connecting links between variants have been lost. This implies that the relative abundance of phylogenetic links between variants is not necessarily a good guide to the closeness of their relation with one another. The precise arrangement of variants achieved in the 'families' of combinations, cannot therefore,be very usefully compared with the arrangement of variants which appears in the polar diagram. Although because of this it is not possible to draw deductions from the relative abundance of links between variants, there is still no reason to suppose that the presence or absence of individual combinations is any less meaningful. Twenty-one such combinations occur, and of these only three do not join variants placed adjacent to each other in the polar diagram. The exceptions are the links between V and W, A and C, G and J. This level of agreement must indicate that typological inter-relationships between these prosternal variants also reflect their phylogenetic inter-relation.

If it can be assumed that phylogenetic relationships between prosternal variants are reflected in their shapes, it is meaningful to discuss which shapes are probably plesiomorphic and which are probably apomorphic. Even so, this does not necessarily mean that the individual variants recognised here correspond with degrees of shape difference that have evolutionary meanings. In fact, examination of the possible functions of the prosternum has shown that minor differences in shape which segregate variants from one another, might well be due to differences in function that have only trivial evolutionary significance. At the same time, discussion of function has exposed categories of variant, which are most probably of major functional significance.

If these categories reflect fundamental differences in function, it is to be expected that they also represent major evolutionary trends in the prosternum. Because of this, it is more realistic to use these categories of variant, rather than individual variants, as the units for discussion of the direction of evolutionary processes in the prosternum.

The first of these categories comprises the 'reduced' shapes (A, B, I, J, S). A trend towards reduction is general in Dipteran morphology. For example, the number of antennal segments and wing veins is progressively reduced in the higher Diptera. Similarly, the pro- and meta-thorax decrease both in size and degree of differentiation. This makes it unlikely that the reduced shapes gave rise to the other, less reduced, prosternal variants, as this would be a trend in the opposite direction. The general principle of the irreversibility of evolution also implies that it is unlikely for these reduced shapes to be the most plesiomorphic Acalypterate sternal variants, since otherwise the other variants should be equally reduced, or more so.

Although many sternal variants fall into a second functional category because they make a precoxal bridge with the propleura, these are not necessarily closely related by shape. In fact, most of them are more similar to some basiliform variant than to other precoxal bridges types. It has been established that similarity of shape is correlated with phylogenetic relationship, so it is unlikely that the precoxal bridges are all closely related to each other. This means that in order to postulate that the most plesiomorphic prosternal variants are found among the precoxal bridges, it is also necessary to suggest that some precoxal bridge types evolved from basiliform shapes which have previously lost the precoxal bridge. A simpler explanation is that precoxal bridges are apomorphic sternal variants.

The sort of theoretical objections which can be made to suggestions that either the reduced or precoxal-bridge bearing variants are plesiomorphic, do not hold for the remaining cateogry of variants, the basiliform shapes. As a group they are closely inter-related by shape. Also, the shapes involved seem equally preadapted to developing into the forms found in both of the other categories. The enlargement necessary to derive a precoxal bridge from basiliform shapes is minimal. At most an elongation of the basisternal wings is necessary and this is reduced through the part played by the precoxalia. Reduced shapes can be derived simply by reduction, a trend well established in the evolution of other characters. In fact, for the basiliform shapes to have been derived from other categories of variant, they must have evolved over and over again along different paths, judging by the differences in shape between the other variants.

These various arguements all point to the same conclusion. Namely, that evolution of prosternal shape has progressed in two directions away from a condition represented by the basiliform shapes, to produce reduced variants on the one hand, and precoxal bridges on the other.

It is useful to look at the distribution patterns of the different categories of variant, in the light of this conclusion. If reduced shapes and precoxal bridges represnnt alternative specialisations, it is to be expected that they would be mutually exclusive in groups of closely related species. Conversely, if basiliform shapes represent a plesiomorphic condition, they could occur in combination with both categories of apomorphic shapes. It would also be unlikely for plesiomorphic variants to provide the dominant variant in groups of closely related species, where both plesiomorphic and apomorphic shapes occur.

Examining the combinations which are present in individual genera, it is found that the three categories of variant never all occur in the same genus.

Combinations between basiliform variants and members of either of the other categories are more than five times as frequent as combinations which involve precoxal bridges and reduced types. Combinations between a reduced type and a precoxal bridge invariably involve bridge type V, and it is argueable that this variant has evolved along a different path from the other precoxal bridges (see below). Among well-established families precoxal bridges and basiliform variants occur together 10 times. Only three times are the two apomorphic categories represented in the same family. In two of these, single species bearing precoxal bridges are present in families from which they are otherwise absent (Neriidae and Sciomyzidae).

Returning to the question of dominance, precoxal bridges are exclusively present in eleven families, reduced shapes in ten and basiliform shapes in only six. Precoxal bridges provide the dominant variant in 60% of the families in which they occur. Reduced shapes are dominant in the same way for 35% of their range, and basiliform shapes for 20%. Were all dominants to an equal extent, frequency of dominance throughout would be 25%.

There are two principle objections to the use of these data in support of the theory of prosternal evolution here proposed. Firstly there is the implication of the anomalous distribution of sternal variant V. Since an individual variant is involved, discussion of this point has been left until the finer detail of prosternal evolution is examined (below). Secondly, there is the general implication of the fact that the closer the resemblance between sternal variants, the closer is believed to be their evolutionary relationship to each other. If this is so, it is not surprising that the most dissimilar categories of variant are found least often together in groups of closely related species, whilst the category comprising variants intermediate in shape can be found in combination with each extreme. However true this is, it does not explain the relative frequency with which members of the different categories provide dominants. The simplest explanation for the subordinate position of the basiliform variants is that they represent a plesiomorphic condition. If so, then the distributional segregation of the other categories of variant probably occurs not only because they are distantly related, but also because they represent alternative specialisations.

This discussion has established the directions in which evolutionary trends in basisternal shape have most probably occurred. The arrangement of sternal variants in the Polar diagram is such that this involves the relationship between its periphery and centre, the believed apomorphic shapes lying distal to the plesiomorphic ones.

The polar diagram provides a convenient framework for discussing the likelyhood of apomorphic variants having developed along discrete evolutionary paths, a problem translated there to the relationship which exists between sectors cut off by different radii. The question of convergent evolution can be examined at the same time.

The range of sternal variation found in each family is in most cases restricted to a narrow sector of the polar diagram, but may involve more than one apomorphic shape. Further, a comparison of of the sectors occupied by different families shows that they overlap (see figs: 63 onwards).

The unusual distribution pattern of sternal variant H, shown as the hub of the polar diagram, is of significance here, In all, this has been found in combination within genera, with 18 other variants. No variant apart from H has been found in combination with more than 9 others. Also, combinations which involve H embrace the complete range of sternal shapes. In other words this shape acts as a connecting link between nearly all of the radii of the polar diagram.

These facts suggest that although apomorphic variants can develop along routes different from one another, it is possible for the same apomorphic variant to develop along a number of different paths, and to have the same origin as other apomorphic variants. Thus in Scionyzoidea A variants A and V may both have arisen from variant B, while in Pallopteroidea,A types appear to be derived from variant C and in Chloropoidea type V may well have developed from a second precoxal bridge shape, type W (W may also have developed from V here).

To summarise, both theory and the data suggest that prosternal shape provides a reliable guide to Acalypterate prosternal evolution, the principle trends in which have culminated either in reduced prosterna or in precoxal bridges. These in either a different shape or even the same shape may have developed on more than one occasion among Acalypterates. The precise course of development leading to any particular apomorphic shape-variant varies somewhat with the taxonomic group involved, and convergent evolution, producing symplesiomorphy, appears to have occurred between the prosterna of some families.

If this theory is accepted as a reasonable one, previous views of prosternal evolution among Acalypterates must be regarded as over-simplified. In other words, it is not sufficient merely to gauge relationship by establishing either presence or absence of a precoxal bridge. The particular shapes of precoxal bridge and both the types and shapes of the other variants involved, must be considered. Unless this is done, flies can be segregated from one another on a basis of whether or not they possess a precoxal bridge, although they are closely related (see under Sciomyzoidea) and a more comprehensive analysis of prosternal variation would reveal this.

3g) SYSTEMATIC SURVEY

Twenty-three families are considered in detail here. The order in which they are discussed follows Hennig's (1958) arrangement of Acalypterates and the groups concerned represent all the families consigned to six of his superfamilies:

- Archischiza
  - Conopoidea
    - Conopidae
- Muscaria
  - Sciomyzoidea
    - Helcomyzidae
    - Dryomyzidae
    - Coelopidae

Sepsidae
Rhopalomeridae
Sciomyzidae

Pallopteroidea

Piophilidae
Thyreophoridae
Neottiophilidae
Pallopteridae
Lonchaeidae

Milichioidea

Canaceidae
Tethinidae
Milichiidae (including Carnidae)
Sphaeroceridae
Braulidae

Drosophiloidea

Diastatidae
Curtonotidae
Drosophilidae
Camillidae
Ephydridae

Chloropoidea

Chloropidae

Discussion of each superfamily follows the same course:

1. Introduction; an outline of the taxonomic history and present status of the superfamily.

2. The families; constituent families taken individually to

discuss their prothoracic morphology, taxonomic status and interrelationships.

3. Discussion; the status and constitution of the superfamily, considered in the light of deductions made using the prothoracic morphology of individual families.

In the Conopoidea and Chloropoidea, each of which contains only one family, the three parts to the discussion of the superfamily have not been separated as individual headed sections.

CONOPOIDEA

NO. GENERA EXAMINED = 27
NO. SPECIES " =118
DOMINANT ST.VARIANT =H/Y

CONOPIDAE

Hennig (1958), separates the Conopidae from other Schizophora and puts them on their own in a group he calls the 'Archischiza' while all other Schizophora (including the Calypterates) go into the 'Muscaria'. Here Hennig follows a scheme proposed by Enderlein(1936). Enderlein based his action on the fact that Conopids share with other Schizophora the possession of a ptilinal suture, but otherwise resemble Aschiza. Hennig justifies the procedure by quoting Enderlein.

Conopids are found throughout the World, apart from in the the polar regions and Pacific islands. According to Smith (in press), there are about 800 known species belonging to some 45 genera. These are divided between four well-defined subfamilies: Dalmanniinae, Stylogasterinae, Conopinae and Myopinae. All known larvae are internal parasites of other insects.

Hennig believes the family is a well founded monophyletic group. He bases this conclusion on the following facts:

1. The larvae are all internal parasites.

2. The larvae possess peculiar and characteristic posterior spiracular processes.

3. In the female, the 7th and 8th sternites bear a scale-like clasping appendage pointing posteriorly, which plays against the point of the abdomen.

Characters which are normally used to define Acalypterate families are no help in Conopidae, because in this family they are usually found in a plesiormorphic condition:

1. Cephalic bristles are undifferentiated, though tufts of hairs occur (Stylogaster provides an exception, see below).

2. Thoracic bristles are undifferentiated, the thorax being either bare or with a scattering of hairs (Stylogaster is again an exception - see below).

3. Costa complete.

4. Subcosta complete.

5. Anal cell and vein and cell complete.

6. Female with 4 spermathecae (except in Stylogaster and Dalmannia).

Most authors appear to agree with Hennig that the Conopids form a group distinct from other Acalypterates, but avoid discussing their phylogenetic position by placing the family at the beginning of the Acalypterate series. Stone et al (1965) take an alternative course, removing the Conopidae from Schizophora and placing them in the Aschiza.

The status of the various subfamilies is a much-debated subject. Rohdendorf (1964) maintains that the Stylogasterinae are sufficiently different from other Conopids to be given family status. Smith (1967) considers that there is insufficient grounds for such a course and points out (pers.comm.) that some of Stylogaster's unusual features are shared with the Dalmanniinae. If a family Stylogasteridae were to be recognised, this would imply that Dalmanniinae should also be given family rank, though Zimina (1960) provides reasons for relegating this group to tribal rank within the Myopinae.

The Stylogasterinae differ from other Conopids as follows:

1. Vertical bristles present.
2. Propleural bristle present.
3. Pteropleural bristles present.
4. Prescutellar dorsocentrals present.
5. Pre-apical tibial bristle present.
6. Female with 2 spermathecae.

The Dalmanniinae are distinct in that only five abdominal segments are visible in the male, while the female has only two spermathecae.

Through these features both of these subfamilies show a closer resemblance to the rest of the Schizophora, than do other Conopids.

There is nothing very distinctive about the prothoracic morphology of the Conopidae. The sclerites of the cervical region remain orientated so that there is a distinct but short neck region - a feature shared with Micropezoid and Otitoid families. The cervical organ complex remains relatively simple and does not include the prosternum, as it does in many Acalypterates. In the Conopinae the presternum is nearly always a large, well sclerotised plate, closely associated with the anterior margin of the basisternum, while in other subfamilies (except Sicus) it is vestigial.

Precoxal bridges are absent from the Conopidae, but basisternal shape varies from subfamily to subfamily. The Conopinae possess two basiliform variants (H/C and H/Y) which have not been found in the Muscaria and are not included on the polar diagram (see fig.13). These two types grade both into each other and into type H, which also present in Conopidae. The sternal variants in the other subfamilies are rather different, nearly always being of a reduced type. Variants A and I occur in the Myopinae and type S is found in all but the Conopinae. Variant H is absent only from the Dalmanniinae (see fig: 57). A feature of the prosternum found throughout the Conopidae, but apparently absent elsewhere among Acalypterates, is the elongation of the postero-lateral corners of the clerite. This produces basisternal 'tails', which can be made out whatever shape the plate takes (see fig: 57).

The isolated phylogenetic position within the Schizophora which is occupied by all Conopid genera, confuses the question of the relationships between the various sections of the family. On the one hand, the difference between the various families of the Aschiza is so great that judged by this all Conopid genera would be consigned to one 'family'. On the other hand, Schizophoran families are so imprecise that jucged by this the Conopidae could be divided into a number of 'families'.

Prothoracic morphology provides no clear lead in this problem. There is not sufficient difference between the prothoraces of Aschizous and Schizophorous Diptera to make it possible for the

Conopid prothoracic sclerites to demonstrate a clear allegiance with one or the other Group. The range of morphological variation potentially available to Conopidae is not therefore much wider than that exhibited by the Acalypterates proper. In fact Conopid prothoracic morphology is much less variable than it might be. Only six sternal variants occur in the family (admittedly above average for a well-established monophyletic group in the Acalypterates) and although these fall into two groups, each group comprises shapes which are closely related to one another. In addition, Conopid prosterna all possess a peculiar feature in common: the basisternal 'tails' which distinguish them from other Schizophoran prosterna. Further, it cannot simply be argued that because Conopid sternal variants fall into two groups, there is some justification for subdividing the family. One of the groups of variants involved (C, H, H/C, H/Y) contains shapes which may well resemble the plesiomorphic condition of Schizophoran sterna, in which case they cannot provide much information on the interrelationships between Conopid genera.

The picture becomes clearer when the actual distribution of variants in the family is examined. The two variants (H/C, H/Y) found only in the Conopidae are in fact confined to the Conopinae, where no reduced shapes are found. The same reduced shapes predominate in each of the other three sub-families, which share with Conopinae only the generalised variant H. Even if H/C and H/Y are plesiomorphic shapes, this distribution suggests that within the Conpidae, the biggest difference is between the Conopinae and the other three subfamilies. However, it tells very little about the relation between the Conopidae as a whole and other Schizophoran families. Differences which might have been anticipated between the prosterna of Stylogasterinae or Dalmanniinae and all other Conopids, do not appear. On the contrary, the similarity between the sternal shapes of Myopinae, Stylogasterinae and Dalmanniinae is such that among the Muscaria (Schizophora minus Conopidae) it would be expected only in a family which is regarded as a good monophyletic group.

The specific prosternal variants found in the Conopidae are widely distributed among Schizophora and occur in both the Acalypterae and the Calypterae. This reduces their value as indicators of affinity. Even so, a great number of Schizophoran families do not have reduced prosterna and many have precoxal bridges, which are absent from the Conopidae. So, if the Conopidae do have close relatives among the Schizophora, it is likely that these are to be found among the families which have reduced prosterna, but not among those with precoxal bridges.

To summarise, prothoracic morphology does not help to clarify the relationship between Conopidae and either the Aschiza or the Schizophora, although it provides some indication that Conpid genera are all more closely related to one another than to other Diptera. As to the taxonomic status of the subfamilies, prosternal variation does not support the segregation of either Stylogasterinae or Dalmanniinae as separate families, whether the family concept applied in Aschiza or Schizophora is used.

SCICMIZOIDEA

Introduction

In this concept Hennig(1958) includes Helcomyzidae, Rhopalomeridae, Coelopidae, Dryomyzidae, Sepsidae and Sciomyzidae. He comments that this superfamily is no more satisfactorily established as a monophyletic group than is the Nothyboidea, since no one apomorphic character can at present be cited to unite the families it contains. However, these families have been grouped together before, firstly by Hendel(1916), who excluded the Sepsidae. Crampton(1944) provides a contract with Hennig. Basing his deductions on the structures of the male terminalia, Crampton erected a superfamily for Sciomyzidae and Sepsidae, a second for Dryomyzidae and Rhopalomeridae and a third to contain Coelopidae (with Clusiidae and Heleomyzidae).

More than anything else, the taxonomic concept"Sciomyzoidea" seems to have arisen as a result of the process of disintegration of earlier, ill-defined family groups which has occurred throughout the Acalypterates, as it affected one or two families. Thus Dryomyza was once regarded as a Sciomyzid or a Helcomyzid,whilst the Helcomyzids used to be included in the Coelopidae. Rhopalomerids were unknown to most early authors. Until 1952 the Rhopalomeridae embraced the genera now put elsewhere as the family Rhinotoridae.

In this group of families more tham any other, the state of prosternal sclerites has in the past been used as a criterion of relationship. Subdivisions mentioned above are more or less dependent upon prosternal differences, though recently work on terminalia by Steyskal has provided independent information.

Discussion of the affinities of Sciomyzoid families has in the past been more or less confined to analysing their precise relation with one another, their relationship to other Acalypterates remaining virtually undiscussed. Even so, it has been suggested that various Sciomyzids are more closely related to Heleomyzids than Hennig would allow, while Sepsidae have been given a diversity of positions (see under Sepsidae).

HELCOMYZIDAE (SCIOMYZOIDEA)

NO. GENERA EXAMINED: 4
NO. SPECIES EXAMINED: 7
STERNAL VARIANT: V

This family comprises only a handful of genera restricted to the Antarctic, New Zealand and northern areas of the Holarctic. These are strand-line species, apparently developing in rotten seaweed.

It seems to be agreed that the genera at present consigned to this family (Helcomyza, Heterocheila, Paractora, Maorimyia) comprise a monophyletic group. However, arguements over the taxonomic status of the group are confused and based on few facts.

Until Malloch (1933) introduced the character of the prosternal precoxal bridge as a means of segregating Helcomyzids from Coelopids, the two were put together in Coelopidae. Since then, no author has discovered further characters which separate these families. Even Malloch said of the 'Helcomyzidae', "not in my opinion entitled to full family rank". The division between Helcomyzidae and Dryomyzidae has the same history, though Helcomyzids may still be included in Dryomyzidae: vide Colyer and Hammond (1951) and Oldroyd(1954).

It is difficult to find apomorphic features in Helcomyzid morphology. Hennig comments that the larval spiracles are peculiarly situated in Helcomyzids, in a fashion very similar to that seen in Rhopalomeridae. This character might provide useful information on the relation between Helcomyzids and other Sciomyzoids, when further studied. The same can be said of the number of spermathecae in Sciomyzoid families. The only satisfactory character which has been anywhere sufficiently studied is the precoxal bridge, but to date the possible significance of its precise shape has never been discussed. In fact the precoxal bridge has been used merely to distinguish Helcomyzids from Coelopidae and Dryomyzidae and the condition of the prosternum in other Acalypterates goes unconsidered.

In order to recognise Helcomyzids at present, the following combination of characters has to be used:

1. Clypeus normal, undeveloped.
2. Vibrissae absent.
3. Post-vertical bristles divergent/parallel.
4. Prosternal precoxal bridge present.
5. Pre-apical tibial bristles present.
6. Costa and subcosta complete.
7. Anal cell and anal vein present.
8. Seven sclerites before the hypopygium in the male; movable surstyli present.

The cervical organ, pronotum and propleura show no distinctive features in this family. The basisternum is of a constant form (variant V) in all four genera: an elongate precoxal bridge, narrowing basally (see fig. 40). Hennig (1958) figures the prosternum of Helcomyza.

The specific form of precoxal bridge seen in Helcomyzidae is found elsewhere among Acalypterates only in Sciomyzidae, Coelopidae, Heleomyzidae and Chloropidae. This makes it one of the more restricted variants. Because of this, and because precoxal bridges as a group are probably apomorphic and also only the one variant occurs in Helcomyzidae, the form of the prosternum provides strong evidence that this family is a monophyletic group. Equally though, these data, together with the fact that this variant occurs elsewhere in Sciomyzoidea, undermines the family status of the 'Helcomyzidae'. This is especially so when the family status of this group is based so heavily on their possession of a precoxal bridge. When the family Helcomyzidae was erected by Malloch precoxal bridges were believed to be a much rarer phenomenon than this study has demonstrated them to be, and their existence in Helcomyzidae is by no means so unique as Hennig thought it to be. Unless more evidence comes to light, that supports keeping the Helcomyzidae as a separate family, there seems little reason why Helcomyzid genera should not be resorbed into the Coelopidae, or combined with the Dryomyzidae.

The distribution of sternal variant V, associated with its rarity, can be regarded as positive indication that Helcomyzids are correctly placed in the Sciomyzoidea: there is little doubt that Helcomyzid genera are only distantly related to the Chloropidae, from which they differ in a number of characters.

DRYOMYZIDAE (SCIOMYZOIDEA)

NO. GENERA EXAMINED: 1
NO. SPECIES EXAMINED: 3
STERNAL VARIANT: A

This group ranks with Strongylophthalmyiidae and Camillidae as being among the smallest of recognised Schizophoran families. Following work by Steyskal (1957) and Hennig (1958) on the terminalia, the generic names Stenodryomyza and Neuroctena have been sunk under Dryomyza. This leaves the family with only two known genera, Dryomyza and Cedoparena, the former with about a dozen species, the latter monotypic. Species of Dryomyza are described from both the Holarctic and the Oriental, while Oedoparena is Nearctic. Known larvae develop in rotting fungi.

Discussion of the relation between Dryomyzids and other Diptera has been almost entirely confined to arguing the family's taxonomic status relative to other Sciomyzoids. As a result the relation between the Dryomyzidae and Acalypterates outside the Sciomyzoidea has hardly beeen considered. Because of the dearth of usable apomorphic features in Dryomyzid morphology, even the relation between them and both Helcomyzids and Coelopids remains a vexed question. This is described in detail elsewhere in this account.

Although the taxonomic status of the 'Dryomyzidae' is open to question, Steyskal (1957) has provided strong evidence from a study of the terminalia that they represent a monophyletic group. Other characters do not help even this much. For a long time, the enlarged clypeus of Dryomyza (including Neuroctena and Stenodryomyza) was regarded as a family character of the Dryomyzidae. While this feature distinguishes Dryomyza from Helcomyzids it is not found in

Oedoparena, but does occur among Coelopids.

At the moment Dryomyzids are recognised by possessing the following combination of characters:

1. Palpal bristle present (absent in Oedoparena).
2. Clypeus differentiated (not so in Oedoparena).
3. Vibrissae absent.
4. Postvertical bristles divergent.
5. Precoxal bridge absent.
6. Dorsal pre-apical tibial bristle present.
7. Costa entire.
8. Subcosta complete.
9. Anal vein and anal cell complete.
10. Seven sclerites before the hypopygium in the male postabdomen.
11. Female with three spermathecae.

Although the absence of a precoxal bridge has been used by most authors to segregate Dryomyza from the Helcomyzidae, the possible significance of the precise form of the prosternum which is found in Dryomyzids has been ignored.

The pronotum and propleura show no distinctive features in Dryomyza (see fig. 43), providing instead a repeat of the pattern seen in a majority of Acalypterate families. The presternum is here a large slcerite which fills the gap between cervical organ sclerite and basisternum. The basisternum itself is lanceolate and is referred to variant A (see fig. 43).

The basisternum of Dryomyza anilis (Neuroctena anilis) is very similar to the basisterna of other Dryomyza species. This backs up Steyskal's deduction that *Dryomyza* and *Neuroctena* can be regarded as one genus. It is not very strong support though, seeing the overwhelming frequency with which different Acalypterate genera in the same family bear basisterna of the same shape. Further, variant A is a very common and widely distributed shape of prosternum.

Although the shape of the prosternum of *Dryomyza* certainly serves to distinguish the genus from Helcomyzids, it is not sufficiently unusual to help separate Dryomyzids from all other Acalypterates. Nine families share sternal variant A with the Dryomyzidae, even after other families have been excluded from consideration because of other morphological differences. These nine are:

Coelopidae
Sepsidae
Sciomyzidae
Neottiophilidae
Pallopteridae
Rhinotoridae
Periscelidae
Heleomyzidae
Trixoscelidae

These include a majority of the other Sciomyzoid families, which at least helps to establish the Dryomyzidae as members of this superfamily. The relation between Dryomyzids and Heleomyzidae/ Trixoscelidae may well be closer than Hennig suggests, as Crampton (1944) believed. Similarily, the Rhinotoridae could be closer to all Sciomyzoidea (see discussion) than in Hennig's arrangement of the Acalypterates. At present there is little justification for suggesting that *Dryomyza* is closely related to either Neottiophilidae or Pallopteridae: the similarity between the prosterna here could well be due to convergence.

It is unfortunate that no material of Oedoparena has been available for examination. However, whether or no the prosternum of this genus is similar in shape to that of Dryomyza, it cannot help to establish the Dryomyzidae as a discreet monophyletic group, seeing that sternal variant A is so widely distributed. This is especially so since the same shape is predominant in Sciomyzoidea.

To summarise, the prosternum of Dryomyzids does not help to establish the family as a monophyletic group, neither does it aid in assessing the taxonomic status of the 'Dryomyzidae'. It does, however, show Dryomyza to be satisfactorily placed among the Sciomyzoidea. This means that there is still no character by which Dryomyzids may be distinguished either from all related groups, or the rest of the Acalypterates. A good case can be made out for combining Dryomyza in either Helcomyzidae or Coelopidae: this would seem the most sensible course unless information does appear which demonstrates that Dryomyzids warrant family status.

COELOPIDAE (SCIOMYZOIDEA)

NO. GENERA EXAMINED: 5
NO. SPECIES EXAMINED: 10
STERNUM VARIANTS: A, B, V.

The Coelopidae, or Kelp flies, are another family of shore inhabiting species. They are represented along most coasts of the world although there are few genera and species: some species are very widely distributed.

In his review of the family, Malloch (1933) says, "I am confining this group to those species in which the prosternum is well separated from the chitinous propleura by a well-defined sunken membranous strip and the epistome in side view projects well beyond the level of the anterior margin of the frons". Since then, other authors have used the same criteria to define the family, but with varying degrees of exactitude (see below).

Hennig suggests there is no reason to doubt that the family Coelopidae is monophyletic. Even so, the only evidence he cites to support this statement is that Coelopid postverticals are convergent (in some, such as Protocoelopa, postverticals are absent). He adds that Coelopids also have in common a number of other cephalic characters, but that these cannot be precisely defined. Presence of convergent postverticals is of little significance by itself, because at least a third of all Acalypterate families contain genera with this feature.

Apart from in the state of the postverticals and the condition of the prosternum, Coelopids are so similar to Helcomyzids that the list of characters used to define either family could also be used to define the other.

In most Coelopid genera a 'clypeus' is differentiated similar to that found in Dryomyza. This might also be of phylogenetic significance, but is, however, lacking in at least Protocoelopa.

In classificatory systems, the Coelopids are often placed next to Helcomyzidae and Dryomyzidae. However, Malloch (1933), who more than anyone else has been responsible for present definitions of the family, allies them with the Sphaeroceridae. Hendel (1922, 1936-37) and Crampton (1944) put the Coelopidae in a group containing the Heleomyzidae. Coelopids have also been placed next to this family by Oldroyd (1954) and Harrison(1959). Hennig himself says he can find no morphological justification for his inclusion of the family in Sciomyzoidea. There certainly seems no greater morphological difference between Coelopidae and Heleomyzidae than between Coelopidae and other Sciomyzoids.

A number of problematic genera are believed by many authors to belong in this family. *Cedoparea*, now synonymised with *Heterocheila* (see Steyskal 1957), has recently been removed to the Heleomyzidae. Hennig gives a long and involved discussion of the possible position of *Apetaenus*, concluding it belongs more in the 'circle of relationships' of the Heleomyzidae than in the Coelopidae. Both Hennig and Steyskal now consider *Orygma* to be a Sepsid, though in the past it has been either left in Coelopidae or given separate family status.

Apart from in the shape of the basisternum, the prothorax of Coelopids is similar in structure to its counterpart in the Helcomyzidae. The pronotum shows no distinctive features, precoxalia are not in evidence and there is a small but separate presternum intervening between cervical organ and basisternum.

In *Chaetocoelopa*, *Malacomyia* and some *Coelopa* species the basisternum is lanceolate/spatulate (variant A, see fig. 57) or almost linear. In *Coelopa curvipes* Hutt. the plate is expanded anteriorly (variant B) and a pigmented ridge of membrane connects it with the propleura. Hardy (1962) illustrates this condition as a precoxal bridge. In *Baeopterus* the sternum is expanded in a similar manner, but there is no sign of any connection with the propleura. Protocoelopa philpotti Mall. possesses a precoxal bridge (variant V). This was not mentioned by either Malloch (1933) or Harrison (1959), despite their definition of the family (Hardy did not examine this species). Both species of Apetaenus have been examined here and both have precoxal bridges. This seems to have been overlooked by Harrison but it is mentioned for A.watsoni by Hardy, who did not consider the fact sufficiently significant to warrant removing the genus from the Coelopidae. The sternum of Orygma is almost linear, as in Coelopa (see fig. 57).

Since species both with and without precoxal bridges still occur in the Coelopidae it is most unsatisfactory that definition of the family should depend to a great extent upon the precoxal bridge being absent.

Assuming that Apetaenus belongs elsewhere, as argued by Hennig, the only genus in Coelopidae still displaying a precoxal bridge is Protocoelopa. This genus also differs from other Coelopids in further characters critical to the definition of the family, so it is difficult to justify retaining the genus in Coelopidae. With Protocoelopa removed it is more plausible that the Coelopids represent a monophyletic group.

If reasons are found for retaining either Apetaenus or Protocoleopa in the Coelopidae, present definitions of the family break down. From the polar diagram for the superfamily (see fig. 63), it can be seen that Coelopid sternal types are well distributed among the Sciomyzoidea and in no way restricted to the Coelopidae. Variant A, at least, is also of frequent occurrence elsewhere among

Schizophora. This means that if these two genera are included in the Coelopidae, it is necessary to rely upon imprecise characters to define the family. These, such as way of life and adaptation to the littoral environment, have already been discarded once, as unreliable, by Hennig. He has shown that Orygma can with justification be placed in the Sepsidae, despite its general morphological and biological resemblance to Coelopids. It is no great step to extend this arguement to other Coelopids, which might then be regarded as modified Helcomyzids, Sciomyzids, or even Heleomyzids.

SEPSIDAE (SCIOMYZOIDEA)

NO. GENERA EXAMINED: 11
NO. SPECIES EXAMINED: 53
DOMINANT STERNAL VARIANT: A

Sepsids are a cosmopolitan group with more than two hundred species known. The larvae develop in decaying matter, particularly faeces.

Morphologically this family is very homogeneous. Sepsids not only possess a combination of characters which distinguishes them from other Acalypterates, but also have in common features which are apparently rare elsewhere among Acalypterates. Thus established, the family is one of the clearest Acalypterate monophyletic groups. The features which characterise Sepsids may be listed as follows:-

1. Palpi vestigial.
2. Vibrissae present (not always).
3. Post-verticals divergent.
4. Metastigmatic bristles present.
5. Costa complete.

6. Subcosta complete.
7. Anal cell complete.
8. Anal vein abbreviated.
9. Pre-apical tibial bristles absent.
10. Hypopygium without movable surstyli.
11. Female with abdominal spiracles 6 and 7 (at least) in the tergites.
12. General appearance very ant-like, the abdomen being petiolated, the legs elongate and the head globose.

The first, fourth and last of these are the characters which above all single out Sepsids as being closely inter-related. According to Hennig the condition of most of the other characters on the list is plesiomorphic in Sepsidae, and thus of little use in determining the affinities of the family.

It is more difficult to assess the phylogenetic significance of the unusual elements in Sepsid morphology, than it is to decide similar issues in other families. The fact that Sepsid palpi are reduced, was first used as a taxonomic character by Melander and Spuler (1917), to separate Sepsids from Piophilids. The condition of the palpi has been little used in the classification of other Acalypterates, and the literature has yielded comment on their state in only seventeen families. In these seventeen the palpi are either normal or enlarged: but their state in the other forty families is a matter for conjecture.

Even less frequently referred to is the character of the metastigmatic bristles. Mention of these has been found in accounts of sixteen families, four of which are said to possess them.

If either of these characters were thoroughly investigated, it seems quite possible that their condition in Sepsidae would be found to be much less unique than it is at present believed to be.

At present it is not at all obvious to which other Acalypterate family the Sepsidae are most closely related. Authors such as Curran (1939), Imms (1957) and Harrison (1959), place the family next to the Piophilidae. As Melander and Spuler (1917) demonstrated, the earlier idea that these two families are one has no foundation, leaving little justification for believing that Sepsids are more closely related to Piophilidae than to many other families. Megamerinidae are chosen by Oldroyd (1954) and Brues, Melander and Carpenter (1954). The latter authors put Rhopalomeridae on the other side of the Sepsids. McAlpine J.F. (1963), says of this relationship that Sepsids, "appear to have arisen from a Rhopalomerid-type ancester". In coming to this conclusion he relies heavily upon the "unique character of the metastigmatic bristles", present in both groups. Sepsids have also been placed next to Heleomyzidae, Sciomyzidae and Tanypezidae. Crampton (1944), puts Sepsidae and Sciomyzidae in their own superfamily. Hennig (1958) bases his placing of this family in the Sciomyzoidea on characteristics of the post-abdomen, but it is a moot point as to whether or no these have yet been adequately investigated. Hennig himself says that more work is needed before the real relationship between the Sepsidae and the rest of the Sciomyzoidea can be established.

The prothoracic region of Sepsidae is similar in structure to that of many other Acalypterates, including Pallopteroidea and Sciomyzoidea. The humeral calli are small and well-defined, but neither pronotal not propleural sclerites show any distinctive features. The presternum is a small plate which, although associated with the cervical organ, is not incorporated into it. Apart from where type H is present, the basisternum is reduced (but see Apterosepsis below). Sternal variant A is present in seven of the eleven genera examined here (including Orygma), but the sternal shape involved is not quite the same as that of Sciomyzid, Dryomyzid and Coelopid sterna referred to the same variant. Whereas in these families the widest part of the plate comes right at its distal end, posterior to which it narrows for the whole of its length, in Sepsids the greatest width normally occurs after the anterior end and otherwise even closer to the base of the sclerite (see fig. 57). Sternal variant S, also found among Sepsidae but nowhere else in the Sciomyzoidea, is of a similar construction.

The remaining Sepsid sternal variants are I and B. Type B appears with other sternal types in Sepsis, Themira and Nemopoda. Type I is found in Sepsis and AustraloSepsis. Altogether, sterna referable to four different variants are found in Sepsis. This is a large number when compared with the range of variation in most Acalypterate genera, and perhaps indicates that Sepsis contains species better placed in other genera. Other than those considered here to represent the genus, one species (Sepsis fuscipes Walker) examined is definitely wrongly placed. It possesses a precoxal bridge and characters diagnostic of the Chloropidae (the determination of this species as a Chloropid has been confirmed by J.C.Deeming). The only other species at present put in the Sepsidae, known to possess a precoxal bridge, belongs to the monotypic genus Apterosepsis, where variant T is found.

Sepsids are, then, as similar to one another in prothoracic morphology as they are in general morphology. The basisterna of fifty-two of the fifty-three species examined form a compact group of shapes closely inter-related (see polar diagram). Apterosepsis provides the exception. It has been argued that if precoxal bridges and reduced shapes are apomorphic forms of the prosterna, it is unlikely for both to occur in the same family. Such a situation is certainly unusual. This makes it desirable to re-examine the phylogenetic position of Apterosepsis.

In discussing Apterosepsis, Richards (1962) says, "The absence of wings and the very reduced chaetotaxy make it hard to place. The palpi are not properly visible but they do not seem to be quite so reduced as would be expected in a Sepsid." At present only the female of this genus is known. The metathoracic spiracle is absent, also, so that the metastigmatic bristles cannot be identified; they in any case appear to be absent.

Put together, these various features suggest that Apterosepsis is less closely related to Sepsidae than is at present believed. The genus may well belong outside the family, but its phylogenetic position must remain in doubt until more specimens are known. At present all that may be said is that it probably belongs in one of the families where precoxal bridges are found.

Excluding Apterosepsis from consideration, prothorac morphology of Sepsids is very constant throughout the family. This gives no reason for believing the family to be anything other than monophyletic. Because the sternal shapes found among Sepsids are well distributed among Acalypterates in general, they are not very useful in deciding the probable affinities of the family, or of problematic genera associated with it. Thus the prosternal shape seen in Orygma is common to both Sepsidae and Coelopidae. Similarly, variant A is dominant in Sepsidae and in other families both in and out of Sciomyzidea, which does not help to establish the position of Sepsids in the superfamily. Nonetheless, the precise combination of prosternal shapes present in the Sepsidae is very similar to the combinations present in other Sciomyzoid families. Outside Sciomyzoidea, the closest parallel to these combinations seems to occur in the Pallopteroidea. Here also, prosternal shapes more precisely like the Sepsid variant A are found. Further, the Piophilidae, for a long time believed to be closely related to Sepsids have been consigned to the Pallopteroidea by Hennig.

In conclusion, it can be said that Sepsid prothoracic morphology supports the contention that this family is a valid monophyletic group, so long as Apterosepsis is excluded from the family. It in addition supports the placing of Sepsidae in Sciomyzoidea, while at the same time suggesting that the family is closely related to others outside this superfamily, particularly, perhaps, Pallopteroids.

RHOPALOMERIDAE (SCIOMYZOIDEA)

NO. GENERA EXAMINED: 2
NO. SPECIES EXAMINED: 4
STERNAL VARIANT: W

Little is known about the Rhopalomeridae, a small neotropical family.

According to Hennig (1958), the only known morphological feature which perhaps unites the members of this family as a monopyletic group is their thickened femora. However, enlarged femora are found in many Acalypterate families, lessoning the significance of their occurrence in Rhopalomeridae.

Rhopalomerids are recognised by their own specific combination of characteristics, all of which are found individually in a large number of Acalypterate families. Apart from the fact that they possess metastigmatic bristles, Rhopalmerids show the same combination of features as is found in Helcomyzidae.

The condition of the prosternum has been known in Rhopalomeridae for some time, and Hennig lays some stress on the presence of a precoxal bridge both here and in Helcomyzidae. His conclusion that the two families are closely related is apparently based upon this fact, but he nowhere discusses the precise form of the precoxal bridges involved.

Since Rhopalomerids are confined to tropical America their phylogenetic position has not been discussed very frequently. J.F.McAlpine (1963), does not agree with Hennig's placing of the family, and believes Rhopalomerids to be, "relatively remotely related" to Helcomyzidae. He concludes instead that Rhopalomerids and Sepsids are closely related. "The Sepsidae appear to have arisen from a Rhopalomerid-type ancestor which, among other things, lost the precoxal bridge." Curran (1939) also places Rhopalomeridae next to the Sepsidae.

Considering families outside Hennig's Sciomyzoidea, it was once supposed that Rhinotoridae are closely related to the Rhopalomerids, the two families being regarded as one. Hennig (1952) separated the two groups: his action has since been supported by work on the terminalia, carried out by Steyskal (1957).

The basisternum is the only prothoracic sclerite with a distinctive appearance in the Rhopalomerids examined here (Rhopalomera and Willistoniella). It takes the form of a wide precoxal bridge referable to variant W (see fig. 57).

Apart from Strongylophthalmyia (Strongylophthalmyiidae) and Ulidia (Otitidae), sternal variant W does not occur outside the Drosophiloid complex. This leaves the Rhopalomeridae somewhat isolated in the Sciomyzoidea. The relationship between variant W and the other precoxal bridge type found in Sciomyzoidea (variant V) is obscure. They are both found in the Chloropidae, but there none of the reduced shapes occur, which are dominant among Sciomyzoids, and to which there is every indication that variant V is closely related. So then, variant W is not only absent from the families to which it is believed that Rhopalomerids are related, but also apparently remotely related to the variants which are found there. This does not substantiate the claim that Rhopalomerids should be placed within the Sciomyzoidea. However, it does provide positive indication that the Rhopalomeridae form a monopyletic group, particularly since W is very probably an apomorphic variant. But this point cannot be discussed further until the form of the prosternum is known in all Rhopalomerid genera.

The prosterna of Rhopalomerids are also different from those of Rhinotoridae, where reduced types occur. Although this adds to the data supporting Hennig's segregation of these two groups, and involves variants belonging to two different apomorphic categories, it does not help to show that the two families are only remotely related: Rhopalomerids are assigned to the Sciomyzoidea where species with reduced prosternal variants are abundant.

To summarise, the precise shape of the prosternum in the Rhopalomeridae might help to establish the family as a monophyletic group, but does not clarify its position within the Sciomyzoidea. None of the special relationships between this family and others which have been put forward are provided with much support. Superficially, the most likely of these is the relationship with Helcomyzidae suggested by Hennig, based as it is upon common possession of a precoxal bridge. However, when he made this suggestion Hennig was unaware of both how widely distributed are precoxal bridges among Acalypterates and of the probable significance of the differences in shape between the bridges in these two families.

SCIOMYZIDAE (SCIOMYZOIDEA)

NO. GENERA EXAMINED:	33
NO. SPECIES EXAMINED:	84
DOMINANT STERNAL VARIANT:	B

According to Knutson (1965), there are some 450 species of Sciomyzidae known, the family being distributed among all the continents of the world and extending from Tierra del Fuego to the Franz-Joseph Islands. Sciomyzids have become known as the "snail-killing flies". Known larvae are predatory or parasitoid on land or water mollusca. Hennig (1958) is unable to find any apomorphic character that demonstrates this family to be a monophyletic group. Other authors are in the same position, although the unusual diet of Sciomyzids might well be regarded as a unifying feature (see Berg 1961).

In order to define the Sciomyzidae at the moment, it is necessary to make use of a combination of characters which, according to Hennig, are most of them present among Sciomyzids in a plesiomorphic condition:

1. Vibrissae absent.
2. Cephalic bristles complete
3. Postverticals divergent (convergent in Huttonina)
4. Palpi normal.
5. Clypeus normal.
6. Pre-apical tibial bristle present (absent in Teutonomyia)
7. Metastigmatic bristles absent.
8. Costa entire.
9. Subcosta complete.
10. Anal cell and anal vein complete (anal vein short in Colobaea and Huttonina.

This list may be compared with the lists of characters for other Sciomyzoid families. Such a comparison shows that this family is distinguished by lacking apomorphic features the others possess.

Curiously enough, although the condition of the prosternum has previously been noted for other families of the Sciomyzoidea, it seems to have been ignored in Sciomyzidae. J.F.McAlpine (1963) provides the only exception: the absence of precoxal bridges in Sciomyzidae is noted in a chart of characters demonstrating inter-family relationships in Sciomyzoidea/Lauxanioidea. He makes no comment on this fact. Until recently this family has been divided into two major sub-families and a varying number of small ones. Steyskal (1965) has re-assessed the situation. He recognises five sub-families. The first of Steyskal's sub-families, the Huttonininae, differs from all other Sciomyzids in possessing convergent post-verticals and an abbreviated anal vein. It is difficult to see how this sub-family is any less different from Sciomyzidae than are, for example, Sepsids, without subjectively 'weighting' the importance of the characters used. In this instance the metastigmatic bristles of Sepsidae would have to be regarded as of more phylogenetic significance than the convergent postverticals of Huttonininae.

The other four sub-families are distinguished from each other by a combination of characters none of which is unique to any one sub-family. More than anything else, the number of spermathecae and characteristics of the male terminalia are used. As previously, there is great disparity between the sizes of the various sub-families. This has been accentuated by combining most genera from the two larger sub-families of earlier authors (Sciomyzinae and Tetanocerinae) in one sub-family, the Sciomyzinae. Three of the five sub-families are monogeneric:

Huttonininae : Huttonina

Salticellinae : Salticella

Phaeomyiinae : Pelidnoptera

The remaining sub-family, Helosciomyzinae, contains only Helosciomyza, Xenosciomyza and Polytocus.

No distinctive protheracic features separate Sciomyzids from other Acalypterate families. The antepronotum is reduced to a narrow ring round the top of the cervical cavity. The humeral calli are large but ill-defined. The suture marking the pleuro-sternal apophysis may continue upwards to meet that from the first phragma. This perhaps marks out the extent to which the prothorax contributes to the humeral calli, but it would be necessary to examine the associated musculature in some detail to establish if this were so. Most of the pleural sutures are lost and there is no precoxale present. The posterior cervical sclerites may be fused to the propleura. The presternum is a small elongate sclerite, variable in shape and lying more or less free in the cervical membrane. Only the shape of the basisternum is sufficiently characteristic to provide points for discussion.

Most forms of the basisternum found here are reduced types. The one found in the largest number of genera is type B, while the only other found with any frequency is the generalised shape H. Types A and V also occur.

The distribution of the various sternal types is not correlated with the accepted subfamily classification of the group. Using Steyskal's 1965 scheme, all the variants found in the family occur together in Sciomyzinae. His other sub-families are so small that it is impossible for all five variants present among Sciomyzidae to occur together in any of them. If the family is sub-divided according to older schemes, the same range and relative abundance of types is found in both Sciomyzinae and Tetanocerinae.

An anomalous feature of the prosternal variation in this family is the presence in one species of Pherbellia (Sciomyzinae) of a precoxal bridge, referrable to type V. Dr. Steyskal has kindly examined the material (including the type) of this species which was used in the present study. He considers it a typical Sciomyzid.

It can be seen that the form of the prosternum cannot be used to help define the various sub-families of Sciomyzidae. The alternative is to argue that the sub-family classification of Sciomyzidae is inadequately understood and that the distribution of sternal variants in the family provides a way to sub-divide it more satisfactorily. This is not very likely seeing the large numbers of features used by Steyskal in his analysis of the inter-relationships of the various Sciomyzid genera. Elsewhere among Acalypterates sternal variation is not in general correlated with present ideas of the sub-division of families.

Although there is no obvious relationship between the distribution of the sternal variants found in Sciomyzidae and sub-family classification, taken together the various sternal shapes seen in this family form a closely related group (see fig. 57). Because of this the shapes of Sciomyzid prosterna do not imply that the family is polyphyletic. The same variants are widely distributed among Acalypterates, however, so they do not provide strong evidence that Sciomyzids form a monopyletic group. This is particularly so when it is realised that these same variants are common to most of the families which are currently believed to be closely related to the Sciomyzidae. Because of this, on the basis of the shape of its basisternum, the aberrant genus Huttonina could be placed just as logically in Heeomyzidae as in Sciomyzoidea.

The body of general morphological date available indicates that it is exceedingly unlikely for the Sciomyzidae to be closely related to all those other Acalypterate groups bearing Sciomyzid-like prostern. However, these groups include those judged to be closely related to Sciomyzids on the basis of their general morphology. Together with the fact that Sciomyzid sterna are all closely related by shape, this suggests that prosternal shape provides a general reflection of the phylogeny of this group of families, even if it fails to indicate the precise position of Sciomyzidae in the complex.

SCIOMYZOIDEA: Discussion

Hennig's justification for grouping together the families he puts in the Sciomyzoidea is tortuous. In fact, judged by the criteria he lays down himself to assess the validity of monophyletic groups, this superfamily cannot be regarded as satisfactory. It is useful only as a conveniently sized taxonomic unit. According to Hennig, before a group can be established as monophyletic it is necessary to find some unique apomorphic characteristic shared by its members. But the Sciomyzoid 'families' are grouped together on negative evidence: they none of them possess features which show they have strong affinities with families outside Sciomyzoidea, and can only with difficulty be distinguished from one another.

The preceeding pages show how some of the deductions made about Sciomyzoid phylogeny from general morphology, could equally easily be made from a study of the prothorax. The prosterna of Sciomyzoids are (with the exception of Rhopalomerids) all closely related to one another by shape, forming as compact a group as is found in any Acalypterate superfamily. For this reason it is difficult to distinguish sub-groups of the Sciomyzoidea from one another by prosternal shape: which makes Sciomyzoid 'families' look less well founded. In addition, most of the sternal shapes found are by no means unique to Sciomyzoidea, reducing their usefulness in determining relationships.

It is here, however, that these similarities end. One of the probably apomorphic Sciomyzoid sternal variants (V) has a very restricted distribution among Acalypterates, occurring in only two families outside the Sciomyzoidea. One of these (Heleomyzidae) might well be closely related to Sciomyzoids. This can be regarded as strong evidence that the Sciomyzoid 'families' with genera which bear this variant are closely related (unless there were independent evidence suggesting any of these families is polyphyletic, which there is not).

Use of these data as evidence that the Sciomyzoidea represent a monophyletic group, can be criticised because of the peculiar distribution of sternal variant V, which suggests it may have evolved independently within Sciomyzoidea at least twice. Otherwise, since it appears (from the same distribution pattern) that variant V has evolved from a reduced shape of sternum, it seems necessary to postulate either that the Coelopidae have developed from the Sciomyzidae, or vice versa, and that in one or the other family the precoxal bridge has been secondarily lost. However, a third explanation is possible. Both of these families, and other Sciomyzoids, could have arisen from an ancestral group in which both reduced prosterna and this specific type of precoxal bridge were found. Assuming for the moment that all four families are valid monophyletic groups, this would mean that both Coelopidae and Sciomyzidae have maintained this dual capacity, while Helcomyzidae (with sternal variant V only) went one way and Dryomyzidae (with reduced shapes only) went the other.

This explanation of the distribution of sternal variant V also shows how the relation between Sciomyzoid genera is perhaps revealed by variation in sternal shape. If so, then it also demonstrates that prosternal shape cannot be used in this superfamily to help distinguish between the families, since it would be potentially possible for all shapes of prosterna found in the superfamily to turn up in any of its constituent families.

If this hypothesis is correct, the way in which the prosternum has been used in the definition of families in the Sciomyzoidea, is inadequate. As much has already been suggested in discussion of individual Sciomyzoid families, using other arguements. This means it is obviously unjustifiable to use presence of absence of a precoxal bridge to segregate Sciomyzoid genera between different families, in which case ways of segregating Coelopid, Dryomyzid and Helcomyzid genera from one another more or less disappear, and with them goes the justification for regarding these families as discrete monophyletic groups. The most logical course at present would seem to be to combine them under one heading as a single family.

The Sciomyzidae possess almost exactly the same combination of sternal variants as is found in Coelopidae/Dryomyzidae/Helcomyzidae and there is little doubt that the four groups are closely related. The situation in the Sepsidae is slightly different though, where the exact combination of variants seen more closely resembles that found in Pallopteroidea: see polar diagrams for Sciomyzoidea and Pallopteroidea (figs.63,64). But the difference between the combinations of sternal variants present in Pallopteroidea and Sciomyzoidea is in any case quite small and of doubtful significance. Whatever basis is used for discussion, the Sepsidae really seem to occupy a position somewhere between these two superfamilies.

The position of Rhopalomerids is enigmatic and made more so by the condition of their prosterna, which are shaped differently from those of all other Sciomyzoid/Pallopteroid/Heleomyzid families. Elucidation of the relationships of this family will obviously have to wait until more information is available. No great significance should be put on the precise shape of the prosternum in the Rhopalomeridae at present, since conceivably this has been derived from variant V, though there is no evidence to prove this.

Since there is little certainty as yet that the Sciomyzoidea represents a valid monophyletic group, it is perhaps premature to consider the relation of this superfamily to other Acalypterate groups. However, whether taken individually or collectively, Sciomyzoid families (apart from the Rhopalomeridae) seem from their prothoracic morphology to be closely related to the Pallopteroidea and to Heleomyzidae/Trichoscelidae: exactly as has been deduced from general morphology by many authors. Judged solely by prosternal shape, the Rhinotoridae, Anthomyzidae and Cpomyzidae could also be closely related to Sciomyzoids (see appendix), but at least at present, the condition of too many other morphological characters which are regarded as significant, rules against this.

Summarising, the prothoracic morphology of Sciomyzoids provides some evidence in support of grouping these families in one superfamily, though it does not help to clarify the relationships of the Rhopalomeridae. It also shows that the separate family status of three of the Sciomyzoid families is of doubtful phylogenetic value, especially as founded upon previous deductions making use of the prosternum in determining relationships, which were based upon inadequate information. As more becomes known, especially about the Heleomyzidae, it seems quite likely that Sciomyzoidea, Pallopteroidea and Heleomyzidae/Trickoscelidae will be regarded as more closely related than they are at the moment.

PALLOPTEROIDEA.

Hennig confines this superfamily to the families Piophilidae, Thyreophoridae, Neottiophilidae, Pallopteridae and Lonchaeidae; none of which has more than a handful of genera. These families have not been formally grouped as a superfamily previously, though they are usually placed very close to each other in recent classificatory systems. The Neottiophilidae form a partial exception, both the content and systematic position of the family being treated differently by other authors.

In part this superfamily has arisen in the same way as the Otitoidea: by splitting originally broader concepts into a number of related families. Thus, until recently, Pallopteridae and Lonchaeidae have been grouped as one family, while the family status of the Thyreophoridae, as separate from the Piophilidae, is still questioned.

Other families for which relationship* to various Pallopteroids has been claimed are Sepsidae, Lauxaniidae, Heleomyzidae and Otitidae s.l. Most authors suggest that some relationship exists between Heleomyzidae and one or other of the Pallopteroid groups.

Hennig is cautious in his comments on this superfamily. While he says that as a group they cannot be more easily related to other families than to one another and that they are morphologically difficult to separate, he also suggests it is almost impossible to establish the superfamily as a monophyletic group. The one character Hennig stresses as of possible potential in uniting the group is the structure of the terminalia, but at present insufficient data are available for this to be used with any certainty. On other morphological characters the superfamily tends to fall into two parts, which Hennig suggests bear a "sister-group" relationship to each other. Thus, while true vibrissae are present in Piophilidae - Thyreophoridae and Neottiophilidae, they are absent from the other two families. Similarly, the anal vein, reduced in Piophilidae - Thyreophoridae, is complete in Lonchaeidae-Pallopteridae. This character varies in the Neottiophilidae, which as Hennig implies occupies a somewhat intermediate position in the superfamily, closer to the Piophilidae - Thyreophoridae than to the Pallopteridae - Lonchaeidae, but without specializations of either group (see below).

PALLOPTERIDAE (PALLOPTEROIDEA)

NO. GENERA EXAMINED: 7
NO. SPECIES EXAMINED: 11
STERNAL VARIANT: A, C, H

This family probably contains more genera than any other among Pallopteroidea. Even so, the Pallopteridae is a small group.Most of the species are Holarctic, some are found in the temperate Neotropic and one genus (Neomaorina) occurs in New Zealand.

Many authors do not recognise this group of genera as warranting family status, treating them as genera of Lonchaeidae - Oldroyd(1952) and Imms (1957). When the Lonchaeidae were not accorded family s status e.g. in Melander (1913), but regarded, with the Lauxaniidae, as genera of "Sapromyzidae", Palloptera was also included. Just as Hendel maintained the position of Pallopterids within Lonchaeidae, so did Malloch maintain their segregation. He said (1948), that although by no means convinced that Pallopterids make a valid family group, he did believe "they are as far removed from Lonchaeidae as the latter are from several other so called families in their immediate vicinity in the scheme of classification." Hennig (1958), comments that Pallopteridae are no closer to Piophilariae - Neottiophilidae than they are to Lonchaeidae. He believes that Pallopteridae - Lonchaeidae form a "sister-group" to the other three Pallopteroid families.

Separate family status is also given to the Pallopteridae in Malloch and McAtee (1924), Curran (1934), Colyer and Hammond (1952), Brues, Melander and Carpenter (1954), Harrison (1958) and Morge (1959).

It has been suggested that a vaguer relationship exists between Pallopteridae and Heleomyzidae, Lauxaniidae or Otitids, by various authors: Curran (1934), Malloch (1948), Shewell (1965 in Cat.N.Am. Dipt.).

Two somewhat imprecise characters separate Pallopteridae from Lonchaeidae. Pallopterids tend to have the frontal lunule concealed, while this is exposed in Lonchaeids; Lonchaeids all possess black halteres: McAlpine (1960), a phenomenon not found in Pallopteridae. In other features the families grade into one another. Thus the post-scutellum is enlarged in Lonchaeidae and some Pallopteridae; vibrissae are absent in Pallopteridae and most Lonchaeidae; pro - pleural and pre-apical tibial bristles are present in Lonchaeidae and some Pallopteridae (Eurygnathomyia). The two families agree in venational characters, cephalic chaetotaxy and (limited data available) in the form of the postabdomen. In post-abdominal structure the Pallopterids show a condition that could be regarded as antecedent to that of Lonchaeids, but more advanced than that of Piophilariae-

Neottiophilidae - Hennig (1938-41 and 1958). Crampton (1944), related Pallopteridae to Ctitoids on the basis of the male terminalia.

Pallopterids and Lonchaeids differ from the other Pallopteroids in: (1) they possess only one pair of front-orbitals, (2) the anal vein is complete (plesiomorphy), (3) they frequently possess a pre-apical dorsal tibial bristle.

Pallopteridae show no unusual feature in the structure of the prothorax. The pre-sternum is undeveloped, or else a small, undifferentiated and more or less triangular sclerite interposed between sella and basisternum. The basisternum in most Pallopterid genera and species is of type H. *Pseudopyrgota* and *Heloparia* exhibit type A and *Aenigmatomyia* type C. *Neomaorina* is uniform with the majority condition (see fig. 58).

The four genera mentioned above have all been taken as being to some extent problematic. The most recent discussion of *Neomaorina* is in Harrison (1958), who considers the genus to have "far greater affinity with Pallopteridae than Lonchaeidae". The genus was originally described as an Opomyzid by Malloch (1930), but later placed by him in the Pallopteridae. Hendel (1937) placed the genus in Pallopterinae under Lonchaeidae. Since the sternal variant found in the genus occurs in a majority of other Pallopteridae, but not in Lonchaeidae or elsewhere in Pallopteridea, it provides no evidence to suggest *Neomaorina* is at present wrongly placed by systematists. Were it suggested by other characters that *Neomaorina* lay outside the Pallopteroidea, then the probasisternum would provide little evidence as to the correct position of the genus, since variant H is not only widespread, but also possibly one of the most generalised of sternal variants.

The only Pallopteridae deviating by not possessing sternal variant E are among those Malloch regarded as problematic. He in fact uses the character of the shape of the prosternum to segregate Heloparia and Pseudopyrgota from other Pallopteridae (1948 p. 337). There seems little precise morphological difference between these genera and other Pallopterids, their aberrance taking the form of a close general resemblance to species in entirely unrelated families. Heloparia was independently described by Hendel (as Neodryomyza) and placed by him in Pallopterinae. As already stated, the sternal shape(A)exhibited by Pseudopyrgota and Heloparia is the commonest type seen among Pallopteroidea, even though it does not occur in other Pallopteridae. Its occurrence here is not therefore very surprising and cannot,in itself, be regarded as evidence for the exclusion of these genera from the family.

Malloch regarded Aenigmatomyia as resembling Neomaorina, with which it shares the Lonchaeid feature of a narrow frons. It is thus interesting to find that alone among Pallopteridae, Aenigmatomyia possess the sternal variant C, which is dominant in the Lonchaeidae. Again this is a sternal variant found elsewhere in Pallopteroidea, so that its occurrence here no more suggests close alliance with the Lonchaeidae, than it does confirm the position of the genus among Pallopteroidea. The fact that different sternal variants are dominant in Lonchaeidae and Pallopteridae, coupled with the fact that one of the dominants is absent from the other family, indicates there is justification for separating the two groups of genera by the characters at present used. However, if the theory of the evolution of the prosternum put forward earlier in this account is to be accepted, the sternal variants found here cannot in themselves help to establish the two families as discrete monophyletic groups: the dominant variant H in the Pallopteridae is very probably plesiomorphic. Nonetheless, the _combination_ of sternal variants found in the Pallopteridae replicates what is found in other Pallopteroid groups (see polar diagram, fig. 63) helping to place the family within Pallopteroidea. The probable significance of the occurrence of similar combinations outside Pallopteroidea, notably in Heleomyzidae and Sciomyoidea, is discussed elsewhere (see under Pallopteroidea: discussion).

THYREOPHORIDAE (PALLOPTEROIDEA)

NO.GENERA EXAMINED: 3
NO. SPECIES EXAMINED: 4
STERNAL VARIANT: A

Less than ten genera of Thyreophoridae are known, most of which are monobasic. These genera are scattered about the world, Australia apparently possessing the most species, in the genus _Choetopiophila_ - Paramonov (1954). The various species seem excessively rare, so that it has been suggested that the family is on the verge of extinction - Paramonov (1954), Oldroyd (1964).

Due to their rarity the Thyreophotidae are not well known morphologically. The three palaearctic genera, (_Centrophlebomyia_, _Thyreophora_ and _Thyreolepida_) have normally been allied to the Piophilidae in literature (see under Piophilidae). The Australian

Choetopiophila was described by Malloch as a Piophilid, while Paramonov's account of the genus (l.c.) would suggest that it lies between Piophilidae and Thyreophoridae. Omiomyia, a North American genus, has recently been placed in Thyreophoridae by Steyskal (Cat. N.Am.Dipt. 1965). This fly was originally put in Coelopidae by Coquillett and then into Pallopteridae by Curran (1934).

In those morphological characters which have been used throughout the Acelpyterates to compare the different families, the Thyreophoridae agree reasonably well with the Piophilidae. At least, there is no more disagreement between the two families than there is between the various Thyreophorid genera. Besides these characters, the Thyreophoridae possess an enlarged (especially in the male) and usually tuberculate scutellum and pronounced anternnal grooves. It is here that Chaetopiophila is intermediate, some species approaching the specialised Thyreophorid condition, others the less differentiated Piophilid state. Characters such as these are, however, to be found in odd genera scattered throughout the Acalypterates. Thus Epicelyphus among Chloropidae has a scutellum as overdeveloped as any found elsewhere, yet this is not used to separate the genus from Chloropidae.

So, while there is general agreement that the Thyreophoridae and Piophilidae are closely related, there is little basis for argueing whether or no the former group demands separate family status. The structure of the postabdomen is insufficiently known in the two families for any comparison between them to be made - it cannot be said whether or no those that have been examined are in any way "typical" of the family they are supposed to represent.

There seems to have been little attempt to associate the Thyreophoridae with any Acalypterate family other than the Piophilidae. Families of Hennig's Nothyboidea have been placed adjacent to the Thyreophoridae as have other Pallopteroid families, but without comment - Brues, Melander and Carpenter (1954), Imms (1957).

In the structure of the prothorax the Thyreophoridae show no unique features. As in so many other Acalypterates, the antepronotum is reduced to a ring-shaped sclerite bordering on the cervix; the humeral calli are moderately developed antero-lateral swellings; the propleura are more or less undifferentiated and precoxalia are undeveloped; the presternum is very reduced. In the genera examined (Centrophlebomyia, Thyreophora, Chaetopiophila) the basisterna are very similar, all being referrable to variant A.

The form taken by the prosternum in Thyreophorids provides no evidence for the segregation of these genera from the Piophilids, since type A is dominant in both families. This form of basisternum is also dominant for the Pallopteroidea as a whole, however, so that its presence in Thyreophorids does not ally them much more strongly to Piophilids than to other Pallopteroids. This is especially so when it is recognised that all sternal variants found in Pallopteroidea are closely related by shape. As to the vaguer relationships which the Thyreophorids supposedly have with Nothyboids, the most frequent form of Nothyboid sternum is a precoxal bridge - the converse of the Thyreophorid condition.

These characteristics of Thyreophorid prosterna provide no reason for doubting that Thyreophorid genera are closely related either to one another or to other Pallopteroids. But on the other hand their distribution outside Thyreophoridae makes it impossible to use them as indicators that the family is monophyletic, and could also be used to place Thyreophorids near families excluded from the Pallopteroidea (Heleomyzidae and Dryomyzidae) but with which it has in the past been suggested that Thyreophorids have a close relationship.

PIOPHILIDAE (PALLOPTEROIDEA)

NO. GENERA EXAMINED: 5
NO. SPECIES EXAMINED: 12
STERNAL VARIANTS: A, C

The Piophilidae enjoy a world-wide distribution, but comprise only a small number of genera. In fact all the genera can be treated as sub-genera of Piophila - a course taken in the recent Catalogue of North American Diptera (eds. 1965).

Piophila s.l. was originally placed in the Sepsidae, but this course has been abandoned since Melander and Spuler (1917) discussed in detail the morphology of these flies. They came to the conclusion that combined, "such a family is polyphyletic and must be separated into two groups, Sepsidae and Piophilidae, each of which has more evident relationships with other Acalypterate families than the two have with each other." The characters they used to segregate the two families are those used for comparing and contrasting Acalypterates today - venational characters, presence/absence of vibrissae etc. In addition they pointed out that Piophilids do not possess the specifically Sepsid character of much reduced palpi. Their suggestion is that the general resemblance of Piophilids to Sepsids is due to convergence (symplesiomorphy), rather than due to close phylogenetic (synapomorphic) relationship. Since 1917 only Hendel has held that Piophilids and Sepsids are closely related. Both Curran (1954) and Malloch (1948), suggest there is little relation between the two families, while other authors, although they put the families adjacent to each other in classificatory systems (Imms 1957, Harrison 1959), always preserve the family status of the Piophilidae.

Other than a rather flattened, triangular scutellum, there is no morphological feature which characterises the Piophilidae, beyond their own particular combination of a number of widely occurring Acalypterate characters.

Only the Sepsidae and Pallopteroid families have been put forward as having any special relationship with the Piophilidae, but both Malloch (1948) and Hennig (1958) indicate some less precise relation to exist between Piophilids and Heleomyzidae.

When allied to other Pallopteroids in classificatory systems, Piophilids are usually placed next to either Thyreophoridae or Neottiophilidae, or both - Hendel (1916), Oldroyd (1954), Imms (1957). The Thyreophoridae may even be included in Piophilidae, as advocated by Paramonov (1954). Hendel (1922) includes these two families under the one heading Piophilariae - a term also used by Hennig (1958) when he is discussing these families.

The difference between Piophilidae and Thyreophoridae is mainly one of degree - Thyreophorids have a more extreme form of scutellum and extremely well-developed antennae grooves. The genus

Chaetopiophila (Thyreophoridae) occupies an intermediate position (see under Thyreophoridae). At present the postabdomen has only been examined (by Hennig) in one Thyreophorid and one Piophilid, so that little can be deduced from its structure. Suffice it to say that those examined show agreement (Hennig 1958). It may be added that on the basis of the male terminalia, Crampton (1944) placed Piophilidae with the Otitoid families.

The prothorax of Piophilidae shows no feature to characterise the family and only the basisternum shows any potential for indicating the family's relationships (see fig. 44). Ten of the twelve species examined possess variant A, while the remaining two have variant C (see fig. 58).

These sternal variants are dominant for the Pallopteroidea as a whole and are closely related in shape. It is also true, though, that the dominant Piophilid sternum type is dominant in Sepsidae, and found in many Heleomyzidae: to both of which it has been suggested that Piophilidae are related. It is equally true that this shape of sternum is found in families to which it has never been suggested that the Piophilidae are related e.g. Richardiidae.

Although these sternal variants (A and C) are widely distributed among Acalypterates it is not so common to find them occurring in the same family. In fact, the combination of sternal variants which characterises the Piophilidae is only characteristic of other Pallopteroid families, Sepsidae and Conopidae. Seeing that the sternal variants involved are closely related by shape this represents quite strong evidence that the Piophilidae are closely related to other Pallopteroids. The vexed question of the relation between Sepsids and Pallopteroidea has already been discussed: there is little justification for assuming that the similarity between Sepsid and Piophilid prosterna reflects anything more than the close relation between Sciomyzoidea and Pallopteroidea.

NEOTTIOPHILIDAE (PALLOPTEROIDEA)

NO. GENERA EXAMINED: 3
NO. SPECIES EXAMINED: 6
STERNAL VARIANTS: A, S

The family Neottiophilidae was erected by Hendel for the reception of two monobasic Palaearctic genera, Neottiophilum and Actenoptera. Actenoptera is also found in North American. In addition to these two species, the Australian genus Tapeigaster (with about ten species), has also been assigned to the family: Malloch(1926), Paramonov (1955).

Unless the structure of the postabdomen proves to be unique, the Neottiophilids possess no single morphological feature either to unite them as a group or to distinguish them from other Acalypterates. As in so many Acalypterate families, their segregation from the others results from their possession of a combination of widely occurring characters slightly different from any found elsewhere.

Actenoptera and Neottiophilum agree closely in most features of their morphology, including the structure of the postabdomen (Hennig 1958). Actenoptera differs from Neottiophilum in that it does not possess a spinose costa. Tapeigaster presents more of a problem. Some of its species have a spinose costa, others do not. One would think that since the other Neottiophilids are not in agreement in this character, it cannot be used to decide the relation of Tapeigaster to Neottiophilidae. However, Paramonov (1955) allies the genus to Neottiophilidae since costal spines are in the main sbsent, saying that this distinguishes it from Heleomyzidae where these spines are present. Hennig (1958) does the converse, saying that the presence of costal spines in some species allies the genus to Heleomyzidae. Almost the same situation is found where the pre-apical dorsal bristle on the tibiae is concerned. Actenoptera and Neottiophilum do not possess this feature, while Heleomyzidae almost invariably do. Most Tapeigaster species are without this bristle, while it may be distinguished in some. Again, Paramonov uses this character to align the genus with Neottiophilidae, while Hennig uses it to associate the genus with Heleomyzidae. However, Hennig also discusses two other characters. In Neottiophilum and Actenoptera the postverticals are divergent, while they are convergent in both Tapeigaster and the Heleomyzidae. Hennig regards the convergent condition as apomorphic and therefore relates Tapeigaster to the Heleomyzidae by this feature. Hennig also says that, as far as can be seen without research, Tapeigaster does not show the peculiar features found in the postabdomen of other Neottiophilids. He does not, however, compare the condition in Tapeigaster, or that of the other Neottiophilids, with that found in Heleomyzidae. Neither does he state how many species, in this variable genus, he has examined.

Looked at within the framework of Hennig's Pallopteroidea, the only aberriant feature Tapeigaster definitely possess is convergent postverticals. On the other hand, it could just as easily be said that the only features separating the Neottiophilidae s.s. from the Heleomyzidae are a couple of variable bristle characters, plus that of the postverticals. Hennig appears to be the first author to state that the family Neottiophilidae is allied to others of the Pallopteroidea, though it usually keys out among Pallopteroid familes: Oldroyd (1954), Brues, Melander and Carpenter (1954), Imms (1957), Malloch (1926) and Czerny (in Lindner 1931) relate the Neottiophilids to Dryomyzidae. In Imms (1957) they are placed between Dryomyzidae and Lauxaniidae, while Colyer and Hammond (1952) put them between Dryomyzidae and Thyreophoridae.

Apart from in the shape of the basisternum, the prothorax shows no feature that sheds light on the relationships of these three genera (see fig. 46). In Neottiophilum the basisternum is weakly sclerotised and of type S. The presternum is evansecent, but is present as a long bar between basisternum and cervical organ. Both in Tapeigaster (4 spp. examined) and Actenoptera, the basisternum is of type A (see fig. 58) and well sclerotised, while the presternum is similar to that of Neottiophilum but more readily distinguishable.

The two sternal shapes A and S are very closely related. They both occur elsewhere among the Pallopteroidea, while variant A is dominant for the whole superfamily. There is thus no suggestion from the form of the prosternum that any of these genera lie outside the Pallopteroidea, or even that there is good reason for assigning them to different families. However, sternum type A is one of the most frequent sternal variants and is particularly a feature of Sciomyzoidea and Heleomyzidae, to both of which the Neottiophilids have been related by different authors. This situation is perhaps as much an indication of the overall close relationship of these different Acalypterate families, as it is of any precise phylogenetic relation between the Neottiophilidae and any one of them.

There is some reason to believe the reduced sternal variants (including type A) represent a more specialised state. If this is accepted, then since within this superfamily these reduced types (A, S, C) dominate to an extent not seen in other superfamilies, the Neottiophilid s.l. genera might as well be retained within the Pallopteroidea as removed elsewhere, whatever happens to the 'Neottiophilidae' as a family.

LONCHAEIDAE (PALLOPTEROIDEA)

NO. GENERA EXAMINED: 6
NO. SPECIES EXAMINED: 27
STERNAL VARIANTS: C, S

Lonchaeids are found in all the major zoogeographic regions of the World. They comprise a small number of genera, but each of these has many species. There are no Lonchaeids recorded from New Zealand, but Harrison (1958) suggests that New Zealand Pallopterids lie somewhere between Lonchaeidae and Pallopteridae.

Unlike so many Acalypterate families, the Lonchaeids form a well-defined monophyletic group because they possess a number of unusual apomorphic characters. As a result authors have not sought to challenge the validity of the family: see Collin (1953), Morge (1959).

In all members of the family the postscutellum is much expanded and the males show a marked tendency to be holoptic. Lonchaeids are in fact so remarkably homogenous morphologically that even colour characteristics can be used in defining them: all species are strongly aeneous (nearly always blue-black) and have black halteres. Admittedly none of these characters is restricted to the Lonchaeidae among Acalypterates, but equally none of them could be used to define any other Acalypterate family and so far as is known, this combination of characters is absent outside the Lonchaeidae.

One of the more noticeable features of this family is a strongly sclerotised, tubular ovipositor. For a long time this character was said to show a close relationship between Lonchaeids and Trypetids, where a similar structure is found. This similarity is now thought to be due to convergence. Whether or not this deduction is correct it is difficult to find differences between Lonchaeids and Trypetids, using the morphological characters usually employed to compare and contrast Acalypterates. Thus in both families the costa is normally broken both near the humeral cross vein and at the end of the subcosta; the first radial vein possesses bristles; vibrissae are absent (apart from doubtfully, in some Lonchaeids); the post-verticals are divergent; pre-apical dorsal tibial bristles are absent (present in some Lonchaeids).

Because of this, the Lonchaeids are frequently placed next to the Trypetids or other Otitoid families, in classificatory systems: Malloch (1948), Colyer and Hammond(1952), Oldroyd (1954) and Imms (1957).

The Pallopteridae otherwise resemble Lonchaeids both in generally used morphological characters and to some extent in the more specialised Lonchaeid characters (see under Pallopteridae). As already stated these two families have often been combined.

The Lonchaeidae were once included in the "Sapromyzidae", a group now recognised as being a polyphletic concept, which included Lauxaniidae, Lonchaeidae and Pallopteridae. While the postscutellum may be expanded in Lauxaniidae, this family does not agree very well with Lonchaeidae in either venational characters, or in chaetotaxy. Malloch and McAtee (1924) considered there to be "little real similarity" between Lauxaniids and Lonchaeids. These families have, however, been placed next to each other in the literature - Curran (1934), Oldroyd (1952). Where keys are provided in the literature Lonchaeids usually come down in couplets with other Pallopteroid families.

The prothoracic region of Lonchaeids is unexceptional. One uncommon feature is the presence of a pair of sclerites lying free in the cervical membrane; these are probably of secondary nature, but may represent some element of a prothoracic trochantin (see fig. 45). There is no precoxale, but the posterior cervical sclerites are large and obvious. The presternum is recognisable, separate from the sella and interposed between that plate and the basisternum. Only two of the possible thirty-odd prosternal variants have been found in the family - types C and S (see fig. 58). These two occur with about equal frequency and as often as not in the same genus.

The sternum segregates C and S are very similar, so similar that at least in Lonchaeidae there is gradation between them. All in all, the Lonchaeid prothorax reflects the general homogeneity of Lonchaeid morphology, and the family provides a good example of closely related genera showing similar sternal characteristics. Both of the Lonchaeid sternal shapes occur elsewhere in Pallopteroidea but are dominant elsewhere only in Pyrgotidae and Sphaeroceridae. Associated with the narrow range of variation in the Lonchaeid sternum this perhaps helps to confirm the close relation between different Lonchaeid genera. Conversely, since these variants are rare in the Pallopteridae, prosternal variation provides some support for the segregation of these two groups (see also under Pallopteridae).

Apart from in the aberrant genus Phytalmia (type C), neither of the sternal variants found in Lonchaeidae occurs among the Trypetids: these variants are also lacking in the Lauxaniidae.

To summarise, the morphology of the Lonchaeid prothorax does not support the view that the family is closely related to either Trypetidae or Lauxaniidae. The prosternal variation in the family is compatible with the view that Lonchaeids are related to other families of Hennig's Pallopteroidea, while not really reflecting any special relationship with the Pallopteridae. At the same time prosternal variation suggests that the family Lonchaeidae is a satisfactory monophyletic group.

PALLOPTEROIDEA - Discussion.

Hennig discovered no character which unites the Pallopteroidea, but neither did he find reason to suppose any Pallopteroids are more closely related to other Acalypterates than to each other.

Only sixty Pallopteroid species have been examined here, but this is a small superfamily and this number probably represents a proportion of the total number of species in the superfamily similar to that examined in others.

Compared with other superfamilies, the number of sternal variants found in Pallopteroidea is small and the range of variation is narrow. The variants involved are all closely related by shape (see polar diagram fig. 64) and most of them are probably apomorphic.

The Pallopteroidea thus show a greater cohesion of sternal variation than is found in other superfamilies (polar diagrams, fig. 63 onwards). This suggests that if any of Hennig's groups is to be regarded as valid, the Pallopteroidea should surely be one of them.

On the question of the relationship Pallopteroid families bear to families outside the superfamily, the prosternum indicates that families without a precoxal bridge are most likely to be involved.

Relationships which have been suggested primarily involve Lauxamoidea, Sciomyzidea and the Helcomyzidae, but members of all of these three groups have precoxal bridges. It is difficult to make deductions from this though, since individual Acalypterate families may contain genera with and without precoxal bridges.

From other morphological features and the predominant lack of reduced types of sterna in the Lauxamoidea, this appears to be the least likely of the three groups to come close to the Pallopteroids. The Sciomyzoidea may be equally distant, though most of the sternal variants seen in Pallopteroidea occur (see also discussion of Sciomyzoidea). There is least morphological distinction from the Heleomyzids,which also include reduced types among their prosterna. Here, however, there is the difficulty that the Heleomyzidae may be polyphyletic (Hennig 1958). Perhaps further work will reveal that, as Hennig suggests, elements of the Heleomyzidae are more closely related to Pallopteroids than the present classification indicates.

Prothoracic morphology seems to show therefore that it is unlik unlikely for Pallopteroid families to be more closely related to other Acalypterates than to one another. In addition, the prosterna show a uniformity within Pallopteroidea which probably indicates a close relationship between the contained families.

Hennig suggests that a sister-group relationship exists between Piophilariae/Neottiophilidae and Pallopteridae/Lonchaeidae. The former sub-group certainly shows a greater uniformity in sternal shape than is shown by the Pallopteroidea as a whole (both in presternum and basisternum), but the sterna of Pallopteridae show no closer resemblance to those of Lonchaeidae than to those of other Pallopteroids.

MILICHIOIDEA

INTRODUCTION

Five families make up Hennig's Milichioidea: Sphaeroceridae, Tethinidae, Milichiidae (inc. Carnidae), Canaceidae and Braulidae. A comparable grouping of families was suggested by Hendel (1916), with Agromyzidae included, but without Canaceidae. In later work, Hendel does not refer to such a grouping however and apart from Hennig, no author has since suggested these families are closely related.

There is no general pattern provided by the literature in the placing of these families, other than a predominant separation of them from one another. More often than they are placed next to each other, Milichioids have been associated with various Drosophiloids. They have also been placed next to the Chloropidae, Nothyboids, Lauxanioids, Agromyzidae, Opomyzidae and Clusiidae. It has been questioned whether Braula is an Acalypterate at all.

This superfamily is, then, a more or less new concept, not based upon widely accepted ideas about the relationships of it's families.

Hennig (1958) suggests that the Milichioidea cannot be so satisfactorily established as a monophyletic group as can the Drosophiloidea. He lists seven apomorphic characters to define the group. Six of them are presence/absence characters and all seven are found elsewhere among Acalypterates, so there is no unique feature to distinguish this superfamily from others. These seven characters are as follows:

1. Postvertical bristles convergent.

2. Vibrissae present.
3. One/two rows of interfrontal bristles present, each on an interfrontal ridge.
4. Costa interrupted at its junction with the subcosta.
5. Anal vein abbreviated and not reaching wing margin.
6. Anal lobes of wing enlarged.
7. Male postabdomen with a single composite sclerite between the fifth tergite and the hypopygium.

It goes without saying that within the superfamily exceptions are found to each of these. The instability of the group is increased by the fact that there are grounds for considering two of the families (Milichiidae and Tethinidae) are themselves polyphyletic: Hendel (1921), Malloch (1948) : while Braula is placed here on a single morphological character.

CANACEIDAE (MILICHIOIDEA)

NO. GENERA EXAMINED: 7
NO. SPECIES EXAMINED: 10
STERNAL VARIANTS: N, U. W

This is a small family: Wirth (1951) provides a World revision of the group, in which he recognises eight genera containing a total of 32 species. Nonetheless, the family has a world-wide distribution. Most of its species are coastal.

Hennig (1958) considers this family to be a well-established monophyletic group, but has been unable to find any character unique to it, in support of his belief, unless hooked cerci (found by Hennig in female Canaceids) are absent elsewhere among Acalypterates He cites divergent post-verticals, enlarged buccal cavity and enlarged mouthparts as other features of significance. This combination certainly distinguishes the Canaceidae from most other Acalypterates, but is repeated in the Ephydridae. The Sphaeroceridae also have an enlarged mouth cavity, but are without an expanded clypeus.

Since Hennig believes that convergent post-verticals are an apomorphic feature, the Canaceids exhibit an apparently plesiomorphic condition of this character, when compared with other Milichioidea and most Drosophiloids. However, he suggests (without providing reasons), that the condition in Canaceidae is to be regarded as secondary, the postverticals having been originally convergent here. Be this as it may, there is little justification for using the possession of divergent post-verticals in arguing a family's phylogenetic status, since post-verticals are found in this condition in at least a third of all Acalypterate groups.

Authors other than Hennig seem hardly to have considered the question of whether the Canaceidae represents a monophyletic group.

In the past, discussion of the taxonomic position of the Canaceidae has been concerned with the family's relation to the Ephydridae. Usually Canaceids are still placed next to this family, or even considered to be part of it: Cresson (1931), Malloch (1948), Curran (1934), Colyer and Hammond (1951), Oldroyd (1954), Imms (1957) and Harrison (1959). Only Wirth (1951, 1965 in Stone et al) and Hennig suggest that Canaceids are more closely related to families of Hennig's Milichioidea.

Although Hennig firmly asserts that the Canaceids are more closely related to other Milichioidea than to Drosophiloids, the reasons for his opinion are by no means clear. Only in the possession of divergent fronto-orbitals do Canaceids show a specialised condition common to other Milichioids, but absent from the Drosophiloidea. Hennig lists a number of other apormorphic characters in his definition of Milichioidea, which are usually present in Drosophiloids in a plesiomorphic condition. In the Canaceidae these characters (e.g. inter-frontal bristles) are in a state which is as reminiscent of many Drosophiloids as it is of Milichioids. The same may be said of the condition in Canaceids of features which Hennig uses to define the Drosophiloidea.

Hennig and Wirth disagree about the condition of one morphological feature in Canaceidae. According to Hennig there are only five abdominal segments in the male (based on a species of Xanthocanace), a fact which he uses in support of placing the family in Milichioidea. Wirth, in his world revision, says that Canaceids possess seven abdominal segments.

The Canaceid prothorax presents no unique structural features (see fig. 47). Pronotum and propleura are reduced to the condition found in most Acalypterate families. Precoxalia are absent, as is any trace of a trochantin. The presternum is relatively well developed, being a largish quadrate or triangular sclerite, fused at its anterior margin to the sella. The basisternum may form a precoxal bridge (variants W, fig. 47 and U, fig. 15), or is otherwise basiliform in shape (variant N: see fig. 59). Variant W is dominant for the family. Apart from Braula, the Canaceids are the only members of the Milichioidea that possess these sternal variants.

Elsewhere, variant W is dominant in Drosophilidae and present in Otitoidea (Otitidae), Nothyboidea (Strongylophthalmyiidae), Sciomyzoidea (Rhopalomeridae), Cryptochaetidae and Chloropidae. Variant N is otherwise found in only Drosophilidae and Otitidae and Variant U is peculiar to the Canaceids.

As the sternal variant dominant among Canaceids is widely distributed among Acalypterates and also occurs in a closely related superfamily, prosternal shape does not provide any immediate indication that Canaceid genera form a group distinct from related families. All three Canaceid sternal variants are closely related by shape though, so they cannot be said to show that the family is polyphyletic. Further, the average number of variants found in well-established Acalypterate monophyletic groups is four, so the presence of three in Canaceidae is not quite so disconcerting as it might appear at first (only ten species having been examined, despite the seven genera). Neither can the presence of two categories of variant (precoxal bridge and basiliform type) be taken as very significant when the shapes concerned are closely related, because much more satisfactorily established families (e.g. Diopsidae and Sciomyzidae) show a similar condition.

Assuming that Canaceid genera can be considered en bloc, the combination of sternal variants they possess can be used to explore the phylogenetic status of the group. Although Canaceid sternal variants are represented in both the Milichioidea and the Drosophiloidea (and Chloropidae), they are confined in Milichioidea to Braula and in Drosophiloidea to Drosophilidae. Judged by the situation found in other Acalypterate families (including those regarded as well-established monophyletic groups), if the Canaceidae no not represent a discrete monophyletic group, it is most surprising that none of their sternal variants are present in any family with which they might be combined on other morphological grounds. This forces the conclusion that the Canaceids do form a discrete group. The presence of a unique sternal variant in the family (U) implies the same thing.

The individual sternal variants found in the Canaceidae do not suggest any exact position for the family within the Milichioidea/Drosophiloidea/Chloropoidea complex. Thus the dominant variant (W) is found in all three superfamilies and variant U is restricted to the Canaceidae. However, among these families, variants W and N occur in combination only in the Drosophilidae and variant N is otherwise absent from the Milichioidea. These facts gain in significance for two reasons. Firstly, it is only marginally justifiable to retain Braula (the only Milichioid with sternal variant W, apart from the Canaceids) in Milichioidea (see under Braulidae). Secondly, the sternal variants present in Canaceids occur outside Milichioidea/Drosophiloidea/Chloropoidea only in four families (Cryptochaetidae, Otitidae, Strongylophthalmyiidae and Rhopalomeridae), to which it is very unlikely that Canaceids are related.

Only Hennig and Wirth (op.cit.) consider that Canaceids are closer to families in Hennig's Milichioidea, than to others he puts in the Drosophiloidea. Even though previous deductions have been partly based on a false premise: that Canaceids have a special relationship with the Ephydridae, judged by prosternal shape authors may well have been correct in concluding that Canaceids are closely related to Drosophiloid groups. Prosternal variation certainly does not support the idea that Canaceids belong in the Milichioidea as it is constituted at the moment.

In summary, Canaceid prosternal morphology helps to establish the family as a monophyletic group. It also suggests that while the Canaceids are placed logically somewhere in the Milichioidea/Drosophiloidea/Chloropoidea complex, their position in Milichioidea is suspect and a truer (or at least equally true) representation of fact would be to consign them to the Drosophiloidea.

TETHINIDAE(MILICHIOIDEA)

NO. GENERA EXAMINED: 2
NO. SPECIES EXAMINED: 11
STERNAL VARIANT: T

Eight genera, none of them large, are at present consigned to this family. Like Canaceids they are found in most parts of the World except New Zealand and are characteristic of littoral situations.

Most authors have treated the Tethinidae as a monophyletic group, though there has been controversy over such an idea. Attempts to establish the Tethinidae as monophyletic have been frustrated by the lack of unique features in Tethinid morphology, a limitation of so many of the so-called families of Acalypterates. Hennig (1958) suggests that the pair of epistomal bumps found in the family might perhaps be regarded as a characteristic apomorphic feature, but this is as yet insufficiently known for its phylogenetic significance to be assessed.

In earlier work, Hennig (1936) suggested that Rhicnoessa is related to the Ephydrids, while Malloch (1948) believed Pelomyia would eventually be placed the the Canaceinae (as a sub-family of Ephydridae) and Tethina in the Milichiidae. Melander (1951) includes all of these genera in Tethinidae and discusses the morphological basis for the differing opinions. He ends with the confusing statement that, "in view of such conflicting evidence the Tethinidae may be regarded as a single comprehensive family". Both Collin (1960) and Vockeroth (in Stone et al 1965) appear to accept Hennig's definition of this family, since they include Pelomyia, Rhicnoessa and Tethina here.

In a significant proportion of the morphological characters generally considered of some phylogenetic significance among Acalypterates, Tethinids resemble many families of Hennig's Milichioidea, Drosophiloidea and Chloropoidea. The difficulty lies in finding satisfactory evidence for any more precise alignment. Excluding Braula (see under Braulidae) from the discussion, Tethinids share with these other familes:

1. Presence of vibrissae.
2. Presence of a costal break at the end of the subcosta.
3. Convergent postvertical bristles.
4. Reduced anal vein.
5. A single composite sclerite between the fifth abdominal tergite and the hypopygium in the male (usually).

This combination of characters places the Tethinids just as reliably anywhere among these three superfamilies. Hennig puts the Tethinidae in Milichioidea because they possess inter-frontals and divergent fronto-orbitals. Tethinids share an additional feature with Milichoodae and Canaceidae (Hennig's Milichioidea s.s.). This is the triangular anal cell, which contrasts with the condition in Drosophilidae where it is rectangular. However, this is about the only real distinction between Tethinids and the Drosophiloidea (many Ephydrids possess both inter-frontals and divergent fronto-orbitals).

Other authors have not associated the Tethinidae with families of Hennig's Milichioidea. Colyer and Hammond (1951), Oldroyd (1954) and Imms (1957) agree in placing Ephydridae on one side of the Tethinids, but put different families on the other: Clusiidae, Opomyzidae and Chloropidae. Hendel (1922), using Frey's work (l.c.) on the mouthparts of the Schizophora, placed Tethinids and Milichiids in quite different superfamilies.

There is no morphological feature of the Tethinid prothorax (in Pelomyia and Tethina) that could be used to characterise the family. Only in the shape of the basisternum, which in all species (eleven) examined is referable to variant T (see fig. 59), does any prothoracic feature provide a basis for discussing Tethinid affinities.

As only two genera have been examined, little can be said about the questionable monophyletic nature of the family, However, since Tethina and Pelomyia possess the same shape of sternum, there is no support here for Malloch's contention that these genera belong in different families. In possessing a precoxal bridge, these genera resemble many other Milichioids, all Drosophiloid families and the Chloropidae: to all of which it has at various times been suggested that Tethinids are closely related. The specific sternal variant involved is prevalent among Drosophiloidea, but absent elsewhere among Milichioids. Outside the Drosophioidea, this variant occurs only in Tachiniscidae, Helcomyzidae and Chloropidae, from which Tethinids can be separated by a number of important characters.

In other words, the prosternal characteristics of Tethinids suggest that the family is as closely related to Drosophiloidea as to other Milichioidea: a situation also more or less indicated by general morphology. It certainly appears that the Tethinidae could with equal facility be put in either of these superfamilies. This must mean either that the family Tethinidae is polyphyletic, or that these superfamilies are closely related to each other.

SPHAEROCERIDAE (MILICHIOIDEA)

NO. GENERA EXAMINED: 21
NO. SPECIES EXAMINED: 80
STERNAL VARIANTS: J, S

The Sphaerocerids, or Borborids, make up a large, morphologically homogenous family of some 500 species, which is represented throughout the World. Their uniformity is reflected in the small number of genera recognised. A feature of the taxonomy of this family is subgenera, by which large genera like Leptocera are broken down into manageable units.

Sphaerocerid morphology is not only very uniform, but also includes a feature found throughout the family, which is sufficiently distinct and unique to establish the Spharoceridae quite firmly as a discrete monophyletic group. This is the enlarged hind basitarsus, by which Sphaerocerids can be separated from almost all other

Acalypterates. However, this character does not help to decide the affinities of the family.

By employing characters normally used to judge Acalypterate inter-relationships it is possible to conclude only that Sphaerocerids lie either somewhere in the Milichioid/Drosophiloid complex, or close to the Heleomyzidae/Trichoscelidae. Any attempt to be more specific is thwarted by the peculiar combination of characters that Sphaerocerids possess:

1. Inter-frontal bristles present, on inter-frontal plates.
2. Postvertical bristles (when present) convergent.
3. Vibrissae present.
4. Costa broken opposite the end of the subcosta, and often by the humeral cross vein as well. (Wings may be reduced or absent).
5. Sub-costa incomplete.
6. Anal vein reduced, anal cell (when present) complete and regularly rounded (i.e. not angular as in Drosophiloidea).
7. Male post-abdomen with one complex sclerite between tergite five and the hypopygium.

Hendel, basing his view on Frey's work on the mouthparts of Schizophora (l.c.), associated Sphaerocerids with the Ephydridae. Crampton (1944) suggests a similar relationship, basing his opinion on the genitalia. Hennig (1958) dismisses similarity in the mouthparts as probably due to convergence and, anyway, as insufficiently studied. He does not discuss Crampton's work, although he points out that the structure of the post-abdomen is similar in Sphaerocerids and Milichioids.

There is a general lack of firm feeling about the relationships of this family, which is demonstrated by the diversity of positions it has been given in systems of classification. Families belonging to the Nothyboidea (Nothybidae), Lauxanioidea (Periscelidae), Milichioidea (Canaceidae, Tethinidae) and Drosophiloidea (Drosophilidae, Ephydridae) have all been chosen for places next to the Sphaeroceridae in recent literature, so have the Heleomyzidae, Clusiidae and Asteiidae.

Although Hennig (1958) places this family in the Milichioidea, he suggests the relationship is only a loose one, relying as it does on "triviale Indizien". The features he cites to establish this relationship are: the regular nature of the anal cell and the presence of inter-frontal bristles on well defined inter-frontal plates: both of these characters are common to the other Milichioids (excluding Braula). Albeit not so well developed as in most Sphaerocerids, apparent inter-frontals are also found elsewhere, for example in Drosophiloidea, Chloropidae, Clusiidae and Anthomyzidae. Such sporadic occurrence limits their usefulness in determining relationships.

There is a number of problematic genera associated with this family. Protoborborus is put here by Malloch (1933), but this genus does not possess an enlarged hind basitarsus, and its systematic position is still in doubt. Brues, Melander and Carpenter (1954) separate Leptocera, Ceroptera and Nerea from the Sphaeroceridae because they have a humeral costal break (normally absent in Sphaeroceridae), putting them in a family "Leptoceridae". However, these genera do have an enlarged hind basitersus and other authorities do place them in the Sphaeroceridae.

In this family the ventral part of the prothorax is largely membranous, since prosternal plates are reduced so much that they only occupy the mid-line and there is no incursion into the area by pleural elements. Precoxalia and all evidence of a trochantin are absent. As in so many families, the ante-pronotum is vestigial (see fig. 50).

The Sphaerocerid presternum is somewhat variable in form. Behind it is normally contiguous with the basisternum, while in front it is fused to the sella of the cervical organ. In Copromyza it is large and more or less boat-shaped, but in Leptocera it is almost linear, though bifurcating posteriorly into a pair of short arms, each of which bears a noticeable tubercle. These two conditions represent the extremes.

In assessing the variation in form of the basisternum here, use has been made of information (both published and unpublished) gathered by Professor Richards. In a paper on the genus Mesaptilotus (1963), he discusses this plate in Sphaerocerids and its possible taxonomic use in the family, He says that, "in fully winged Sphaerocerids (it) is nearly always absolutely linear", but that, "in some flightless species......the prosternum is more or less broad and often blunt anteriorly". The former description corresponds with variant I as recognised here, the latter to variant S.

On the strength of this paper and evidence provided by unpublished data involving 53 species belonging to 20 genera, it was considered to be unnecessary to examine here as large a sample of Sphaerocerid species as has been taken in other families of a similar size. As a result, twenty six species, representative of seven genera (*Archileptocera*, *Sphaerocera*, *Copromyza*, *Archiborborus*, *Ceroptera*, *Antrops* and *Leptocera*) have been examined.

The shape of the basisternum is very stable throughout the family. It is always reduced, and either linear (variant I) or else short and expanded posteriorly giving a more or less triangular shape (variant S: see fig. 59). Variant A provides an intermediate condition.

Such a narrow range in the shape of the prosternum as is found in the Sphaeroceridae, does not occur in any other large Acalypterate family. This reflects the morphological homogeneity of the family and provides a further indication that the Sphaerocerids form a satisfactorily established monophyletic group.

Comparing the combination of sternal variants found in Sphaeroceridae with that in other Milichioid families,shows that there is little similarity between them. Precoxal bridges predominate in all of the other families and reduced sterna occur in only a few genera of the Milichiidae (*Phyllomyza* etc.). Looking outside the Milichioidea, reduced sternal variants are virtually unknown in the whole of the Milichioidea/Drosophiloidea/Chloropoidea complex, and characterise only Heleomyzidae/Trichoscelidae and Rhinotoridae of those families to which Sphaeroceridae could be related on general morphological grounds. This being so, any deductions about the relationships of the Sphaerocerids, based upon prosternal shape, must conflict with the views of both Crampton and Hennig (l.c.) However, these two authors differ widely in their placing of the family and other writers exhibit an even greater diversity of opinion, in which case this contradiction looses much of its significance. Professor Richards (pers.comm.) considers that Sphaerocerids occupy an isolated position: this would certainly provide a simple explanation of the confusion.

Summarising, the narrow range of prosternal variation found in this family provides added confirmation that the Sphaerocerids make up a monophyletic group. At the same time, the combination of sternal variants involved suggests a completely different picture of Sphaerocerid relationships from that produced by Hennig: the family may be related to Heleomyzidae/Trichoscelidae and seems definitely out of place in the Milichioidea.

MILICHIIDAE (MILICHIOIDEA)

NO. GENERA EXAMINED: 14
NO. SPECIES EXAMINED: 32
STERNAL VARIANT: G, Gb,Gt.

It is difficult to give any estimate of the size of this family, because comprehensive accounts of the group are lacking. Some idea can be gained from the fact that in Stone et al (1965) fifty two species belonging to 15 genera are recorded from North America, while 26 species are known to occur in Britain. In fact, genera consigned to the Milichiidae are found in all regions of the World, but few seem to contain many species: it is likely that many wait to be recognised, especially outside the Holarctic.

Known Milichiid larvae are either saprophagous or coprophagous and are usually associated with the nests of other animals, including Hymenoptera, birds and mammals.

This family is one of the most neglected among Acalypterates, the last general revision of the group being by Melander (1913), when it was still regarded as a sub-family and contained many genera now placed elsewhere. Hendel was the first author to give the group family status. In reality the Milichiidae comprises the genera which remained when the Agromyzidae (as recognised at present), plus a number of other distinct groups, were separated from an older and broader concept of Agromyzidae.

As yet, there is no known morphological character which establishes the Milichiidae as a monophyletic group. The family is divided into three sub-families, the Carninae, Madizinae and Milichiinae, and the inter-relationships between these groups remains a matter for controversy. Both the Carninae and the Milichiinae possess unusual features which suggest they are monophyletic groups. In the case of the Carninae (with parallel post-verticals, not found elsewhere in Milichioidea/Chloropoidea) this has been used by some authors to give the group separate family status; Hendel (1921), Brues, Melander and Carpenter (1954). The third sub-family, Madizinae, does not have any distinguishing features, and is recognised by its lack of the apomorphic characters which define the others.

At present the family Milichiidae is separated from other Acalypterates by the following combination of characters:

1. Post-verticals parallel or convergent.
2. Inter-frontal bristles present.
3. Costal breaks at both the humeral cross vein and the end of the sub-costa.
4. Anal vein much abbreviated.
5. Vibrissae present.
6. Only one composite sclerite between the fifth tergite and the hypopygium.
7. Anterior fronto-orbital bristles convergent.

These features occur, in combination, in genera belonging to about half of the families Hennig puts in Milichioidea/Drosophiloidea and Chloropoidea. Where this happens Milichiid genera are distinguished primarily by their lack of the apomorphic characters found in the other families (such as the plumose antennae of Drosophilids or the enlarged hind basitarsi of Sphaerocerids).

This family has been given a variety of positions in classificatory systems. Only Hendel (1916) and Malloch (1948) have associated Milichiids with any of the families Hennig consigns to the Milichoidea. Hendel erected a group similar to Hennig's Milichioidea, which also included the Agromyzidae, but no longer referred to such a group in later work. Malloch associated Milichiids with the Tethinidae. Other authors have adopted a traditional approach and placed Milichiids between the Agromyzidae and some other family; Curran (1934), Colyer and Hammond (1954), Oldroyd (1954). The second family chosen varies, including Odiniidae and Chloropidae.

In most of its features the Milichiid prothorax shows nothing distinctive (see fig. 48 and 49). The elements of the pronotum are vestigial and the propleura are undifferentiated from adjoining sclerites. However, well developed precoxalia are present in Milichiinae and Madizinae, though they appear to be absent in the Carninae. The presternum is evanescent in Milichiinae but present as a triangular piece in Madizinae and Carninae. In Australimyza it is lunulate.

The form of the basisternum varies between the different sections of the family. In Milichiinae and Madizinae it is of a very characteristic transverse and heavily sclerotised type: G (see fig. 48), Gt and Gb. Where a precoxal bridge is formed here, the sternum is attached to the propleura via the precoxalia, the suture between the plates often being well developed (see fig. 15). Amongst Milichiinae only Milichia dectes Collin shows a different type of sternum; variant H.

Basisterna of the Madizinae fall into two groups. Those of Desmometopa, Madiza, Leptometopa etc. are as described above, whilst Phyllomyza, Neophyllomyza and Paramyza have reduced sterna: variants B and L (fig. 59).

The basisterna of Meoneura (only genus of Carninae examined) are intermediate: variants H and F. As such they differ from those of both of the other subfamilies.

The aberrant genus Australimyza, placed in Milichiidae by Harrison (1953), exhibits a further sternal variant: C (see fig.59).

The Milichiidae is one of the few Acalypterate families in which all three categories of sternal variant occur. Further, the variants concerned are not very similar in shape to one another (see polar diagram, fig. 65) as they are in other families where this situation is found (for example the Sciomyzidae). The sheer number of different variants found is high (eight) and equals the highest number found in any Acalypterate family regarded as a well-established monophyletic group. These facts certainly do not support the idea that the Milichiids represent a monophyletic group. In fact, with the range of variation in prosternal shape which occurs among Acalypterates, the condition in Milichiidae probably represents the strongest possible evidence suggesting the group is polyphyletic.

There is more order to the distribution of prosternal variants between the different Milichiid sub-families. The variants found in Carninae are both basiliform, while those in the Milichiinae, although belonging to two categories, are closely related by shape. It is in the third sub-family, the Madizinae, that unrelated variants occur together (see polar diagram, fig. 65). The sterna of one section of the Madizinae resemble those of the Milichiinae, but the other, typified by Phyllomyza, has sterna of a type absent from the rest of Milichiidae, and, apart from the Sphaeroceridae, from the rest of the Milichioidea/Drosophiloidea/Chloropoidea complex. Among Milichiids, these sterna are most similar to those of Australimyza, whose sterna are also different from those of other Milichiids.

This situation argues that the position of at least Phyllomyza and its allies needs to be revised, and that Australimyza is also probably wrongly placed in the Milichiidae.

As it seems probable that this family is polyphyletic, it is necessary to discuss its relation to other Acalypterates part by part.

Seeing the predominance of precoxal bridges in the Milichioidea/Drosophiloidea/Chloropoidea complex, the state of the prosternum in the Milichiinae and the Leptometopa section of Madizinae suggests these genera are probably satisfactorily placed at present. Even so, the actual variants involved, especially associated with precoxalia as they are (absent elsewhere among these families), are rather different in character from those of the other Milichioidea/Drosophiloidea/Chloropoidea families, and could well represent a separate evolutionary line. The position of Carninae remains problematic since basilform sterna are found in this sub-family. These do not help to decide if the Carninae should be retained within Milichiidae. However, by being unspecialised, they certainly lend no support to the idea that Carninae should have separate family status. The reduced sterna of Phyllomyza etc. indicate that these genera may well be closer to the Anthomyzids, with which the Milichiids have been associated in the past.

In summary, prosternal variation in this family demonstrates that the group is probably polyphyletic and that while some Milichiid genera seem correctly placed in the classification system at present, others probably fall outside the Milichioidea/Drosophiloidea/Chloropoidea complex.

BRAULIDAE (MILICHIOIDEA)

NO. SPECIES EXAMINED: 1
NO. GENERA EXAMINED: 1
STERNAL VARIANT: W

The monotypic genus Braula is sufficiently distinct from all others of the Schizophora to warrant its segregation from them in a family of its own. Braula coeca Nitzsch is a commensal of the honey bee (Apia mellifera) and as such is found in most parts of the world. It has earned itself the common name of the "Bee louse".

The systematic position of this fly has long been in doubt: the specialisations it exhibits in both life history and structure make it impossible to use here many of the characters upon which Dipteran classification is based.

Borner (1908) related Braula to the Phoridae. Massonat (1909), Skaife (1921) and other authors have concluded its position is among the Pupipara, while Jobling (1936), Hendel (1936-37), Hennig (1938, 1958) and Imms (1944, 1957) reason that it should be put among the Acalypterates.

That Braula belongs among the Schizophora is determined by the fact that it possesses three-segmented antennae (Massonat, 1909) and a functional ptilinal suture (Muggenburg 1892, Skaife 1921). The genus is segregated from the Pupipara by the structure of its mouthparts (Jobling, 1936) and by being oviparous (Skaife, 1921). Despite this, the family Braulidae is still sometimes put among the Pupipara: as in Brues, Melander and Carpenter (1954).

Attempts to relate Braula to the Acalypterates have suggested that various families have a more precise relationship with the genus. Hendel (l.c.) places Braulidae in a group with the Agromyzidae, Coelopidae and Odiniidae. Imms (l.c.) suggests that Braula is most closely related to the Chamaemyiidae. Hennig (1938) included the family in a diffuse concept which incorporated both his later Milichioidea and Drosophiloidea and a number of other families:

Asteiidae, Periscelidae, Mormotomyiidae and Chloropidae.

Imm's conclusions upon the affinities of Braula are based on larval characteristics shared with Chamaemyiidae. Unfortunately, the features used by Imms are not diagnostic of Chamaemyiid larvae (K.V.G.Smith, pers.comm.). Further, four of the five features he quotes are characteristic of the mouthparts, so that the similarity could be due to symplesiomorphy. Finally, as Imms himself says, "no detailed description of any larva of the Chamaemyiidae" was available at the time of his work. Hennig (1958) considers there is more evidence to contradict Imms' view than to support it.

Hennig bases his discussion of Braula's phylogenetic position on characters of the postabdomen. He concludes the genus belongs in the Milichioidea because in the male there is only one composite sclerite between the fifth tergite and the hypopygium. This is a condition particularly characteristic of the families in the Milichioidea, but is found in a total of fifteen Acalypterate families. Hennig's views are summarised in the statement, "Alles in allem muss ich zur Zeit die Zugehorigkeit der Braulidae zu den Milichioidea fur am besten begrundet halten, wenn von einem eigentlichen Beweise, der strengeren Anforderungen genugen Konnte, auch Keine Rede ist".

The prothorax is found at an extreme of reduction in Braula, but its structure is not greatly different from that in other Acalypterates. Its sclerites are almost entirely confined to the antero-ventral face of the thorax.

The ante-pronotum is vestigial, remaining merely as a rim to the cervical cavity. This interpretation conflicts with that of

Hassanein and Abd-el-Salam (1962), who believe the dorsal surface of the thorax to be entirely covered by the pronotum, the pterothoracic terga being, "greatly reduced and usually concealed beneath the first abdominal tergite". These authors do not state why they came to this conclusion.

The functional antero-dorsal edge of the thorax is mesonotal, with the mesonotum curving down anteriorly onto the front of the thorax. Humeral calli are not distinguishable, though the antero-dorsal 'corners' of the thorax are perhaps homologous with the post-pronotum of other flies: the prothoracic spiracles lie high up under these corners, partly on the front of the thorax.

The only pleural suture visible is that marking the line of the pleuro-sternal apodeme. Precoxalia take part in the formation of a precoxal bridge.

In the cervical membrane the lateral cervicalia are reduced: so also is the cervical organ. The corniculae of the cervical organ are sclerotised.

There is no recognisable presternum, but the basisternum is quite normal and developed into a precoxal bridge, referrable to variant W (see fig. 59).

A compound sternellar plate (sternellum of prothorax, plus elements of the mesothoracic presternum) is well marked.

In this fly the members of each pair of thoracic coxae are widely separated in the mid-line. Apart from the Pupipara, the ptero-thoracic coxae of Schizophora are always in close apposition. The condition in Braula (as in Pupipara and other Diptera where this situation has been described) appears to be due to a secondary expansion of pleural elements, the true ptorothoracic sterna being internal. Thus no sutures mark off the apparent 'sterna' from lateral pleural elements, while the suture of the discriminal line continues posteriorly from the point of the pro-sternellar **triangle.**

Despite its specialisation, the prothorax of Braula shows nothing incompatible with the view that the genus is a specialised member of the Schizophora. That the family belongs among the Acalypterates is supported by the presence of a precoxal bridge, since this structure has not yet been found in either the Pupipara or the Calypteratae (except Scatophagids and Mormotomyia). The separated coxae found in both Braula and the Pupipara could be a symplesiomorphic character, associated with an ectoparasitic way of life.

The degree of reduction of the prothorax, the placing of the prothoracic spiracles and the separation of the ptero-thoracic coxae are unique characters which suggest Braula occupies an isolated position among Acalypterates. It is, in fact, hard to justify giving such an aberrant genus a precise position in any Acalypterate superfamily; especially on the basis of two characters found, in combination, in at least three different superfamilies.

MILICHIOIDEA: DISCUSSION

During the course of this systematic survey, six superfamilies are discussed in some detail. Apart from in the Milichioidea, Hennig's arrangement of these families is not radically contradicted by the new information provided by variations in prothoracic morphology. As the previous pages have shown, however, the variation in shape of Milichioid prosterna suggests the group is an unnatural one and could be broken in three as follows:

1. Tethinidae, Canaceidae and parts of Milichioidae.
2. Braulidae.
3. Sphaeroceridae and the remainder of Milichiidae.

Although Hennig puts these families together in one superfamily, it is difficult to know how much such a re-arrangement would conflict with his views. He points out that the Milichioidea is only a tentative grouping, with, as yet, very little solid foundation in fact. He also considers Sphaerocerids to be only loosely associated with the other Milichioids and says that Canaceidae/Tethinidae/Milichiidae form a more certain group within Milichioidea, to which he refers as the Milichioidea s,s.

Since Hennig is the only recent author to hold that these five families are in any sense closely related, the opinions of others do not present obstacles to dissolving the Milichioidea. On the contrary, other authors tend to separate Milichioid families in a way much more in agreement with prosternal data than with Hennig's grouping. Thus the Sphaerocerids have been given an isolated position and Canaceidae/Tethinidae have often been associated with both one another and Drosophiloid/Chloropoid families.

The place of Braula has always been problematic. No two authors seem to have the same opinion on the placing of this genus and attempts to place it precisely (including Hennig's) have only been marginally successful because of the inconclusive nature of their evidence. So, perhaps it is not surprising to find that thoracic morphology indicates Braula occupies an isolated position. It is true that the peculiarity of Braula is acknowledged anyway, in giving the genus the status of a separate family, but is this sufficient? For as long as the families of the Milichioidea/Drosophiloidea/Chloropodea complex are grouped as they are at the moment, this degree of isolation is probably not sufficient. Whether or no Braula is regarded as so morphologically aberrant that it should be given a superfamily by itself, the fact remains that the morphological clues allying it to this complex of families are not sufficiently precise to show where in the complex the genus belongs. In this situation, giving Braulidae a superfamily of its own is a simple alternative. Should it become accepted that most of the families in the Milichioidea/Drosophiloidea/Chloropoidea complex are best all consigned to one superfamily, then discussion of the position of Braula may well revolve around arguing the significance of its aberrant characteristics. These certainly present a problem, since here Braula differs from all members of the complex much more than they differ from other Acalypterates.

Probably the most unexpected deduction from this examination of prothoracic morphology, is that the family Milichiidae is polyphyletic. If Hennig suspected this he certainly has not said so, though he does comment that he doubts the validity of other families, particularly the Heleomyzidae. However, there is no justification for assuming enough is known about Milichiids for it to be possible to comment on the family's validity, since little work has been done on them since 1913, and there is no reason to suppose Hennig made a special investigation of the family. In other words, even if this family is polyphyletic, the fact could well have been missed until now. Unfortunately it has not been possible to examine the relationships between Milichioid genera in detail here, so that these deductions based on prosternal shape remain unsupported just as much as they are uncontested.

As it happens, even though the fact that the Milichiidae may be polyphyletic does not ipso facto affect the validity of the Milichioidea, the actual sternal variants present in part of the family (Phyllomyza etc.) are so different from these of the rest of the Milichioidea/Drosophiloidea/Chloropoidea complex apart from the Sphaerocerids, that they make the concept of the superfamily questionable.

These arguments reinforce the conclusion drawn from considering the families individually: that the superfamily is probably polyphyletic. This conclusion is further substantiated by comparing the combination of sternal variants found in Milichioidea with combinations found in other superfamilies. The sterna found in Milichioid families are so different from one another that all the families occupy different parts of the polar diagram (see fig. 65). In all other superfamilies, the combinations of variants characterising individual families overlap (see figs. 63 - 68). This overlap is sufficient both for a majority of the families to occur together at least once, and for most variants present to occur in more than one family in each superfamily. Another unusual characteristic of Milichioid prosternal variation is that all three categories of variant are found together in the one superfamily. Elsewhere, this only occurs in the Sciomyzidae, and there the variants concerned are all obviously related by shape (see fig. 63).

If it is to be accepted that the Milichioidea is a polyphyletic group, the question of the correct positions for Milichioid families then arises. This problem was discussed when Milichioid families were considered individually and the conclusions can be summarised as follows:

1. Canaceidae and Tethinidae to be added to Drosophiloidea.
2. Braulidae to perhaps be put in a superfamily by itself, or in Drosophiloidea.
3. Sphaeroceridae to be excluded from the Milichioidea/Drosophiloidea/Chloropoidea complex completely and placed near either Heleomyzidae or Anthomyzidae.
4. Placing of the Milichiidae to be left until an up-to-date revision of the family is available.

DROSOPHILOIDEA: INTRODUCTION

Hennig includes in this superfamily Camillidae, Curtonotidae, Diastatidae, Drosophilidae and Ephydridae. It is not a new idea that these families are closely related. The construction of most systems of Acalypterate classification indicates that other authors have held similar opinions.

Both Drosophilidae and Ephydridae are long-established names, which have suffered in the past as 'umbrellas', sheltering a number of distinct groups now recognised as families in their own right. Some of the families produced by the process of dissection are still retained in the Drosophiloidea, viz., Camillidae and Curtonotidae. Other families are excluded: Aulacigasteridae, Canaceidae, Cryptochaetidae.

The Diastatids have arrived in the Drosophiloidea from a different source. Initially this family was ill-defined and heterogeneous, so that its taxonomic position varied with the opinion of each author. As the family has become better known, it has been more consistently associated with the Drosophilidae s.l.

In Hennig's opinion, the Drosophiloidea is one of the most satisfactorily established of Schizophoran superfamilies. However, none of the features which he suggests can be used to characterise the group is quite restricted to it. Even in combination, they occur at least within the Milichioidea and the Chloropoidea. It is also true that these features vary in their expression among Drosophiloids (see following pages). These are the characters which Hennig uses:

1. Costa fractured at the end of the sub-costa.
2. Sub-costa fused to the first radial (R1) distally, or very close to it.
3. Anal cell small and vein Cu-1b recurved.
4. Anal vein abbreviated and not reaching wing margin.
5. Proclinate front-orbital bristles present.
6. Vibrissae present.
7. Post-vertical bristles convergent.
8. Only two spermathecae in the female (character so far investigated in only a few species).

It can be seen that this list is very similar to the one Hennig uses to define the Milichioidea. This is especially so when it is remembered that inter-frontal bristles and a reduced male post-abdomen, leaving a single composite sclerite between the fifth tergite and the hypopygium, are characters widespread among Drosophiloids and not restricted to the Milichioidea, where Hennig uses them in his definition of that superfamily. Because this is so, it is not surprising to find that Milichioids (and the Chloropidae) are among the families which other authors have most frequently associated with members of the Drosophiloidea.

EPHYDRIDAE. (DROSOPHILOIDEA)

NO. GENERA EXAMINED: 62
NO. SPECIES EXAMINED: 155
STERNAL VARIANT: T, Q/T

This is a large and cosmopolitan family, particularly characteristic of littoral habitats, river banks and pond margins. The larvae are aquatic or sub-aquatic. Up to seven subfamilies are currently recognised.

This family has been recognised as a discrete group for many years: Ephydrids possess a combination of distinctive morphological characters which not only segregate them from other Acalypterates, but also make them into one of the most satisfactorily established monophyletic groups among the Schizophora. These characteristics may be listed as follows:

1. Buccal cavity usually large, frons very arched and an apparent clypeus often distinct.
2. Vibrissae and postvertical bristles absent. There is widespread dissension over the interpretation of these characters. Whether or no the scattered oral bristles should be regarded as vibrissae, or the divergent bristles sometimes present on the dormal rim of the occiput are postverticals, the condition in Ephydridae is still distinctive.
3. Arista often plumose, and when so, haired on one side only.
4. Subcosta vestigial, fused with the first radial vein for the greater part of its length.
5. Costa broken both at the humeral cross-vein and by the end of the first radial.
6. Anal cell absent and anal vein reduced.
7. Abdominal spiracles lying in the tergites, abdominal spiracle seven absent in both sexes.
8. No sclerites intervening between tergite five and the hypopygium, in the male.

The first of these characters is found outside the Ephydridae only in Canaceids (see under Canaceidae), a fact upon which much emphasis has been put in the past. The last two characters appear to be unique to the Ephydridae, but they are based entirely on Hennig's own research, and he suggests that as yet it is not certain that they have been examined in enough species.

The rest of these characters place Ephydrid genera firmly among the families divided among Milichioidea, Drosophiloidea and Chloropoidea. They include the characters Hennig uses to define the Drosophiloidea.

Authors seem agreed that the family Ephydridae is a monophyletic group, but there is less uniformity of opinion about the family's closest relatives. Although the family is almost invariably put among others of Hennig's Milichioidea/Drosophiloidea/Chloropoidea complex, the precise position it is given varies with the author. Most often, Ephydrids are sandwiched between Canaceidae and Tethinidae, as in Colyer and Hammond (1952), Brues, Melander and Carpenter (1954) and Oldroyd (1954). Crampton (1944), who bases his groupings on the structure of the male genitalia, puts Ephydrids with the Sphaeroceridae, in a superfamily of their own, Curran (1934) associated Ephydridae with Chloropidae and Canaceidae, while Harrison (1959) puts them next to Opomyzidae and Canaceidae.

These associations strongly reflect the 'traditional' attitude that Canaceids and Ephydrids are related. Equally significant, though, is that at one time or another it has been implied that a close relationship exists between Ephydrids and all groups of the Milichioidea (except the Braulidae) and the Chloropidae, but not between Ephydrids and Drosophiloids.

The prothoracic region has been examined in sixty two genera, representative of all seven subfamilies which have been recognised in the Ephydridae. No consistent difference is noticeable between the prothoraces of members of these different sub-groups, so that variation in prothoracic morphology can be described without reference to them.

In the Ephydridae the head is closely opposed to the thorax. This phenomenon is particularly noticeable in certain genera, such as Peltopsilopa and Scatella. Such a characteristic makes interpretation difficult and in eleven genera (extra to the 62 mentioned above) interpretation was impossible.

As in so many Acalypterates the antepronotum is here no more than a rim to the cervical cavity, fading imperceptibly into the humeral calli. The calli are well developed, but only the line of the pleuro-sternal apodeme gives any indication of the extent to which they include prothoracic elements.

Nearly all sutures are lost in the pleural region, so that pleural sclerites are incompletely differentiated. A suture is sometimes present between the basisternum and the propleura, but this too is usually lacking leaving a wide, strong, precoxal bridge (see figs. 54, 55).

In this family the presternum is joined to the sella of the cervical organ and is usually a well formed transverse sclerite. It has no obvious connection with the basisternum posteriorly.

All 155 species of Ephydrid examined have precoxal bridges. Only four sternal variants can be distinguished, three of which (Q, fig. 60; Q/T, fig. 55; T, figs. 54, 60) merge into one another. The fourth type, variant X (see fig. 15), is known only in the apterous genus Synhoplos and does not occur outside the Ephydridae. This unusual variant does not appear to be correlated with the fact that the genus concerned is apterous, since Amalopteryx, another apterous Ephydrid, has a 'normal' Ephydrid sternum, variant T.

A feature of many Ephydrid sterna not noticeable in other Acalypterates, is the development of a ridge along the front margin of the sclerite; see diagram of Dimecoenia (fig. 6C). This is very pronounced in some genera, but absent in others.

Because the prothoracic morphology of Ephydrids is difficult to examine, its practical value to taxonomy is lessened. Nonetheless, the form of the prosternum does provide information about the phylogenetic position of the family.

Compared with the condition in most Acalypterate families, the range of Ephydrid sternal variation is very restricted. In this family a precoxal bridge is universally present, only four sternal variants occur (the average for a well-established family) despite the large number of genera examined) and these variants are all closely related by shape. Looked at in isolation this situation strongly supports the widely held view that the family Ephydridae is a discrete monophyletic group. However, because the variants present here are also present in families judged to be among the Ephydrids' closest relatives, these variants can only show that Ephydrid genera are closely related both to one another and to these other families. With the exception of the Sphaeroceridae and the Milichiidae, all families of the Milichioidea/Drosophiloidea/Chloropoidea complex share at least one sternal variant with Ephydridae. The same sternal variants do occur in other

Acalypterate families, but Ephydrids are separated from these by a number of morphological features. The closest resemblance to the combination of variants found in Ephydridae, occurs in Chloropidae, Drosophilidae and Curtonotidae. In this case, then, the prosternum does not help very much to determine the precise position of the family.

Summarising, variation in prosternal shape provides no basis for believing that the family Ephydridae is either polyphyletic, or wrongly placed as a member of the Drosophiloidea, but does not help either to determine the family's best place in the superfamily, or to provide characters which demonstrate that the Ephydridae is a discrete monophyletic group.

DIASTATIDAE (DROSOPHILOIDEA)

NO. GENERA EXAMINED: 2
NO. SPECIES EXAMINED: 8
STERNAL VARIANT: T

Few genera of Diastatidae are recognised and none of them contains many species. The genus Diastata has been found in Europe, Nepal, Japan and the Nearctic. Almost nothing seems to be known of the biology of the family.

Little attention has been paid to this scattered group of small flies and references to them are consequently confused and contradictory. As late as 1948, Malloch described a species of Diastata, in the sub-genus 'Spilochroa',as a result of which he put Diastata in the Heleomyzidae. Spilochroa (including Malloch's species), is now consigned to the Trichoscelidae and separated from Diastata completely. With anomalous genera like Spilochroa removed, the family Diastatidae has come to contain only Diastata, Campichaeta, Euthychaeta and Trypochaeta. Different concepts include genera otherwise consigned to the Curtonotidae (see under Curtonotidae). A third approach is provided by Oldroyd (1954) and Imms (1957), neither of whom recognise the family, putting Diastatid genera in the Drosophilidae. Hennig (1958) introduces yet another idea, by suggesting that Diastatids are perhaps closest to Ephydridae/Camillidae. Whichever of these courses is followed, Diastatids are now always put among Drosophiloid families.

Although Diastatids possess a range of morphological features which can be used to show that they are closely related to other families of Hennig's Drosophiloidea, they do not have any morphological character which demonstrates that they form a monophyletic group: Hennig (1958).

In the following combination of apomorphic morphological characters, Diastatids resemble other Drosophiloids, some Milichioidea and the Chloropidae, but differ from the remaining Acalypterate families (except some Heleomyzidae and Anthomyzidae):

1. Vibrissae present.
2. Postvertical bristles convergent.
3. Subcostal vein incomplete.
4. Costal break near the end of the first radial vein.
5. Anal vein reduced.

This list includes most of the features used by Hennig in his definition of the Drosophiloidea. The other definitive features (see under Drosophiloidea) are restricted to Diastatidae and other Drosophiloids.

Diastatids are distinguished from Ephydrids by the fact that they lack the unusual apomorphic characters of the other family. They differ from Camilla in having sternopleural bristles and are separated from Curtonotids only by the relative positions of proclinate and reclinate front-orbital bristles. Diastatids also lack a costal break by the humeral cross-vein: a plesiomorphic character which helps to segregate them from all other Drosophiloidea.

The prothoracic region of both Campichaeta and Diastata (see fig. 53) is uniform with those of a great many other Acalypterates. Pronotal and propleural sutures are incomplete, with the sclerites themselves showing a pattern of reduction repeated in many families. The sternal plates are, however, well developed. A transverse presternum intervenes between cervical organ and basisternum. The latter meets the propleura to form a strong precoxal bridge, which takes the shape of variant T in both genera.

This condition of the prothorax reveals nothing to support the suggestion that the Diastatidae is a distinct monophyletic group worthy of family status. Both genera possess sterna of the same shape, so they could well be closely related, but this particular variant is common to a majority of Drosophiloid families (see polar diagram, fig. 66). At least this demonstrates that Diastatids are probably closely related to the rest of the Drosophiloidea: a deduction which is in keeping with the general morphology of the 'family'. Looking outside the Drosophiloidea, sterna of the Diastatid type occur in Tethinidae, Chloropidae, Tachiniscidae, Heleomyzidae and Anthomyzidae. There is a close resemblance between the first two of these families and the Diastatidae in general morphology. As suggested elsewhere in this account, this is probably because both Tethinidae and Chloropidae are more closely related to all members of the Drosophiloidea than Hennig's grouping of Acalypterate families implies. It is doubtful that Diastatids are closely related to any of the other families that possess similarly shaped prosterna, because of the condition of other morphological features.

To summarise, there is nothing about the prothorax to suggest Diastatids are incorrectly placed as a part of the Drosophiloidea, though using the same evidence they could equally justifiably be put with Milichioids or the Chloropidae. Due to this same ambivalence, Diastatid prothoracic characters do not help to establish Diastatidae as a discrete monophyletic group, though they do imply that Diastatid genera are closely related to each other.

CURTONOTIDAE (DROSOPHILOIDEA)

NO. GENERA EXAMINED: 3
NO. SPECIES EXAMINED: 8
STERNAL VARIANT: Q, Q/T

As defined at present, the Curtonotidae is a small and essentially tropical group of flies. Curtonotum itself is Neotropical and Ethiopian, with one species extending into the Nearctic. Apsinota and Parapsinota, which may be included here, extend into the Oriental. Anaseiomyia is as yet known only from Malaya. Little is known about the biology of the group, but larvae of Curtonotum have been found in North Africa, acting as scavengers in the egg pod beds of Schistocerca (Acrididae): see Greathead (1958).

Almost without exception, Curtonotids have been treated as members of the Drosophilidae, in the past. The views of Brues, Melander and Carpenter (1954) make an exception. Here Curtonotum is regarded as a Diastatid, being put in a sub-family 'Curtonotinae' with Apsinota and Parapsinota. Duda (1935) appears to be the first author to put Curtonotum and its allies in a separate family.

Although Hennig uses the name Curtonotidae, he neither defines the content of his group, nor suggests why he has adopted this course. His only relevant statement is that the family cannot yet be established as monophyletic. He makes no mention of one of the most obvious characteristics of all Curtonotid genera: a greatly expanded mesonotum, which gives these flies a hump-backed appearance. Brues, Melander and Carpenter (1954)use this feature in defining their 'Curtonotinae'. Admittedly this character is not easy to define and like the eye-stalks of the Diopsidae varies in its degree of development in different genera. Even so, this is a character which Curtonotids do not appear to share with other Drosophiloids.

While Curtonotids do not possess any accepted apomorphic character which segregates them from other Drosophiloids, neither do they have any of the distinguishing features of any other Drosophiloid family. Thus interfrontal bristles are undeveloped, the oral aperture is normal, pre-apical bristles are present on all tibiae, the costa is pectinate, the sub-costa is well-developed, the anal cell and vein are present and there are seven tergites to the male pre-abdomen. This makes it very difficult to decide which of the other Drosophiloid groups contains the Curtonotids' closest relatives, whether or no the Curtonotidae is to be recognised as a distinct family.

The status and precise position of the Curtonotidae remain unclear, but there is little doubt that the group is correctly placed in Drosophiloidea. In nearly all characteristics they conform to Hennig's definition of the superfamily and differ only in possessing a well-developed sub-costal vein, which is distally free of the first radial.

The Curtonotids can be confused with certain Milichioidea and the Chloropoidea, using Hennig's definition of the Drosophiloidea. But Curtonotids lack specific apomorphic characters found in these families, and also have a humeral break in the costa: an apomorphic feature lacking in most of them.

In the Curtonotidae, the sclerites of the prothorax take up a smaller porportion of the thorax than they do elsewhere in the Acalypterates, and are almost confined to part of its anterior face. This is most obvious in side view (see fig. 5). The mesonotum is so expanded that it 'overhangs' the cervical region and occupies a major part of the front of the thorax.

The ante-pronotum is vestigial. It is almost divorced from the humeral calli by the sutures of the first phragma and pleurosternal apodeme, which nearly meet externally. The calli themselves are greatly developed, but sutures are incomplete so that their prothoracic content is unidentifiable.

The propleura show no distinctive features. As usual, the main sclerite of the sternal region is the basisternum, which here makes a precoxal bridge with the propleura (see fig. 52). In _Curtonotum_ and _Anaseiomyia_ this takes the shape of variant Q (figs. 52 and 6C) and in _Apsinota_ the shape of variant Q/T. A presternum is apparently present, in contact with both the basisternum and the sella of the cervical organ.

It can be seen that the construction of the Curtonotid prothorax remains as in other Acalypterates and presents no unique characteristics, although the mesonotum is so grossly enlarged.

The shape of the prosternum is the same in Curtonotids as in Diastatids and other members of the Milichioidea/Drosophiloidea/Chloropoidea complex, so it is of no assistance in establishing the family as a discrete monophyletic group. But the variants present in Curtonotidae are similar to one another in shape and both are precoxal bridge types (even though they are segregated from one another on the polar diagram: see figs. 62, 66). Because of this they do not show that Curtonotid genera are unrelated to each other.

Outside the Milichioidea/Drosophiloidea/Chloropoidea complex, the sternal variants present in the Curtonotidae are found only among Nothyboidea and Ctitoidea. Curtonotids are separated from families of these groups by a number of characters, so the prosternal resemblances are presumably due to symplesiomorphy. There is no justification for assuming that the similarity between the sterna of Curtonotids and other Drosophiloids is due to symplesiomorphy, since so many other morphological characters also indicate that these groups are closely related. However, seeing that the prosternal variants present in the Curtonotidae are widely distributed in this complex of families, prosternal shape does not help to decide the <u>precise</u> place of the family.

Prothoracic morphology is not, then, much help in establishing the phylogeny of the Curtonotidae. It does show that the group is well placed as a member of the Drosophiloidea, but provides no conclusive evidence that it is a monophyletic group worthy of family status. Neither does it help to show which families of the Milichioidea/Drosophiloidea/Chloropoidea complex are the Curtonotids' closest relatives.

DROSOPHILIDAE (DROSOPHILOIDEA)

NO. GENERA EXAMINED: 31
NO. SPECIES EXAMINED: 67
STERNAL VARIANT: W

This is one of the larger Acalypterate families, and is usually sub-divided into two sub-families, Drosophilinae and Steganinae. Many genera are known, distributed among all the zoogeographic regions of the World. Most of the known larvae are saprophagous.

The family name Drosophilidae is long established in Acalypterate systematics, and present concepts of the group have been achieved primarily by progressive exclusion of genera as the family became more precisely defined. Genera now put in the following families have in the past been regarded as Drosophilids:

Asteiidae
Aulacogasteridae
Camillidae
Cryptochaetidae
Curtonotidae
Diastatidae
Periscelidae

Various of them may still be included in Drosophilidae.

Despite the 'pruning' this family has received, Drosophilid genera have no feature in common to establish them as members of a monophyletic group distinct from other Acalypterate families (Hennig, 1958).

In the morphological characters normally used to compare Acalypterate families, Drosophilids resemble most closely families within Milichioidea/Drosophiloidea/Chloropoidea, and the Cryptochaetidae:

1. Costa with two breaks.
2. Subcosta incomplete.
3. Anal vein abbreviated with anal cell reduced in size.
4. Vibrissae present.
5. Proclinate anterior front-orbitals present.
6. Postvertical bristles convergent.
7. Only one composite sclerite between the fifth abdominal tergite and the hypopygium.

The Braulidae, Sphaeroceridae, Ephydridae, and Chloropidae are all recognisably distinct from Drosophilids, because they possess unique apomorphic features lacking in the Drosophilidae, but means of distinguishing the family from the other Milichioid/Drosophiloid groups are of doubtful phylogenetic significance (see under families concerned).

Most previous authors can be said to agree with Hennig in his assessment of the relationships of the Drosophilidae, since they normally included in Drosophilidae most of the families he consigns to his Drosophiloidea. However, the families which other authors have recognised as being closely related to the Drosophilidae s.l. are excluded from Hennig's superfamily. Thus Curran (1934), Colyer and Hammond (1952) and Harrison (1959) all place the Drosophilids next to Asteiidae. Crampton (1944) puts Drosophilidae and Chloropidae on their own in a superfamily and Malloch (1948) flanks the Drosophilidae with Chloropidae and Tethinidae. Opomyzidae, Agromyzidae and Sphaeroceridae have also been placed next to Drosophilidae.

Apart from in variations in the shape of the basisternum, the prothoracic sclerites in Drosophilidae remain much the same throughout the family. The pronotum and propleura are, as usual, incompletely differentiated (see fig. 51). The presternum is articulated to the cervical organ sclerite and contacts the basisternum behind.

A range of basisternal shapes occurs, but of the 31 genera examined, the vast majority (25) possess precoxal bridges, referrable to variant W (see fig. 51). Variants T and Q each occur in single genera. In addition, variants N (three genera), L (two genera) and F (one genus) are present (see fig. 6C). Of the six genera with basiliform sterna, only one, Cacoxenus (variant L), has previously had any doubt cast upon its position as a Drosophilid. The other genera appear to be typical Drosophilids, morphologically, and are scattered between both sub-families.

The condition of Drosophilid prosterna can be summarised as follows:-

1. Vast majority of genera with precoxal bridges. This includes two genera (Leucophenga and Chymomyza) in which some species do not have a precoxal bridge.

2. Four genera without precoxal bridges: Paraleucophenga, Rhinoleucophenga, Cacoxenus and Dasydrosophila.

Hennig concludes that at present it is impossible to find a morphological basis for supposing that the Drosophilidae is monophyletic. For a number of reasons Drosophilid prosternal variation does not help in this predicament. Firstly, the sternal variants involved are none of them restricted to Drosophilidae and half of them (the three precoxal bridges) occur in closely related families.

Secondly, the number of sternal variants in the family (six) is greater than the average number (four) present in well established Acalypterate families, though not so high as the average number (eight) for families that are doubtful. Thirdly, Chymomyza possesses two variants (F and T) absent from the rest of the family, without also possessing any of the variants which characterise other Drosophilid genera. Fourthly, the variants present in Chymomyza are a basiliform variant and a closely related precoxal bridge. So that, judged by the theory of evolution of basisternal shapes developed here, this precoxal bridge could have developed independently of the variants found in other Drosophilids.

Although prosternal variation does not provide a convenient means of establishing that the Drosophilidae is monophyletic, neither does it show at all convinvingly that the family is polyphyletic. Thus, very few Acalypterate families have unique sternal variants and in even fewer (Nothybidae and Conopidae) are unique variants dominant or unaccompanied by more widely distributed ones. Six sternal variants is not the maximum found in a well-established family, though it may be unusual. Also, it is only just within the range (four to fourteen) of numbers characterising doubtful families. The sternal variants found in Chymomyza may well be problematic, but those in the rest of the family are all closely related and not incompatible with one another. The fact that they do not all appear adjacent to each other on the polar diagram (see fig. 66) is here more a reflection of the inadequacies of the polar diagram than of actual dissimilarity of shapes (see fig. 60). It may well be of some significance that Leucophenga and its allies include a majority of the genera containing species without precoxal bridges,since they belong to the Steganinae. Most genera examined belong to the Drosophilinae. However, Stegana itself has the same sternal variant as most of the Drosophilinae.

This leaves the sternal variants present in the genus Chymomyza as the only data which seem incompatible with the idea that the Drosophilidae is monophyletic. Since in other morphological features Chymomyza is a perfectly ordinary Drosophilid, it does not seem possible to explain the form of its sterna by suggesting that the genus is wrongly placed. If Chymomyza is wrongly placed, then the morphological similarity between it and other Drosophilids would have to be explained as resulting from Symplesiomorphy, and the relation between a great many Drosophilid genera would then become suspect. But these other genera form a compact group, whether judged by general morphology or the shape of the prosternum: in which case if the general morphological resemblance were put down to symplesiomorphy, then the resemblance between Drosophilid sterna would also become suspect. It is far more logical to accept that Chymomyza is correctly placed in the Drosophilidae.

The fact that Chymomyza posses a pair of sternal variants otherwise absent from the Drosophilidae is far less perplexing than is the presence of the particular variants concerned. Most Acalypterate families contain a few genera with sternal variants not found in the rest of the family. However, when there is nothing anomalous about the general morphology of the genera concerned, their sternal variants are closely related to the others found in the family and do not carry any particular implications about the phylogenetic status of the group. Variants Q and L in Drosophilidae, come into this category.

The presence of variants F and T in Chymomyza suggests that the precoxal bridge has arisen more than once within the Drosophilidae. If so, it seems that most Drosophilid genera have arisen from a common stock possessing variant W, probably derived from variant N (both of these occur in Leucophenga). Other genera, scattered through the family, have retained variant N, or another basiliform variant, L. Only by means of very tendentious arguements could it be suggested that variant T in Chymomyza has also developed from variant N (or even variant L) when a more closely similar basiliform variant (F), is present in the same genus.

If T and W have originated from different basiliform variants in the Drosophilidae this is certainly unusual, since there is no evidence to suggest that different precoxal bridge shapes have had independent origins in any of the twenty three other families examined in detail in this survey. However, this is not to say that such a thing could not occur. As suggested in discussing the evolution of prosternal shape, the distribution of sternal variants among the Acalypterates shows that individual shapes have almost certainly evolved more than once, and that individual families have often evolved a number of related shapes. There is, therefore, no reason why different parts of a family, all originating from flies bearing a narrow range of basiliform sternal variants, should not develop different precoxal bridge shapes based on the specific basiliform variants they possess: whether or no the precoxal bridges developed are of a shape also found in other Acalypterate families.

This certainly provides an explanation for the various sternal shapes present in the Drosophilidae, without having to claim either that the family is polyphyletic, or that the proposed theory of the evolution of the prosternum is untenable.

The prosternal region provides less contradictory information about the relationship between the Drosophilidae and other Acalypterates. The only Drosophilid sternal variant absent from the rest of the Milichioidea/Drosophiloidea/Chloropoidea complex is L. This variant occurs elsewhere among Acalypterates only in families to which it is very unlikely that Drosophilids are closely related (various Otitoids and the Psilidae). The combination of variants found in Drosophilidae is most closely paralleled in the Canaceidae (N, W), Ephydridae (Q, T) and Chloropidae (Q, T, W). The only family in the complex not sharing any sternal variant with Drosophilids is the Sphaeroceridae.

There is no reason to doubt that these data demonstrate clearly that the Drosophilidae is correctly placed somewhere among these three superfamilies. But the prosternal region does not help to place the family more precisely. The same can be said of the general morphology of Drosophilids, even though Hennig uses this to put Drosophilidae in a group separate from all Milichioids and the Chloropidae.

Summarising, variations in prosternal shape do not help to establish the Drosophilidae as a monophyletic group. In fact, at first sight they give reason to suppose the family is polyphyletic, a deduction which appears spurious only when the situation is examined closely. Prosternal variation does show that the Drosophilidae is correctly placed somewhere in the Milichioidea/Drosophiloidea/Chloropoidea complex, but does not help to place the family precisely because all three superfamilies appear to be so closely related.

CAMILLIDAE (DROSOPHILOIDEA)

NO. GENERA EXAMINED: 1
NO. SPECIES EXAMINED: 3
STERNAL VARIANT: T

This family is monogeneric and almost confined to the Holarctic region. Less than a dozen species of Camilla are known and their biology remains obscure.

The idea that Camilla might warrant family status was introduced by Frey (1921), on the basis of his work on Acalypterate mouthparts. No author has yet discovered any additional features which support Frey's contention, unless the specialised condition of the female abdomen described by Hennig (1957) can be put in this category. But Hennig examined only one species of Camilla, and abdominal characteristics are very inadequately known in all Acalypterates at the moment, so it is impossible to know how unusual the postabdominal structure of Camilla is. Hennig has undermined the status of the Camillidae himself, by dismissing Frey's work as insufficient and the condition of the mouthparts in Camilla as plesiomorphic.

Hennig does not discuss the taxonomic status of the Camillidae, so if he does regard this family as a satisfactory, discrete, monophyletic group, his reasons remain obscure.

In Camilla most of the morphological characters used in comparing Acalypterates are the same as in other Drosophiloids, apart from where the other families exhibit individual apomorphic conditions of particular features:

1. Postvertical bristles are convergent.
2. Vibrissae are present.
3. Costa broken both by the humeral cross-vein and near the end of the subcosta.
4. Subcosta incomplete.
5. Anal cell incomplete and anal vein absent.
6. Only one complex sclerite between the fifth tergite and the hypopygium in the male.

In this combination of characters Camilla differs from all Acalypterates other than Drosophiloids. The features which help to segregate Camilla from other Drosophiloidea do not help to establish the status of Camillidae. Thus the genus is distinguished from the Drosophilidae by the following characters:

1. Mesopleural bristles present, sternopleurals absent: the converse of the situation in Drosophilids.
2. Anal cell and anal vein incomplete: at least the anal cell is complete in the Drosophilidae.

The first of these characters also helps to separate Camilla from Diastatids, but neither separate Camilla from the Ephydridae. According to Hennig, Camilla differs from Ephydrids only in plesiomorphic characters, and is therefore perhaps closer to Ephydrids than to Drosophilids:

1. Abdominal spiracles free in the pleural membrane: in the tergite in Ephydridae.
2. A segment interposed between the fifth and the hypopygium

in the male: nothing intervenes in the Ephydridae.

3. Postverticals convergent: Hennig suggests that the divergent postverticals of Ephydridae represent a secondary condition.

4. Oral aperture and clypeus normal: enlarged in Ephydridae.

By other authors Camilla is variously treated either as a member of the Drosophilidae: Sturtevant (1921), Brues, Melander and Carpenter (1954), Imms (1957), or as a separate family closely related to the Drosophilidae: Frey (1921), Duda (1935), Oldroyd (1954), McAlpine J.F. (1960).

In Camilla the antepronotum is differentiated only as a rim to the dorsal edge of the cervical cavity; pronotum and propleura are not present as distinct sclerites. Interposed between the sella of the cervical organ and the basisternum, and articulated to both, is a transverse presternum. The basisternum itself forms a precoxal bridge with the propleura, a well-defined suture marking the position where these sclerites meet. In shape the basisternum conforms to variant T (see fig. 61).

The prosternum of Camilla is not distinctive among those of other Drosophiloids: only in the Curtonotidae is sternal variant T absent. This means that the prosternal region provides no support for Frey's contention that Camilla should be put in a family by itself. However, none of the Drosophiloid families are clearly separated from each other by the shapes of their prosterna, so there is no reason why Camillid sterna should be unique. For the same reason, Camillid sterna give no definite indication of the genus's closest relatives among the Drosophiloidea: it would be equally possible to put

Camilla in Ephydridae or Drosophilidae, using prosternal shape.

There is nothing in Camillid prothoracic morphology to gainsay the practice of placing Camilla in the Drosophiloidea. Both sternal plates are of a form dominant within the superfamily, whatever form they take elsewhere (see polar diagram, fig. 66).

Outside the Drosophiloidea variant T occurs in Otitoidea, Heleomyzidae, Anthomyzidae, Milichioidea and Chloropidae. The first three of these groups may be readily distinguished from Camilla by a number of apomorphic characters and no author has ever suggested that the genus is closely related to any of them. Families of the other two groups show many similarities to all Drosophiloids, so there is no reason to suppose that Camillid prosternal shape indicates a special relationship with Milichioidea and Chloropidae, any more than with other Drosophiloids.

To summarise, prothoracic morphology does not help to consolidate the position of the Camillidae as a separate Acalypterate family, but gives clear support to the practice of placing Camilla in the Milichioidea/Drosophiloidea/Chloropoidea complex. At the moment there seems no justification for retaining a separate family for Camilla, but the prosternum is not much help in deciding to which other Drosophiloid group the genus is most closely related.

DROSOPHILOIDEA: DISCUSSION

All sub-groups of the Drosophiloidea share a combination of apomorphic characters which does not occur outside the Milichioidea/Drosophiloidea/Chloropoidea complex. In addition, the morphological characters which segregate Drosophiloid 'families' one from another are of such doubtful phylogenetic significance, that it is by no means clear that the various groups all warrant family status. It can at least be assumed from this situation that Drosophiloid 'families' are all closely related to one another. This means that the two main problems to be decided in this superfamily are: the number of Drosophiloid families that can be justifiably recognised and their relationship to the other members of the Milichioidea/Drosophiloidea/Chloropoidea complex.

The analysis presented in the previous pages shows that there is nothing about the prothoracic morphology of Drosophiloids to contradict the view that Drosophiloid families are all closely related. Various shapes of precoxal bridge predominate in all families and, apart from in Ephydridae (where one genus possesses a unique sternal variant), no family has prosternal variants which do not occur elsewhere in the superfamily. This great similarity between the prosterna of all Drosophiloids makes it difficult to find in prosternal variation, additional grounds for accepting each Drosophiloid family as a distinct group. This is especially so when nearly all Drosophiloid precoxal bridge variants are found together in a related family, the Chloropidae, which is one of the most well defined of all Acalypterate groups.

The case for each doubtful Drosophiloid 'family' has been argued in detail in previous pages. There appears to be some justification for regarding both Curtonotidae and Diastatidae as distinct groups, though the prosternum is of little help in solving the problem. The only aspect of prosternal variation which is of use here is the fact that the dominant variant in Drosophilidae:the family which might otherwise absorb both of these groups, is distinct from the variants they possess. There is less justification for segregating Camilla from Drosophilidae, and here the sternal variant is the same as that dominant among Drosophilids. On balance, it looks as though the family name Camillidae is best sunk under Drosophilidae, but that Curtonotidae and Diastatidae should be retained.

Time and again in discussing the families of the Milichioidea/ Drosophiloidea/Chloropoidea complex, it is necessary to conclude that there is very little basis for deciding the precise place of individual families within the complex. It can also be pointed out that in the main, this conclusion is forced not by indications that these families are unrelated to one another, but by signs, both from general morphology and the condition of the prosternum, that most of them are very closely related.

It is also true that Hennig considered his Milichioidea to be only a doubtful grouping and that many authors do not share his view that the Chloropidae occupies an isolated position. Because there is every reason to believe that Hennig's distribution of families between these superfamilies and the Drosophiloidea is unsatisfactory, an alternative arrangement is suggested here, which could give a better representation of the relationships involved:

1. Sphaeroceridae: separated from the other families of the complex and given closer association with Heleomyzidae/Trichoscelidae or Anthomyzidae.

2. Drosophiloidea: reconstructed, to contain:

Braulidae
Canaceidae
Chloropidae
Curtonotidae
Diastatidae
Drosophilidae (inc.Camillidae)
Ephydridae
Tethinidae

It would probably be equally acceptable to put Braula in a superfamily by itself.

This arrangement is compatible both with the general morphological state of these families and with the condition of their prosterna. The range of prosternal variation found in the new group Drosophiloidea is no greater than that displayed by any of the superfamilies erected by Hennig (see polar diagram, fig. 68), and holds together as well as any of them.

To summarise, Drosophiloid sternal variation is not very successful in determining the correct taxonomic status of doubtful Drosophiloid 'families', but is sufficiently characteristic to show that the Chloropidae and families from Hennig's Milichioidea (which appears to be polyphyletic), should be incorporated in Drosophiloidea rather than segregated from one another in different superfamilies.

CHLOROPOIDEA

CHLOROPOIDAE

NO. GENERA EXAMINED: 185
NO. SPECIES EXAMINED: 78
STERNAL VARIANT: T, W,

This is one of the largest of Acalypterate families, and contains a great number of genera of mostly small flies. Larvae of many species are phytophagous, in which case grasses are very often the host plant. Chloropids are found throughout the World.

Although there are so many genera in this family, their morphology seems to be sufficiently uniform and yet distinctive, for authors to have accepted the validity of the group without much discussion. This is despite the fact that Chloropids are not distinguished from other Acalypterates by possessing in common some unique, apomorphic character (but see Malloch's remarks, below).

Malloch (1948) summarised the family's characteristics as the following:-

1. Strong front-orbital bristles generally lacking.
2. Vibrissae absent.
3. Strong pleural bristles absent.
4. Subcosta incomplete.
5. Pre-apical dorsal tibial bristle absent.
6. Cross-vein separating discal and second basal cells in the wing, absent.
7. Vein M3/M4 nearly always with a flexure near the middle of the discal cell.
8. Anal vein and anal cell absent.

He added: "I have found some of these characters rather variable and propose to use in addition as criteria for the recognition of the family the following: Prosternal plate with a sharp anterior margin, in front of which the surface is abruptly precipitous, the propleura similarly margined at the anterior edge of its lateral exposure. (The) family is one of the most clearly distinguished in the Acalypterate, there being no other with the prosternal and propleural carinae".

Hennig uses Malloch's statement of these prothoracic characters as the key feature in his discussion of the phylogenetic status of Chloropidae. He states that without doubt apomorphic characters are involved, and that Chloropidae must therefore be regarded as a well-established monophyletic group. He does introduce a note of caution though, by commenting that he has had difficulty in interpreting these features himself. He also questions the number of species Malloch examined, when making these deductions.

Hennig uses the following additional features in characterising the Chloropidae:

1. Postvertical bristles convergent.
2. Ocellar triangle much enlarged.
3. Costal break near the end of vein R1.

Among the characters listed above, the Chloropids possess, in an apomorphic condition, a majority of those widely used in comparing Acalypterate groups. Such a combination does not occur elsewhere among the Schizophora. In itself, this is enough to justify regarding the Chloropidae as a monophyletic group. Nonetheless, Chloropids possess no unique apomorphic feature in common: Malloch's description of the Chloropid prosternum includes nothing which does not also apply to precoxal bridges in other Acalypterates, and the sclerite itself does not seem in any way peculiar (see below).

The combination of characters by which Chloropids are recognised is most closely paralleled in the Milichioidea and the Drosophiloidea: the Chloropids have often been placed among these families by previous authors. Hendel (1922) put Chloropidae in his 'Drosophilomorpha'. Curran (1934) sandwiches them between Tethinidae and Ephydridae, while Crampton (1944) puts Chloropidae and Drosophilidae together as the 'Drosophiloidea'. Chloropids are given a more isolated position by Oldroyd (1954) and Harrison (1959), where they are put at the end of the Acalypterate series.

Hennig nowhere states his reasons for isolating the Chloropidae in a superfamily by themselves. He appears to have taken this course because, although Chloropids are clearly related to both Milichioidea and Drosophiloidea and would fit with equal facility in either superfamily, it is difficult to justify making the choice between them. He comments that an equally good case can be made, to show that Chloropids are related to the Asteiidae: a theory he considers to be incompatible with the hypothesis that Chloropids are closely related to either Drosophilidae or Milichiidae.

In Chloropidae, the pronotal and propleural sclerites show the same degree of development as is found in Drosophiloid and Milichioid families (see fig. 56). In all species of the 78 genera examined, the basisternum makes a precoxal bridge with the propleura. The precise form of this bridge is variable: more so than in any other Acalypterate family. Thus some genera (such as Meromyza) exhibit sterna most easily referrable to variant V, whilst others (such as Siphonella), most closely resemble variant Q. A third variant (W) occurs in genera like Lipara. Variants Q/T and T are also present (see fig. 61).

Certain of these variants are much more frequent in the family than are the others. Thus T and Q are found in 22 and 49 genera, respectively. None of these various shapes appears to be more characteristic of the one Chloropid subfamily than of the other.

At first sight, Chloropid sternal variation seems to indicate that the family is polyphyletic, since here five types of precoxal bridge occur together when elsewhere among Acalypterates (apart from in Drosophilidae and Ephydridae) no more than two precoxal bridge variants are found in any family, suggesting an independent origin for most precoxal bridge variants. However, it has been argued (see under sternal evolution) that a given shape of prosternum can have a number of different origins, so, although the precoxal bridge may well be an apomorphic condition of the prosternum, it is possible for a given <u>shape</u> of precoxal bridge to be derived from either topologically similar basiliform variants, or from topologically similar precoxal bridges.

Seeing the number of genera examined (seventy eight), this family exhibits a narrow range of prosternal variation (only five sternal variants). Also, all Chloropid sternal variants belong to <u>one</u> category of sternal type (the precoxal bridge), which is believed to be apomorphic. At least in these characteristics Chloropid sternal variation resembles that found in the most satisfactorily established Acalypterate families, providing support for the idea that the Chloropidae itself is monophyletic. As precoxal bridges are widely spread among Acalypterates and none of the actual variants found in Chloropidae are restricted to the family, the prosternum does not, however, provide Chloropids with any <u>unique</u> apomorphic character.

It is most likely that the closest relatives of the Chloropidae are to be found among those families in which precoxal bridges occur, unless the precoxal bridge evolved among Chloropids after they diverged from other Acalypterates. Judging by the situation in other families, if the precoxal bridge had evolved in isolation in the Chloropidae, some genera should have retained a free prosternum, and the shapes taken by the bridge could well bear little resemblance to the bridge shapes found elsewhere. In fact, the combination of precoxal bridge shapes present in Chloropidae (see fig. 67) closely resembles that present in Ephydridae and Drosophilidae, and is even more similar to that found in the Drosophiloidea as a whole (see fig. 66). Such a combination is not found anywhere else among Acalypterates (apart from partially, in the Milichioidea), and many authors have concluded from a consideration of general morphology that Chloropids <u>are</u> closest related to either Drosophiloids or Milichioids.

It seems then, that variation in prosternal shape supports the generally held view that Chloropids belong among the Milichioid/ Drosophiloid families, but tends to show that evolutionarily, the family does not occupy the isolated position which Hennig ascribes to it. In fact, it looks as though Hénnig's subdivision of this complex into three superfamilies is an artificial one, and that a truer representation of the inter-relationships involved can be obtained by putting most of these families in one group (see under Drosophiloidea). Prothoracic morphology is of less use in assessing whether or no the Chloropidae represents a monophyletic group, because although it shows that Chloropid genera are probably closely related to one another it does not incorporate distinctive features isolating the family from its closest relatives, unless Malloch's character of the propleural carina falls into this category.

SYSTEMATIC SURVEY: SUMMARY

The general significance of deductions made about the systematic use of prothoracic morphology, during the course of this survey, does not depend upon the identity of the taxa they involve, but upon the character of the systematic changes they propose and the likelihood of achieving similar results in Acalypterate groups not covered by the survey.

Looked at in this way, the results of the survey can be summarised as follows:-

1. Forms of prosterna sufficiently distinctive to help distinguish a family group from all other Acalypterates, are rare. They were encountered in only one family (Conopidae) during the course of the survey. In other cases (Dryomyzidae, Coelopidae, Camillidae) the prosternum can provide strong indications that family status for a group, is not justified. More frequently (16 out of 23 families) the prosternum helps to show whether or no the members of a family are all closely related to one another, but fails to distinguish the family from closely related groups. This means that particular genera, like Apterosepsis, stand out as apparently wrongly placed, but their correct position cannot be decided because the prosternum suggests more than one alternative.

2. Families requiring some revision, as judged by prosternal variation,do not include any currently recognised as well-established.

3. Variation in prosternal shape provides a basis for discussing the relationships of each superfamily covered by the survey, but apart from in the Conopoidea, suggests either that

present superfamily groups are too narrowly based (Sciomyzoidea, Pallopteroidea, Drosophiloidea, Chloropoidea) or polyphyletic (Milichioidea).

4. Individual recognisably different shapes of the prosternum have only rarely proved of much systematic use at family and superfamily levels. The great majority of deductions have been made using combinations of prosternal shapes.

SECTION 4: GENERAL DISCUSSION

The general objective of this work has been to assess the potential use of prothoracic sclerites in solving problems of Acalypterate taxonomy and inter-relationships. To do this, the morphology of the prothorax has been surveyed, both to establish homologies of sclerites and to reveal which of them might be suitable for more detailed consideration. This approach led to an exhaustive study of the probasisternum, so that its potential contribution to Acalypterate systematics has been progressively defined by succeeding sections. But the general contribution of the thesis to the study of Acalypterates, has yet to be considered.

Whatever shortcomings the analysis of prothoracic morphology presented here may have, it does provide a system of nomenclature for prothoracic sclerites applicable throughout the Acalypterates, and based on current morphological theory. This overcomes the confusion left by a succession of previous authors who examined a limited range of forms and who concentrated their activities on specialised flies like Braula. It should be possible to correct remaining mis-interpretations without causing further problems, because care has been taken to ensure that individual sclerites have been given the same names in all species examined here, and many difficult species have been illustrated.

The morphological work also shows that whatever systematic use the prosternum is eventually put to, no other prothoracic sclerite has the potential to be generally useful in defining Acalypterate inter-relationships.

Unavoidably, most of this thesis has been devoted to describing and analysing the variability of the prosternum, so that the part which other sclerites can occasionally play in suggesting relationships has been somewhat obscured. Their occasional variations in form have been difficult to use in the past, because of uncertainty over the identity of the plates involved. They have nonetheless sometimes been used (e.g. see under Braulidae), with peculiar results. This survey should make it possible to take advantage of these variations in the future, though most of them are not easy to define. Invasion of the prothoracic region by the mesonotum (as in Curtonotum and Angitula) is probably the most characteristic and distinct of them.

A basis assumption which has been made here, is that before the contribution of a character to understanding inter-relationships can be assessed, it is necessary to distinguish between its apomorphic and plesiomorphic variants. Numerical Taxonomists may challenge this view but it is otherwise accepted. Hennig consistently stresses its importance.

Assuming Hennig and other systematists are correct, the parts of this account aimed at understanding the evolution of the prosternum are critically important. Subsequent discussion is largely dependent upon them for exposing ways in which the prosternum might help to demonstrate relationships between Acalypterates. Consequently, any shortcomings in this theory of prosternal evolution have inevitably influenced the conclusions produced and they must be regarded in that light. Even so, this theory provides a basis for discussion of prosternal evolution. In all other Acalypterate characters ways of distinguishing between plesiomorphic and apomorphic variants have never been discussed in any detail and theories of their evolution have so far been presented as blank statements of belief.

Here it has been attempted to establish the relationship between the evolution of prosternal shape and the evolution of Acalypterates. One source of error in judging the evolutionary significance of some prosternal shapes lies in the limitations of the system used to classify them. Even so, this system has provided a means of comparing the sternal variation found in different Acalypterate groups, and a plausible theory of prosternal evolution, so it would seem perfectly justifiable to use such an artificial classification system in investigations of other polymorphic characters, where the range of variation cannot be divided into discrete sub-units. A more refined system for classifying prosternal variation would probably only alter details of the arguement, changing the number of "variants" to be recognised, defining discontinuities in the "polar diagram" and in other ways providing a more precise understanding of the relationships between variants.

The polar diagram has been used here only to give a visual impression of the relation between variants of a single character, but potentially it has a wider application. It should be possible to prepare polar diagrams for a number of characters and build up from them a "polar family tree" of the organisms concerned. A polar diagram has an advantage over traditional family tree representations, that it can portray relationships between present day groups with less distortion. A disadvantage to using some form of polar diagram is the implication carried with it that the relationships it suggests are the only likely ones, since possible alternative arrangements cannot be indicated upon it. Here the relationship between sternal variants Q and Q/T is obviously inadequately expressed, but this could only be improved by including one of the variants in more than one place on the diagram.

Even if this theory of prosternal evolution is accepted, the practical value of basisternal shape to Acalypterate systematics still depends upon the sort of improvements that using it can be expected to produce. This has been tested in the systematic survey, which certainly suggested ways of improving the present structure of the classificatory system. However, it could be argued that support can be found somewhere in the literature, for almost any more or less feasible relationship between Acalypterate groups suggested by variation in any character, because of the diversity of opinion available. This problem is aggravated by the fact that the data forming the basis of an opinion has rarely been stated, so that it is often impossible to decide whether a recurrent opinion stems from a single author originating an idea, or from different authors arriving at the same conclusion independently. But this, in itself, is a criticism of the present system of classification and indicates where improvements are needed: in this circumstance data on the prosternum at least suggests where investigation of relationships might prove profitable.

The biggest changes suggested by the prosternum are in the superfamily arrangements. This raises the question of the suitability of available characters for use at the superfamily level.

Almost without exception characters used widely at the moment exist only in a single pair of alternative conditions. Because of this, when used individually they cannot divide Acalypterates into any more than two groups, one of which will possess the plesiomorphic condition of the character, the other the apomorphic condition. In order to achieve further subdivision such characters have to be used in combination, a practice which has produced two thirds of the sixty-odd Acalypterate "families" now recognised. In this situation it is not possible to erect major groupings of families without making subjective decisions upon the relative importance of characters (since families within such major groupings will share less characters with each other's genera than with their own), and without basing some superfamilies on plesiomorphic combinations, as Hennig (1958) was forced to.

In contrast the prosternum can exist in some 30 recognisably different conditions. These can be divided into three groups, two of which appear to be apomorphic and to a great extent mutually exclusive in Acalypterate families. As a result, the prosternum can potentially be used by itself to group families into superfamilies, as has been demonstrated. A feature of the superfamilies produced in this way is that they do not normally cut across Hennig's groupings (the exceptions are the Milichioidea and Nothyboidea), but suggest amalgamation of certain of them. It is at this point that discussion reaches an impasse. Use of dimorphic characters in combination produces one set of superfamily groupings, incorporation of data about a polymorphic character, prosternal shape, produces a second. Comparing these sets demonstrates the differences between them but gives no clear indication of which is more likely to be correct. It is true that dimorphic characters, either singly or in combination, seem to be intrinsically less capable of producing natural superfamily groups than polymorphic characters. But the fact that here comparison is forced between systems based on characters of different types means that the reliability of the prosternum remains uncertain. What is really required is superfamily arrangements based on two polymorphic characters to be compared.

Even if this limitation to the systematic survey shows that changes in present classificatory system suggested by the prosternum should be used with caution at the moment, it does demonstrate that polymorphic characters are likely to be the most profitable subjects for investigation of the relationships between Acalypterate families. It is also true that the large measure of agreement between both the arrangement and content of families accepted at present, and their counterparts suggested by the prosternum, shows that it would be wise to take prosternal shape into consideration in future discussions of relationships between Acalypterate families.

On balance it would appear that this form of systematic survey is a useful method of testing the capabilities of a 'new' character. Nonetheless, because of the shortcomings of this form of analysis, the accuracy of deductions made using the prosternum cannot be assessed until more data on other polymorphic characters becomes available. At the moment the prosternum appears to have some considerable ability to demonstrate relationships and it will probably be increasingly used by Acalypterate systematics in the future.

The possible use of the prosternum as a key character has not been specifically explored during the course of this work, but most prosternal shapes could be amply described using few words (or simply illustrated) and could help to distinguish between members of many families and genera, especially in Keys to regional faunas.

Perhaps the central contribution of this thesis to Acalypterate systematics has been to expose the prosternum as a morphological character which might be usefully exploited by systematists. On the other hand, until now there has been no record of any comprehensive investigation of any individual Acalypterate character, and the varying success of components of this investigation should help in the selection of lines and methods of study in future work. Equally, it has not previously been possible to see how ideas about Acalypterate phylogeny could be affected by polymorphic characters, because of insufficient data. Interest in them (particularly, perhaps, in the genitalia), could well be stimulated by the apparent potential of the prosternum for elucidating <u>inter-family</u> relationships.

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APPENDIX ONE : LIST OF GENERA EXAMINED

ARCHISCHIZA

CONOPIDAE	ST.VARIANTS
Aconops Krob.	H/Y
Archiconops Krob.	H/Y
Brachyglossum Rond.	H/C
Chrysidiomyia Krob.	H/Y
Conops L.	H/C, H, H/Y
Dacops Speis.	H/C
Dalmannia R.-D.	S
Heteroconops Krob.	H
Leopoldius Rond.	H/C
Melanosoma R.-D.	S
Microconops Krob.	H
Myopa Fab.	A, S
Neobrachyglossum Krob.	H/Y
Neobrachyceraea Szilady	H/Y
Neoconops Krob.	H/C
Paraconops Krob.	H/Y
Parazodion Krob.	A
Physocephala Schin.	H/C, H/Y
Physoconops Szilady	H/Y
Pleurocerinella Brun.	E
Pseudophysacephala Krob.	H/Y
Psilocephala Krob.	H/Y
Sicus Scop.	H
Stylogaster Macqt.	C, H, S
Thecophora Rond.	I
Zodion Lat.	I, S

MUSCARIA:ACALYPTERAE

MICROPEZIDAE (including TAENIAPTERIDAE & TREPIDARIIDAE of Hennig)

Anaeropsis Big.	S
Aristobata Frey	H, L
Calobatina End.	S
Calycopteryx Eaton	H
Cardiacephala Macqt.	H, S1
Cephalosphen Hennig	S
Cliobata End.	H, S1
Erythromyiella ?	S
Eurybata C.-S.	I
Glyphodera End.	I, S1
Gongylocephala Cz.	S
Grallipeza Rond.	S, S1
Grallomyia Rond.	H, Y
Grammicomyia Big.	S1
Hoplocheiloma Cresson	S, L
Hylobata End.	S
Metopochetus End.	S

MICROPEZIDAE (Cont'd).	**ST.VARIANTS**
Micropeza Mg.	I
Mimegralla Rond.	S
Nestima C.-S	I
Phaeopterina Frey	B
Plocoscelus End.	H, L, S1
Poecilotylus Hennig	H
Ptilosphen End.	F, Y
Raineria Rond.	Y, H, L
Scipopus End.	Y
Taeniaptera Macqt.	H
Trepidaria Mg.	F, H, L, S
Trepidariodies Frey	S
NERIIDAE	
Chaetonerius Hend.	I
Dictyonerius End.	A
Glyphidops End.	A
Gymnonerius	A
Longina Wied.	A
Nerius Wied.	A, I, Z
Oncopsis End.	A,
Paranerius End.	A
Rhoptrum End.	A
Stypocladius End.	A
Telostylinus End.	I
Telostylus Big.	I
CYPSELOSOMATIDAE	
Cypselosoma Hend.	S
Formicosepsis de Meij.	S
NOTHYBOIDEA	
MEGAMERINIDAE	
Megamerina	A
Texara	A
NOTHYBIDAE	
Nothybus Rond.	Z
DIOPSIDAE	
Centrioncus Speis.	A
Cyrtodiopsis Frey	R
Diasemopsis Rond.	R
Diopsina Curran	Y
Diopsis L.	R
Megalobops Frey	R

DIOPSIDAE (Cont'd)	ST.VARIANTS
Pseudodiopsis Hend.	R
Sphyracephala Say.	R, Y
Teleopsis Rond.	R
PSILIDAE	
Chylisa Fall.	D, L
Loxocera Fab.	L
Oxypsila ?	L
Platystyla Mg.	D
Psila Mg.	C, F, L
Schizostomyia Mall.	P
SOMATIIDAE	
Somatia Schin.	C
TANYPEZIDAE	
Neotanypeza Hend.	Q/T
Tanypeza Fall.	Q/T
STRONGYLOPHTHALMYIIDAE	
Strongylophthalmyia Hend.	W
CTITCIDEA	
PYRGOTIDAE	
Adapsilia Waga	C
Apyrgota Hend.	C
Campylocera Macqt.	C
Commoniella Paramonov	C
Epicerella Macqt.	C
Epicerina ?	C
Eupyrgota Hend.	C
Hyptotyphla Loew	C
Leptopyrgota Hend.	C
Nicholsonia Mall.	C
Plectobrachis ?	H
Prodalmannia Bez.	H
Prohypotyphla Hend.	C
Pyrgota Wied.	C
Pyrgotosoma Mall.	G
Ramuliseta Keis.	C
Tephritopyrgota Hend.	K,C
Teretrura Big.	C/P
Toxura Macqt.	X
Tylotrypes Bez.	C

PLATYSTOMATIDAE	ST.VARIANTS
Achias Fab.	O, Q
Achiosoma Hend.	Q
Agrochira End.	C
Amphicnephes Lw.	O
Antineura O.-s.	G, H
Asyntona O.-S.	G,O
Brea Walk.	C
Bromophila Macqt.	O/P
Celetor Lw.	C
Cleitamyia Macqt.	Q
Clitodoca Lw.	Y
Coelocephala Karsch	C
Conicipithia Hend.	H
Dasyortalis Hend.	Y, O/P
Engistoneura Lw.	H
Eosamphicnephes ?	O
Euprosopia Macqt.	O
Euthyplatystoma Hend.	C
Euxestomoea Hend.	Q
Icteracantha Hend.	Y
Laglaisia Big.	Q
Lamprogaster Macqt.	Q
Lamprophthalma Porsch	R
Lophoplatystoma Hend.	C, Q
Loxoceromyia Hend.	L
Loxoneura Macqt.	O, Y
Loxoneuroides Hend.	L
Lule Speis.	C
Mesoctenia End.	O
Mezona Speis.	Q
Naupoda O.-S.	O
Neoardelio Hend.	H
Neoepidesma Hend.	H
Ostracocoelia G.-T.	H
Palpomyiella Hend.	P
Parardelio Hend.	O
Parepicausta End.	Y
Paryphodes Speis.	O
Peltacanthina End.	H, O, Y
Phasiamyia Walk.	C
Philocomptus O. -S.	Y
Plagiostenopterina Hend.	C, R
Platystoma Mg.	Y, O
Poecilotraphera Hend.	G
Pogonortalis Hend.	H
Pseudorichardia Hend.	O, O/P
Pseudoscholastes ?	O
Pseudocleitamia Mall.	O
Pterogenia Big.	C
Rivellia R.-D.	F, H, O
Seleostenopterina Hend.	R

PLATYSTOMATIDAE (Cont'd)	ST.VARIANTS
Scholastes Lw.	O, Y
Traphera Lw.	O
Trigonosoma Gray	O
Valonia Walk.	O
Xenaspis O.-S.	R
Xenognathus Wall.	H
Xiria Walk.	F
Zygaenula Dol.	O

PHYTALMIIDAE

Angitula Walk.	O
Angituloides Hend.	O

TRYPETIDAE

Acanthiophilus Beck.	L
Acanthoneura Macqt.	E, H, L
Acidia R.-D.	H
Acinia R.-D.	H
Acinia R.-D.	H
Aciura R.-D.	H
Acrotaenia Lw.	L
Acrotaeniostola Hend.	M
Actinoptera Rond.	L
Antoxya Mun.	H, L
Adrama Walk.	L
Aethiothemara Hend.	H
Afreutreta Bez.	H, L, M
Afrocmeros Bez.	E, H
Allotrypes Bez.	H
Anastrepha Schin.	H, M
Axiothaumia Mun.	H, L
Bactropota Bez.	H
Baryglossa Bez.	H
Bistrispinaria Speis.	H
Blepharoneura Lw.	H, L
Braciaciura Bez.	H, L
Callantra Walk.	H
Callistomyia Bez.	M
Campiglossa Rond.	L
Carphotrichia Lw.	L
Carpomyia Rond.	L
Carpophthoromyia Austen	H
Carpophthorella Hend.	H
Celididacus Hend.	H
Ceratitis McLeary	H, J, L
Ceriocera Rond.	L
Chaetellipsis Bez.	H
Chaetorellia ?	L
Chaetostomella Hend.	L
Cheesmanomyia Mall.	E

TRYPETIDAE (Cont'd)	ST.VARIANTS
Chelyphora Rond.	H
Clusiosoma Mall.	E, H
Coelopacidia End.	M
Coelotrypes Bez.	B, N
Colobostroter End.	H
Conionota Mun.	H
Contradtina End.	H, M
Craspedoxantha Bez.	L
Cyanodesmops Mun.	H
Cyclopsia Mall.	H
Dacus Fab.	H, L
Desmella Mun.	H, L
Diarrhegma Bez.	H
Dicheniotes Mun.	H, L
Dimeringophrys End.	H
Dioxyna Frey.	H
(Diplochorda Sharp.	H, Y)
(Phytalmia Gerst.	H, P)
Ditrichia R.-D.	H
Elaphromyia Big.	J, L
Elgonina Mun.	B
Enicoptera Macqt.	H
Ensina R.-D.	H, J, L
Euleia Walk.	H
Euphranta Lw.	G, H, L
Euresta Lw.	H, J, L
Eurestella Hend.	L
Euryphalara Mun.	H
Eutreta Lw.	H, L
Eutretosoma Hend.	L
Felderimyia Hend.	H
Gastrozona Bez.	H, L
Gymnaciura Bez.	L
Hemiles Lw.	L
Hexachaeta Lw.	H, L
Hexacinia Hend.	H, L
Hoplobophormia Bez.	L
Hyaloctoides Mun.	L
Icterica Lw.	L
Insizwa Mun.	L
Isoconia Mun.	H, L
Katonaia Mun.	L
Lethyna Mun.	H
Leucotaeniella Bez.	H, L
Lucumaphila Stone	H
Meracanthomyia Macqt.	E, H
Mesoclanis Mun.	L
Migmella Mun.	L
Monacrostichus Bez.	H
Munroella Bez.	H
Munromyia Bez.	H

TRYPETIDAE (Cont'd)	ST.VARIANTS
Myiolia Rond.	H
Myiopardalis Bez.	H
Myopites Blot.	H
Namwambina Mun.	H
Neaspilota O.-S.	L
Noeeta R.-D.	H
Neosadrama Perk.	H
Neosophira Hend.	H
Neothemara Mall.	H
Nototrypeta Perk.	H
Ocnerioxa Speis.	H
Ocneros Costa	L
Oedaspis Lw.	H, L
Orellia R.-D.	H, L
Ortaloptera Edwds.	H
Oxyna R.-D.	H
Paracantha Coqt.	L
Paraciura Her.	L
Parafreutreta Mun.	L
Parahypaenidium Shir.	H
Paroxyna Hend.	E, H
Parasphensiscoides Her.	H
Pediapelta Mun.	G, H
Pelmatops End.	H
Perilampsis Bez.	H, L, M
Perirhithrum Bez.	H
Phalogramma Grims.	L
Phasca Hering.	L
Pherothrinax Mun.	H
Philophylla Rond.	H
Platensina End.	G, J, L
Platomma Bez.	H
Platyparea Lw.	H
Plaumannimyia Her.	L
Pliomelaena Bez.	H
Poecillis Bez.	H, L, M
Polionota v.d.W.	L
Polyara Walk.	H
Protephrites Shir.	L
Psednometopa Mun.	L
Pseudofreutreta ?	L
Pseudospheniscus Hend.	H
Pterops Mun.	H
Ptilona v.d.W.	L
Ptiloniola Hend.	H
Rabaulia Mall.	E
Rhabdochaeta de Meij.	L
Rhochmopterum Speis.	H
Rhacochlaena Lw.	H
Rhagocarpus Rond.	H, L

TRYPETIDAE (Cont'd)	ST.VARIANTS
Rhagoletis Lw.	L
Rhynchoedaspis Bez.	H
Rioxa Walk.	H
Rioxina Her.	H
Rioxoptilona Hend.	E, H, L
Rivelliomima Bez.	H
Schistopterum Beck.	L
Scleropithus Mun.	H
Seraca Walk.	E, H
Soedella Mun.	L
Soita Walk.	E, H
Sophira Walk.	G
Sosiopsila Bez.	H
Spathulina Rond.	H, L
Spenella H.-D.	H, L
Speniscomyia Bez.	H, L
Spilocosmia Bez.	H
Spilographa Lw.	H, M
Stenotrypeta End.	H
Taomyia Bez.	E, H
Taeniostola Bez.	H
Telaletes Mun.	L
Tephritis Lat.	H, J, L
Tephraciura Her.	H, L
Terellia R.-D.	L
Termitorioxa Hend.	E
Themara Walk.	H
Themarohystrix Hend.	H
Themaroides Hend.	H
Thematictera Hend.	G, H
Tomoplagia Coqt.	L
Toxotrypanea Gerst.	H
Trirhithrum Bez.	L
Trupanea Schr.	H, J, L
Trypanocentra Hend.	H
Trypanophion Bez.	M
Trypeta Mg.	H, L
Tylaspis Mun.	H
Urophora R.-D.	L
Vidalia R.-D.	H
Xanthaciura Hend.	H, L
Xanthorrhachis Bez.	H
Xanthorrhachista Hend.	E
Xanthotrypeta Mall.	H
Xarnuta Walk.	H, L
Xyphosia R.-D.	H
Zacerata Coqt.	L
Zonosema Lw.	M

RICHARDIIDAE	ST.VARIANTS
Automola Lw.	A
Coelometopia Macq.	A
Euolena Lw.	A
Melanoloma Lw.	A, C
Odontomera Macq.	A
Ozaenina End.	A
Paneryma v.d.W.	A
Richardia R.-D.	A
Richardiodes Hend.	A
Sepsiosoma Johnson	A, C
Setellia	A, C
Stenomacra Lw.	A
Zeugma Cresson	A

OTITIDAE	
Acrosticta Lw.	N
Anacampta Lw.	H
Atopocnema End.	L
Axiologina Hend.	N
Bothrometopa Hend.	K
Callopistromyia Hend.	K
Chaetopsis Lw.	H
Chrysomyza Fall.	L
Coelometopia Macqt.	C
Conopariella End.	L
Dasymetopa Hend.	D, K
Delphinia R.-D.	F
Dorycera Mg.	H
Eumecosomyia Hend.	B
Eumetopiella ?	A
Euphara Macqt.	O
Euxesta Lw.	H, N
Federeyella Frey	L
Herina R.-D.	H
Hypochra Lw.	H, O
Idana Lw.	F
Machaerocera Rond.	F
Megalaemyia Hend.	K, O/P
Melieria R.-D.	H
Myennis R.-D.	Q
Myrmecomyia R.-D.	F
Neoeuxesta Mall.	H
Notogramma Lw.	N
Oeciotypa Hend.	L
Oedopa Lw.	H
Otites Fall.	H
Paragorgopsis G.-T.	K, P
Plastotephritis End.	L
Pseudoeuxesta Hend.	N, O

OTITIDAE (Cont'd)	ST.VARIANTS
Pseudotephritis Johnston	G
Pterocalla Rond.	H, K, O, O/P
Pterocerina Hend.	K, P
Pterogenomyia ?	L
Pterotaenia Rond.	N
Ptilonota Lw.	H, L
Rhegmatosaga Frey	L
Rhyparella Hend.	K
Seioptera Kirby	H
Stictomyia Big.	H
Stylophthalmyia Frey	P
Terpnomyia Hend.	O/P
Tetanops Fal.	H, O
Timia Rond.	L
Ulidia v.d.W.	H, P, W
Xanthocrona v.d.W.	K
Zacompsia Coqt.	H

TACHINISCIDAE

Anthophasia Speis.	L
Tachiniscia Keretz	T

SCIOMYZOIDEA

HELCOMYZIDAE

Helcomyza Curtis	V
Heterocheila Rond.	V
Maorimyia Tonn. & Mall.	V
Paractora Big.	V

RHOPALOMERIDAE

Rhopalomera Wied.	W
Willistoniella Mik	W

COELOPIDAE

Apetaenus Eaton	V
Baeopterus Lamb.	B
Chaetocoelopa ?	A
Coelopa Mg.	A, B
Malacomyia Hal.	A
Protocoelopa Mall.	V

DRYOMYZIDAE

Dryomyza Fal.	A

SEPSIDAE	ST.VARIANTS
Apterosepsis Richards	T
Australosepsis Mall.	I
Lasiosepsis Duda	S
Nemopoda R.-D.	A, B
Crygma Mg.	A
Palaeopsepsis Duda	A
Paratoxopoda Duda	H
Saltella R.-D.	A, S
Sepsis Fal.	A, B, I, S
Themira R.-D.	A, B, H
Toxopoda Macqt.	A

SCIOMIZIDAE	
Dichetophora Rond.	A
Dichrochirosa Mall.	H
Dictya Mg.	B
Ethiolimnia Verbecke	B
Euthycera Mall.	H
Euthycerina Mall.	A, B
Hedroneura Hend.	B,H
Helosciomyza Hend.	A
Hoplodictya Cresson	B
Huttonina Tonn. & Mall.	H
Hydromyza R.-D.	B
Knutsonia Verbecke	B
Limnia R.-D.	B, H
Lunigera Hend.	B
Melina R.-D.	A, H, V
Notopherbellia Mall.	B
Pelidnoptera Rond.	R
Pherbellia R.-D.	B,H
PherbinaaR.-D.	B
Prosochaeta Mall.	H
Protodictya Mall.	H
Psacadina End.	B
Pseudomelina Mall.	B
Pteromicra Lioy	H
Salticella Rond.	B
Sciogriphoneura Mall.	A
Sciomyza Fal.	H
Sepedon Lat.	A, B
Tetanocera Duda	B, H
Tetanoceroides Mall.	B
Thecomyia Perty	B, H
Trypetoptera Hend.	H
Xenosciomyza Tonn. & Mall.	A

LAUXANIOIDEA	ST.VARIANTS
LAUXANIIDAE	
Cestrotus Lw.	W
Homoneura v.d.W.	Gb, H, W
Minettia R.-D.	H
Poecilohetaerus Hend.	H
Sapromyza Fal.	G, H, W
Steganopsis de Meij.	H
Trigonometopus Macqt.	W
CHAMAEMYIIDAE	
Acrometopia Schin.	H
Chamaemyia Panz.	H
Leucopella Hall.	C
Leucopis Mg.	C
Neoleucopis Mall.	C
Paraochthiphila Czerny	H
Plunomyia Curr.	H
PERISCELIDAE	
Diopsosoma Mall.	A
Periscelis Lw.	A
Schizochaeta Mall.	B
PALLOPTEROIDEA	
PIOPHILIDAE	
Amphipogon Wahl.	A
Mycetaulus Lw.	A
Piophila Fal.	A, C
Prochyliza ?	A
Protopiophila Duda	A, C
THYREOPHORIDAE	
Centrophlebomyia Fab.	A
Chaetopiophila Mall.	A
Thyreophora Lat.	A
NEOTTIOPHILIDAE	
Actenoptera Czerny	A
Neottiophilum Mg.	S
Tapeigaster Macqt.	A

PALLOPTERIDAE	ST.VARIANTS
Aenigmatomyia Mall.	C
Heloparia End.	A
Homaroides Mall.	H
Neomaorina Will.	H
Palloptera Fal.	H
Pseudopyrgota Mall.	A
Toxoneura Macqt.	H

LONCHAEIDAE

Carpolonchaea Hend.	S
Basiops Rond.	C, S
Earomyia Zott.	S
Lamprolonchaea Bez.	C
Lonchaea Fall.	C, S
Silba Macqt.	C, S

UNPLACED FAMILIES

AGROMYZIDAE

Agromyza Fal.	N
Phytomyza Fal.	W

HELEOMYZIDAE

Acantholeria Gar.	V
Aecothea Hal.	H, T
Allophylopsis Lamb.	A, H
Amoebaleris Garr.	V
Anastomyza Mall.	A
Aneuria Mall.	S
Anorostoma Lw.	V
Apophoneura Mall.	A, B
Blaesschaetophora Czerny	V
Cephodapedon Mall.	B
Chaetomus Cz.	B
Dihoplopyga Mall.	V
Eccoptomera Lw.	B, V
Fenwickia Mall.	A, B
Gephyromyza Mall.	A, S
Heloclusia Mall.	A, I, S
Helomyza Fal.	A, S
Heteromyza Fal.	V
Leria R.-D.	B, V
Mayomyia Mall.	K
Morpholeria Garr.	V
Neoleria Mall.	V
Notomyza Mall.	A, S
Prosopantrum Edwds.	V

HELEOMYZIDAE (Cont'd).	ST.VARIANTS
Scoliocentra Lw.	V
Suilla R.-D.	A, B, S
Tephrochlamya Lw.	V
TRICHOSCELIDAE	
Spilochroa Will.	C
Trichoscelis Rond.	A, C, S
RHINOTORIDAE	
Neorhinotora Schin.	A
Rhinotora Schin.	A
ANTHOMYZIDAE	
Amygdalops Lamb.	H
Anthomyza Fal.	A, H, T
Cyamops Melander	Gb
Ischnomyia Lw.	H
Melanthomyza Mall.	H
Paranthomyza Mg.	H
Stenomicra Coqt.	A, H
Teratomyza Mall.	A, S
OPOMYZIDAE	
Geomyza Fal.	B
Opomyza Fal.	A, B
AULACIGASTERIDAE	
Aulacigaster Macqt.	H
FERGUSONINIDAE	
Fergusonina Mall.	H
ASTEIIDAE	
Asteia Mg.	H
Leiomyza Macqt.	H
Phlebosotera Duda	H
CRYPTOCHAETIDAE	
Cryptochaetum Rond.	W

MILICHIOIDEA	ST.VARIANTS
SPHAEROCERIDAE	
Aluligera Rich.	I
Anatalanta Eaton	I
Antrops End.	I
Archiborborus Duda	S
Archileptocera Duda	I
Aubertinia Rich.	I
Binorbitalia Rich.	I
Ceroptera Mg.	I
Copromyza Fal.	I
Frutillaria Rich.	S
Howickia Rich.	S
Leptocera Oliv.	I
Mesaptilotus Rich.	S
Ocellipsis Rich.	S
Cribatomyia Rich.	S
Penola Rich.	I
Pismira Rich.	I
Scutelliseta Rich.	S
Sphaerocera Lat.	S
BRAULIDAE	
Braula Nitzsch	W
TETHINIDAE	
Pelomyia Will.	T
Tethina Hal.	T
MILICHIIDAE	
Australimyza Harr.	C
Desmometopa Lw.	Gb, Gt
Eccoptomma Beck.	Gt
Leptometopa Beck.	Gb
Madiza Fal.	G
Meoneura Rond.	F, H
Milichia Mg.	Gb, Gt, H
Milichiella G.-T.	Gb.
Neophyllomyza Melander	I
Paramyia Will.	I
Pareccoptomma Duda	Gt
Pholeomyia Bilimek	Gt
Phyllomyza Fal.	B
Risa Beck	Gb
CANACEIDAE	
Canace Hal.	W
Canaceiodes Cresson	N

CANACEIDAE (Cont'd)	**ST.VARIANTS**
Macrocanace Tonn. & Mall.	U
Nocticanace Mall.	U
Procanace Hend.	W
Trichocanace Wirth	W
Xanthocanace Hend.	W

DROSOPHILOIDEA

CURTONOTIDAE

Anaseiomyia Mall.	Q
Apsinota v.d.W.	Q/T
Curtonotum Macqt.	Q

DROSOPHILIDAE

Acletoxenus Fraun.	W
Amiota Hend.	W
Anacanthophila Duda	W
Cacoxenus ?	L
Chaetodrosophila Hend.	W
Chymomyza Cz.	F, T
Clastopteromyia Mall.	W
Dasydrosophila Duda	N
Drosophila Fal.	W
Gitona Mg.	W
Gitonides Knab.	W
Hirtodrosophila Mall.	W
Hypselothyrea de Meij.	W
Idiomyia Grimshaw	W
Leucophenga Mik.	N , W
Mycodrosophila Old.	W
Oxyphortica Duda	W
Paradrosophila Duda	W
Paraleucophenga Hend.	N
Parascaptomyza Duda	W
Phortica Schin.	W
Pseudiastata Coqt.	W
Rhinoleucophenga Hend.	L
Samoaia Mall.	W
Scaptomyza Hardy	W
Sphaerogastrella Duda	Q
Stegana Mg.	W
Stegophortica Duda	W
Tristanomyia Frey	W
Zaprionus Coqt.	W
Zygothrica Weid.	W

DIASTATIDAE

Campichaeta Macqt.	T
Diastata Mg.	T

CAMILLIDAE	ST.VARIANTS
Camilla Hal.	T

EPHYDRIDAE	
Actocetor Beck.	T
Allotrichoma Beck.	T
Amalopteryx Eaton	T
Athyroglossa Lw.	T
Atissa Haldy	T
Brachydeutera Lw.	Q/T
Ceropsilopa Cresson	Q
Chaetoscatella Mall.	T

(The family Ephydridae is continued on the next page).

EPHYDRIDAE (Cont'd)	ST.VARIANTS
Chlorichaeta Beck.	Q/T
Cirrula Cresson	T
Coenia R.-D.	T
Cyphops Jaenicke	Q/T
Dagus Cresson	T
Dichaeta Mg.	T
Diclasiopa Hend.	Q/T
Dimecoenia Cresson	T
Discocerina Macqt.	T
Discomyza Mg.	T
Ditrichophora Hend.	T
Dryxo R.-D.	Q/T
Ephydra Fal.	T
Gastrops Will.	T
Glenanthe Hal.	T
Gymnopa Fal.	T
Hecamede Haldy	Q/T
Hecamedioides Hend.	T
Homalometopus Beck.	Q/T
Hyadina Hal.	Q/T
Hydrellia R.-D.	Q/T
Hydrina R.-D.	Q
Ilythea Hal.	Q/T
Karema Cresson	T
Lamproscatella Hend.	T
Leptopsilopa Cresson	Q
Lipochaeta Coqt.	T
Lytogaster Beck.	T
Napaea R.-D.	T
Neoscatella Mall.	T
Nostima Coqt.	Q/T
Notiphila Fal.	Q/T
Ochthera Lat.	Q
Octheroides Will.	Q/T
Paraglenanthe Wirth	T
Paralimna Lw.	Q/T
Parascatella Cresson	T
Paratissa Will.	T
Parydra Sten.	Q/T
Pelina Hal.	Q/T
Phasiosterna Cresson	T
Placopsidella Keretz	T
Plagiops Cresson	Q
Polytrichophora Cresson.	T
Psilephydra Hend.	T
Psilopa Fal.	Q
Psilopina Beck.	T
Rhynchopsilopa Hend.	Q
Scatella R.-D.	T
Scoliocephalus Beck.	Q
Setasera Cresson	T
Stenochthers Hend.	Q/T

EPHYDRIDAE (Cont'd)	ST.VARIANTS
Synhoplos Lamb.	X
Teichomyza Macqt.	Q/T
CHLOROPIDAE	
Alombus Beck.	T
Anatrichus Lw.	Q/T
Anthracophaga Lw.	W
Aphanotrigonum Duda	W
Assuania Beck.	T
Batrachomyia Krefft	T
Botanobia Lioy	W
Cadrema Walk	W
Calamoncosis End.	W
Camarota Mg.	V, W
Cestoplectus Lamb.	W
Cetema Hend.	W, V
Chaethippus Duda	W
Chloromerus Beck.	V
Chloropisca Lw.	Q, W
Chlorops Mg.	T, W
Conioscinella Duda	W
Dactylothryea de Meij.	T
Dicraeus Lw.	W
Diplotoxa Lw.	T, W
Discogastrella End.	W
Echimba Duda	Q
Ectecephala Schin.	W
Elachiptera Macqt.	W
Elachiptereicus Lw.	T
Epicelyphus Beck.	W
Epichlorops Beck.	T
Epimadiza Beck.	V, W
Eurina Mg.	V, W
Eutropha Lw.	W
Formosina Beck.	Q
Gaurax Lw.	W
Goniaspis Duda	W
Goniopsita Duda	W
Haplegis Lw.	T, W
Hippelates Lw.	W
Homops Speis.	Q, Q/T
Hopkinsella Mall.	W
Lagarocerus Beck.	T
Lasiopleura Beck.	T, W
Lasiosina Beck.	V
Leptotrigonum Beck.	W
Liohippelates Duda	W
Lioscinella ?	Q, W
Lipara Mg.	W
Loxotaenia Beck.	Q
Melanum Beck.	V

CHLOROPIDAE (Cont'd)	ST.VARIANTS
Mepachymerus Beck.	T
Merectecephala Duda	Q/T
Meromyza Mg.	Q/T, V, W
Metopostigma Beck.	W
Mimosepsis Sabrosky	Q/T
Monochaetoscinella Duda	T
Oscinella Beck.	T, W
Oscinis Lat.	W
Oscinomorpha Lioy	W
Oscinosoma Lioy	T, W
Pachylophus Lw.	T, W
Parectecephala Beck.	W
Pemphigonotus Lamb.	T
Platycephala Fal.	T
Polyodaspis Duda	W
Pseudeurina de Meij.	W
Pseudogaurax Mall.	W
Rhodesiella Adams	W
Scoliophthalmus Beck.	V, W
Semaranga Beck.	Q/T
Siphonella Macqt.	Q, W
Siphonellopsis Strob.	T
Siphunculina Rond.	Q, W
Stegelocerus Beck.	T
Stenoscinis Mall.	W
Thressa Walk.	Q
Trachysiphonella End.	T
Tricimba Lioy	T
Trigonomma End.	W
Tropidoscinis End.	W

FIGS. 1-10: Various Acalypterates, lateral view of prothoracic region.

1. *Giraffomyia* (Platystomatidae).
2. *Nothybus* (Nothybidae).
3. *Plagiostenopterina* (Platystomatidae).
4. *Diopsis* (Diopsidae).
5. *Curtonotum* (Curtonotidae).
6. *Ochthera* (Ephydridae).
7. *Rainieria* (Micropezidae).
8. *Trepidaria* (Micropezidae).
9. *Micropeza* (Micropezidae).
10. *Angituloides* (Phytalmiidae).

FIG. 11: Giraffomyia (Platystomatidae), dorsal view of prothoracic region.

Abbreviations; Figs. 1-11:

apn: ante-pronotum.

epm: epimeron of propleuron.

eps: episternum of propleuron.

hc: humeral callus.

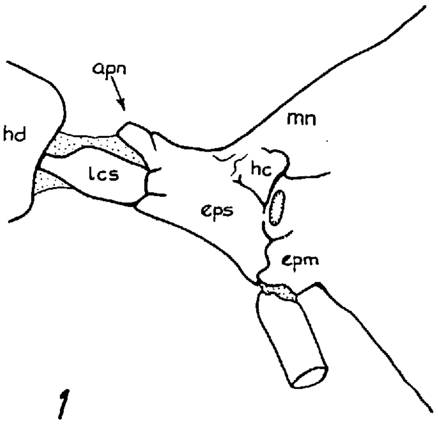
hd: head capsule.

lcs: lateral cervical sclerite.

mn: mesonotum.

sps: spiracular sclerite.

ppn: post-pronotum.



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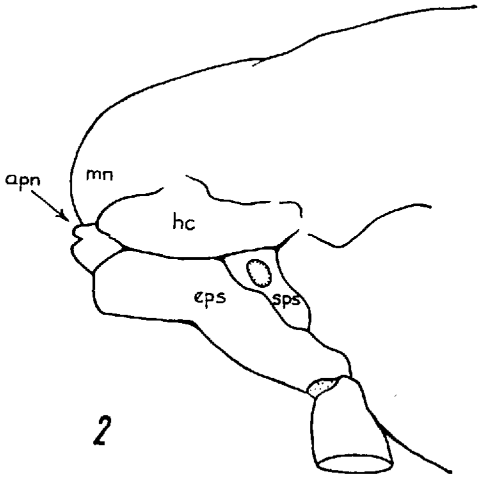

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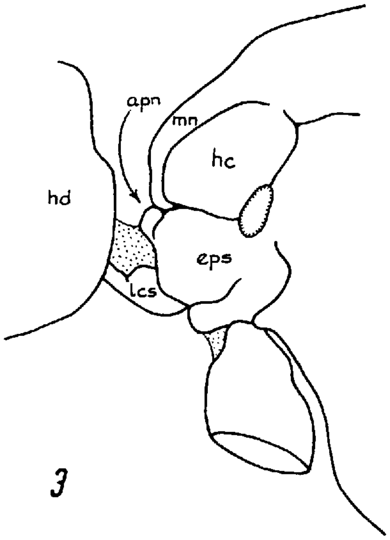

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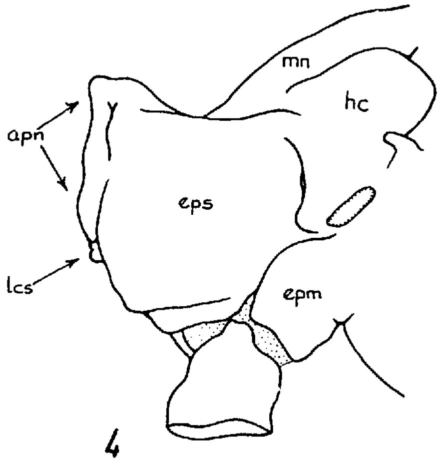

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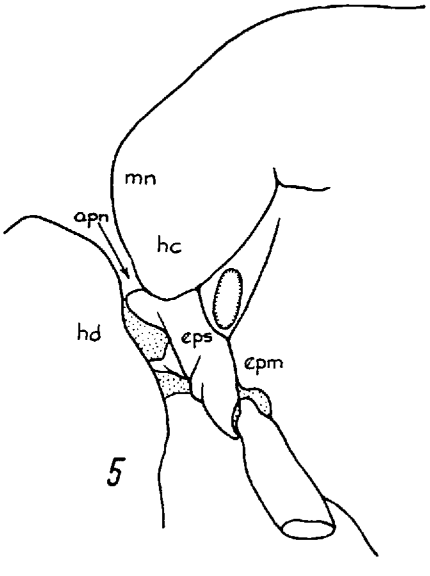

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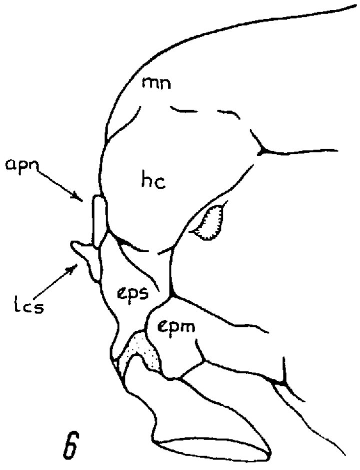
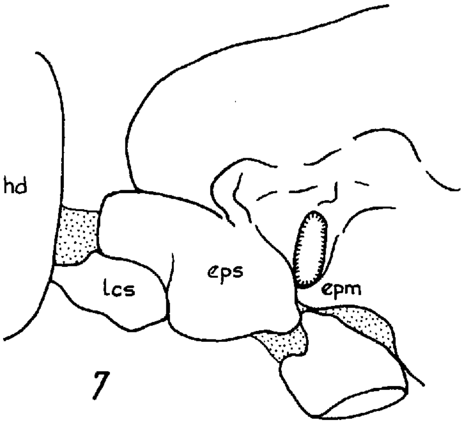


6

FIGS.1-6



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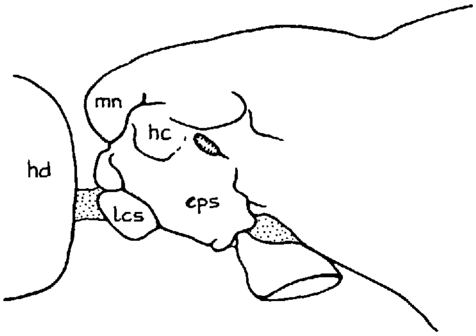

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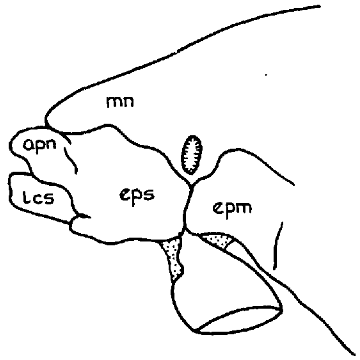

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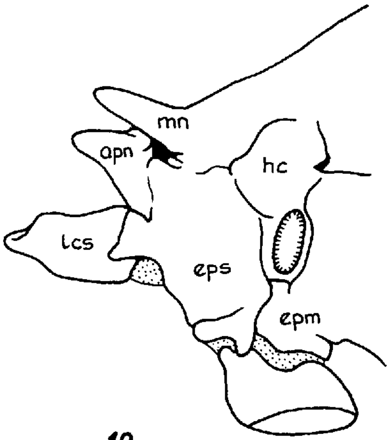

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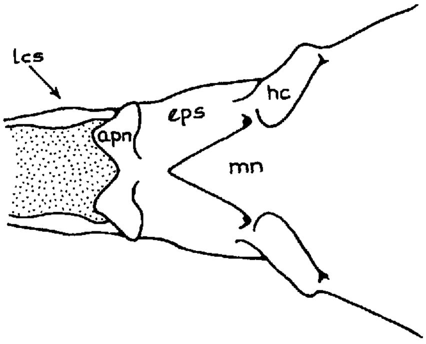


11

FIGS. 7-11

FIG. 12: Plagiostenopterina (Platystomatidae), ventral view of prothoracic region.

acs: anterior cervical sclerite.

apn: antepronotum.

bst: basisternum.

cc: cervical cavity.

cc_2: coxal condyle.

cm: cervical membrane.

co: corniculus.

cx: fore coxa.

epm: epimeron of propleuron.

eps: episternum of propleuron.

hc: humeral callus.

lcs: lateral cervical sclerite.

mf: median flap of cervical organ.

mn: mesonotum.

mp: mesopleur (antoepisternal part).

ps: pleural suture.

pst: presternum.

px: precoxale.

se: sella of cervical organ.

sp: spiracle.

spa: sterno-pleural apophysis.

ss: secondary sclerite.

stp: sternellar pit.

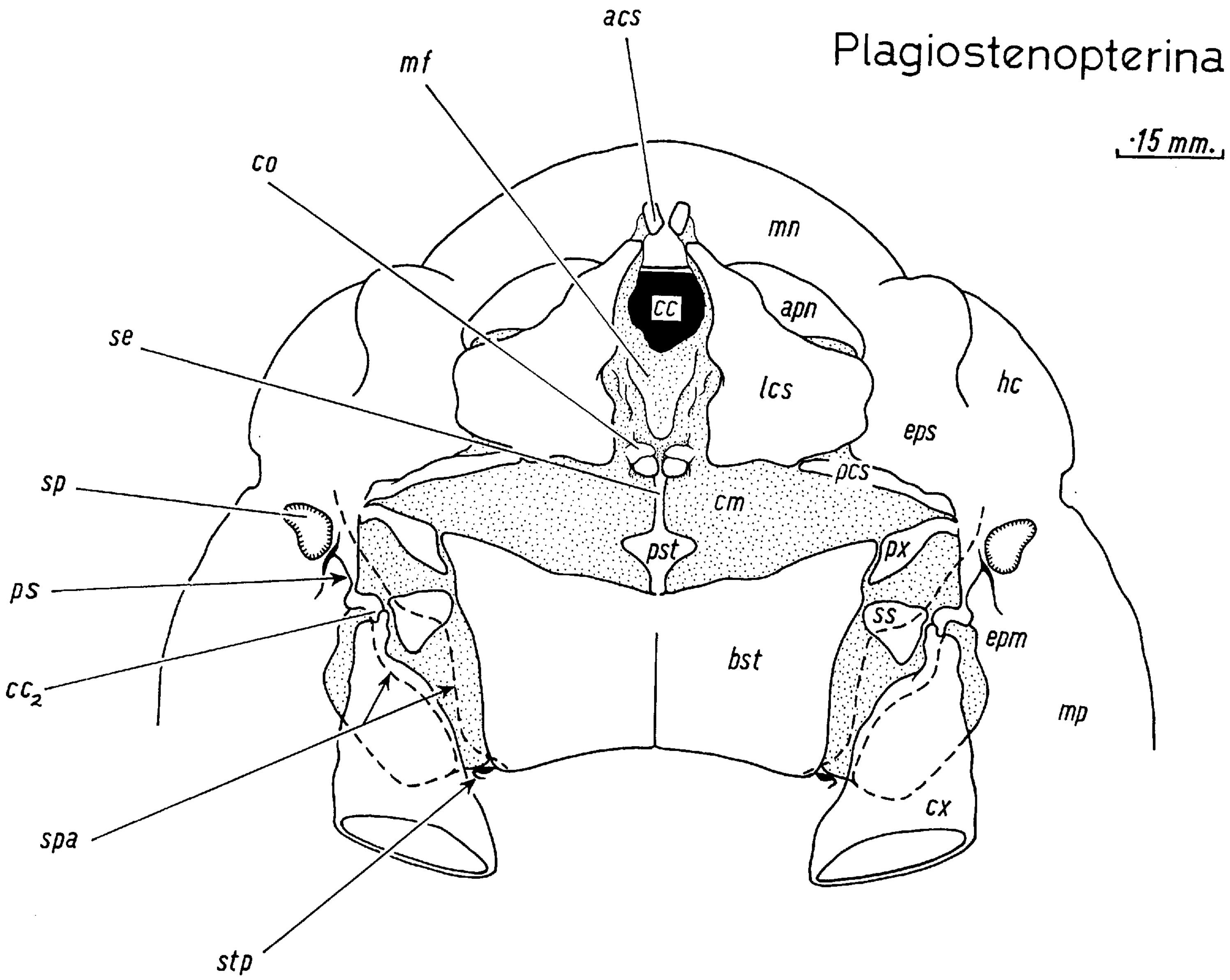

acs
Plagiostenopterina
mf
·15 mm.
co
mn
cc
apn
se
lcs
hc
eps
pcs
sp
cm
px
pst
ps
ss
epm
cc_2
bst
mp
spa
cx
stp

FIG.12

FIGS.13-15: The range of variation in prosternal shape found among Acalypterate Diptera.

Each of the shapes illustrated is regarded as representative of the sector of prosternal variation consigned to an individual 'sternal variant' (see text, p.36). The code letters used in these figures denote the same shapes when used in the text, and in the 'Polar diagram' (fig.62). More intermediate shapes (the 'sternal variants' to which they have been allocated is indicated) are illustrated in figs. 57-61.

ST.VARIANT	REPRESENTATIVE SPECIES
A	Eumetopia rufipes Macqt. (Otitidae)
B	Baeopterus robustus Lamb. (Coelopidae)
C1=C	Epicerlla punctulata Hend. (Pyrgotidae)
C2=C	Pyrgota undata Wied. (Pyrgotidae)
D	Chyliza munda (Walk.) (Psilidae)
E	Adrama determinata Walk. (Trypetidae).
F	Xiria cholobaphes Hend. (Platystomatidae)
G	Antineura kerteszi de Meij. (Platystomatidae)
G_t	Desmometopa sordidum (Fal.) (Milichiidae).
G_b	Milichia speciosa Mg. (Milichiidae)
H	Prodalmannia variabilis Bez. (Pyrgotidae)
I	Sepsis lateralis Wied. (Sepsidae)
J	Platensina sumbana End. (Trypetidae)
K	Pterocalla strigula Lw. (Otitidae)
L	Plastotephritis pannosa End. (Otitidae)
M	Myopites delottoi Munro (Trypetidae)
N	Euxesta apicalis Will. (Otitidae)
O	Loxoneura decora Fab. (Platystomatidae).
O/P	Bromophila caffra Macqt. (Platystomatidae).
P	Phytalmia alcicornis Saund. (Trypetidae).
Q	Duomyia obscura Walk. (Platystomatidae)
R	Sphyracephala hearseiana Westwood (Diopsidae)
S	Cypelosoma gephyrae Hend. (Cypselosomatidae)
Q/T	Parydra fossarum (Hal.) (Ephydridae)
T	Ephydra micans Hal. (Ephydridae)
U	Nocticanace peculiaris Mall.(Canaceidae)
V	Protocoelopa philpotti Mall.(Coelopidae).
W	Ulidia erythrocephala Mg. (Otitidae)
X	Synhoplos neglectus Lamb. (Ephydridae)
H/Y	Physocephala rufipes Fab. (Conopidae)
Y	Platystoma seminationis L. (Platystomatidae)
Z	Nothybus longithorax Rond. (Nothybidae).

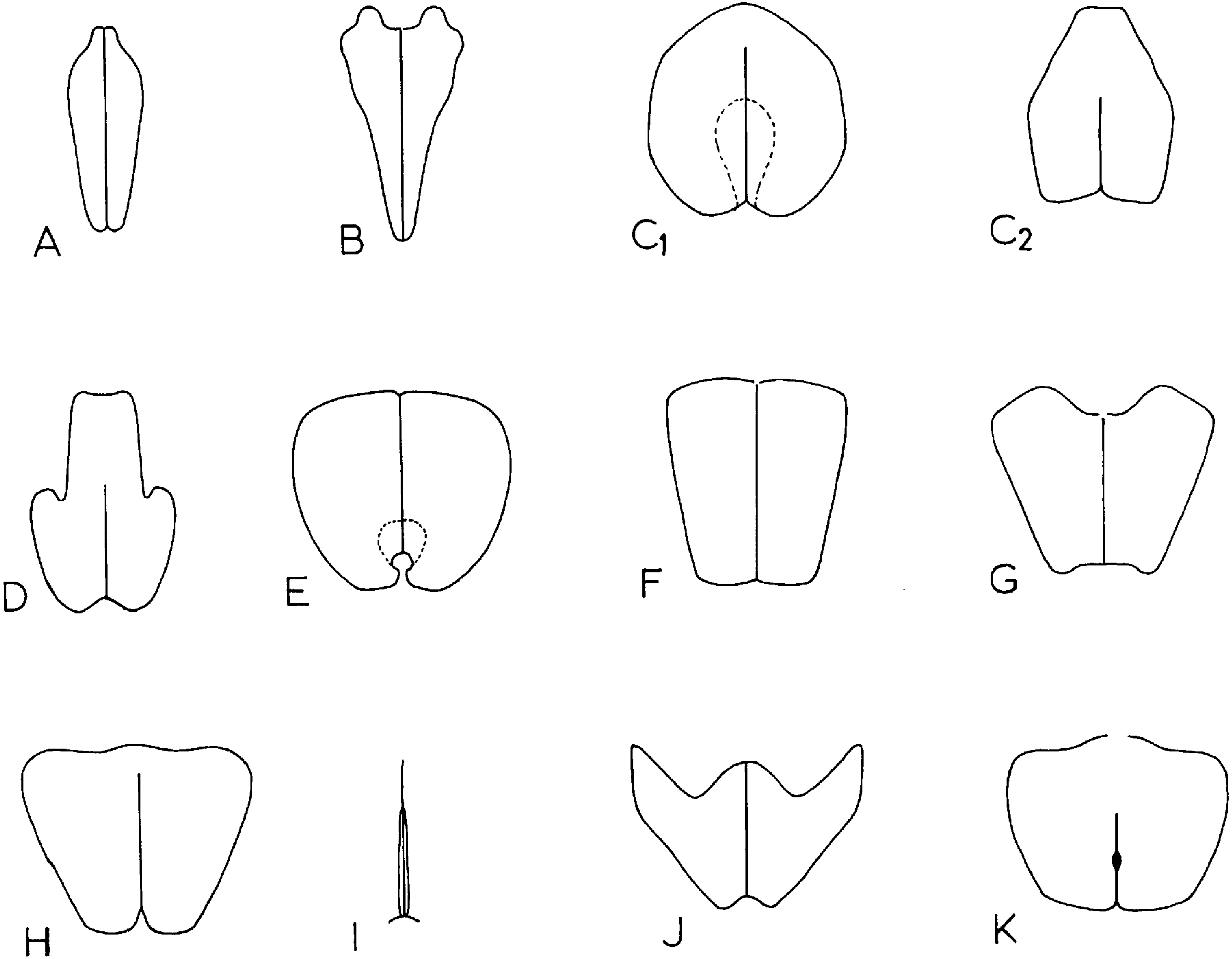


FIG.13

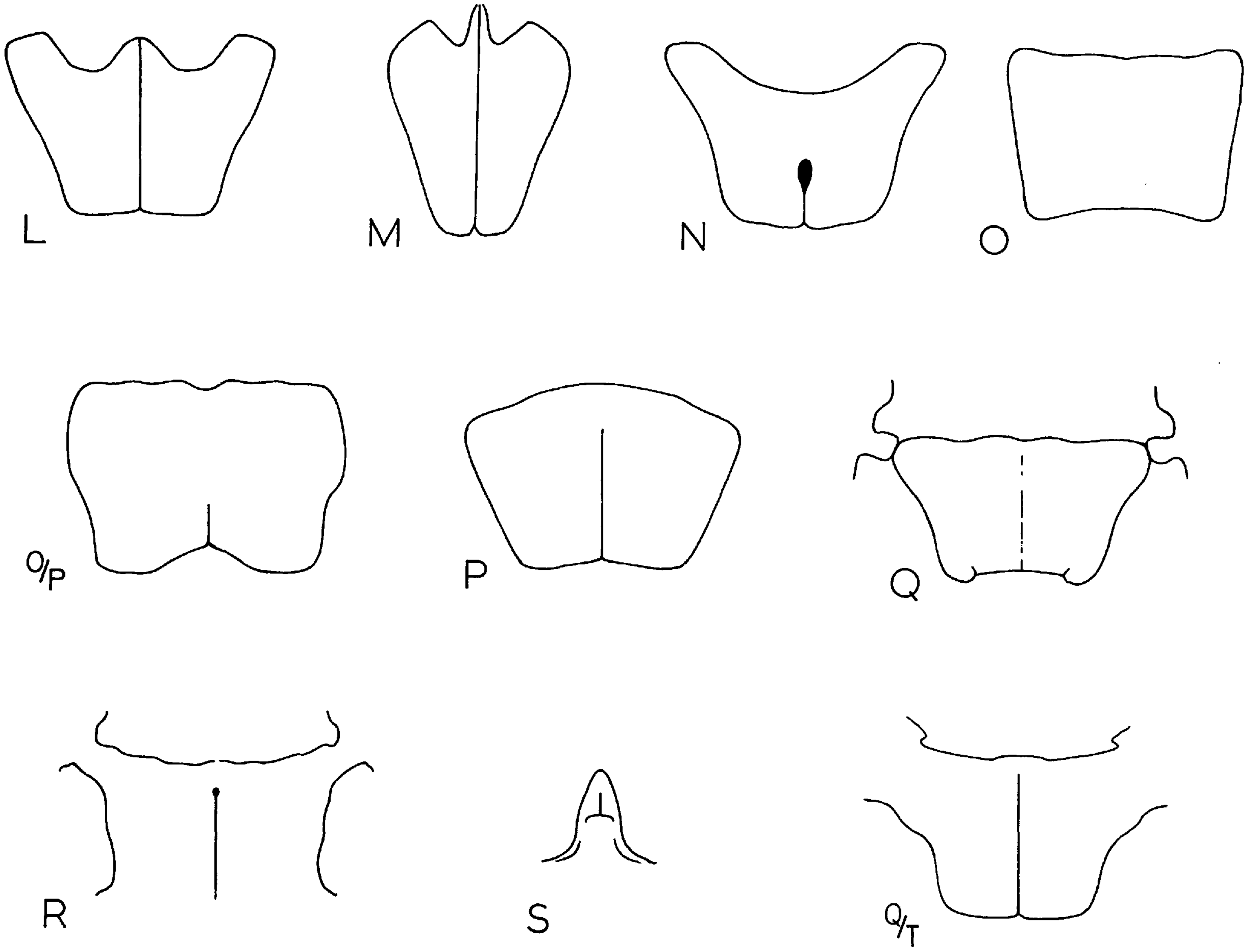


FIG.14

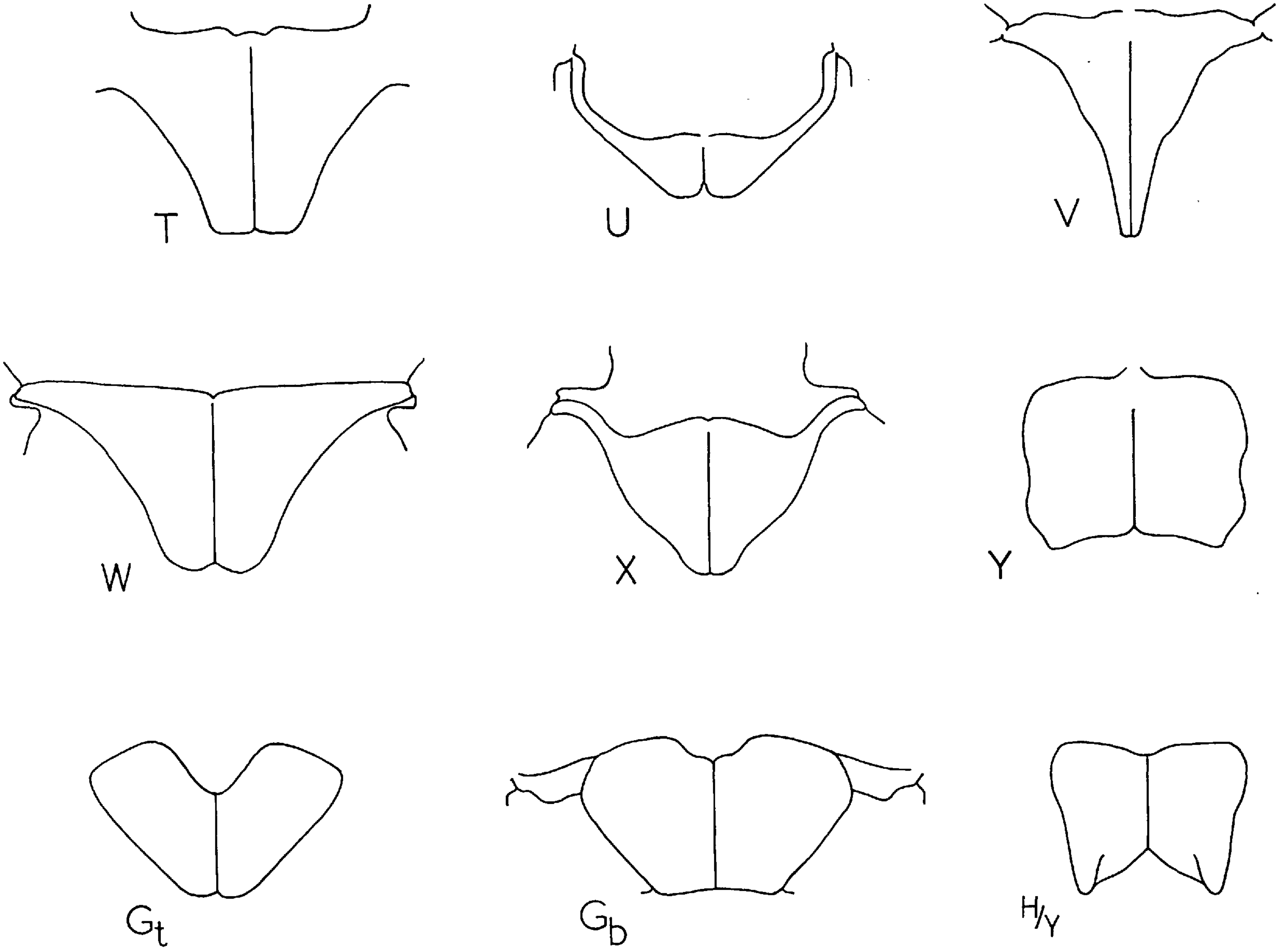


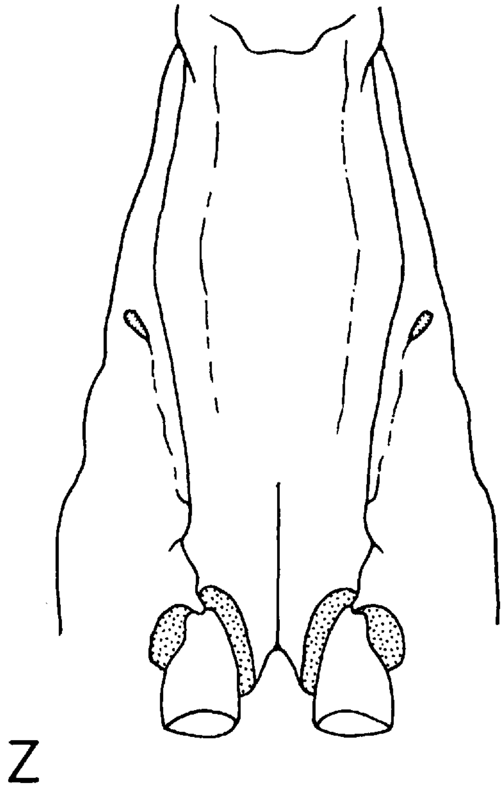
FIG.15(part)

FIGS. 16-20. Ventral view of the neck region, showing the cervical organ complex.

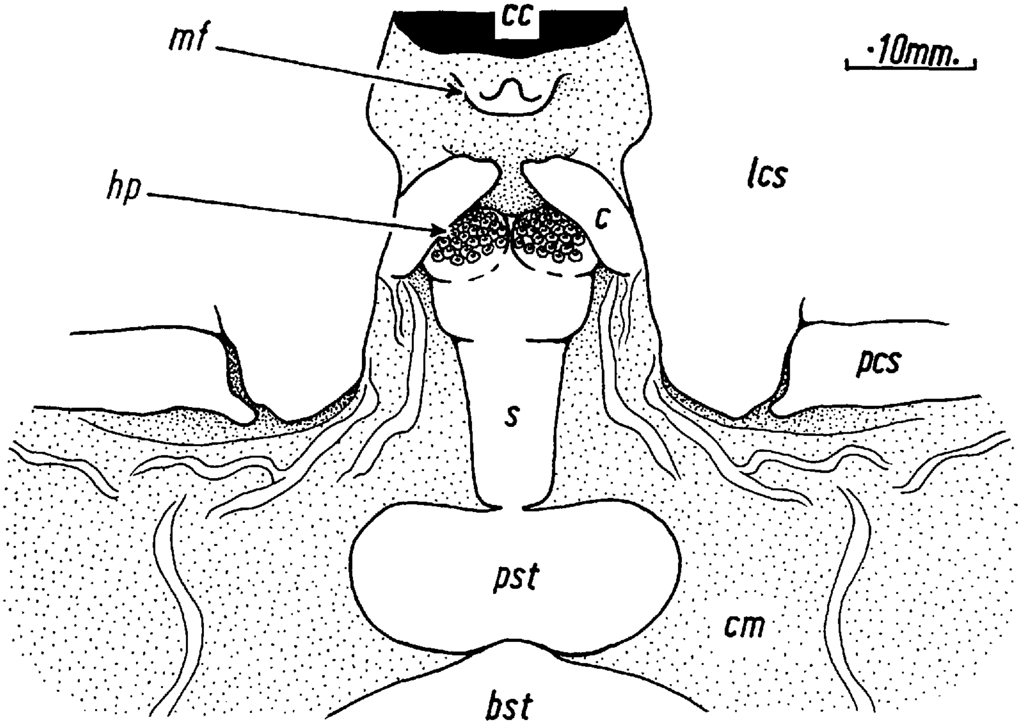
16. Sicus (Conopidae)
17, Megamerina (Megamerinidae)
18. Rivellia (Platystomatidae)
19. Dorycera (Otitidae)
20. Curtonotum (Curtonotidae)

LABELLING OF FIG. 16.

bst = basisternum
c = corniculus
cc = cervical cavity
cm = cervical membrane
hp = hair plates
lcs = lateral cervical sclerites
mf = median flap
pcs = posterior cervical sclerites
pst = presternum
s = sella



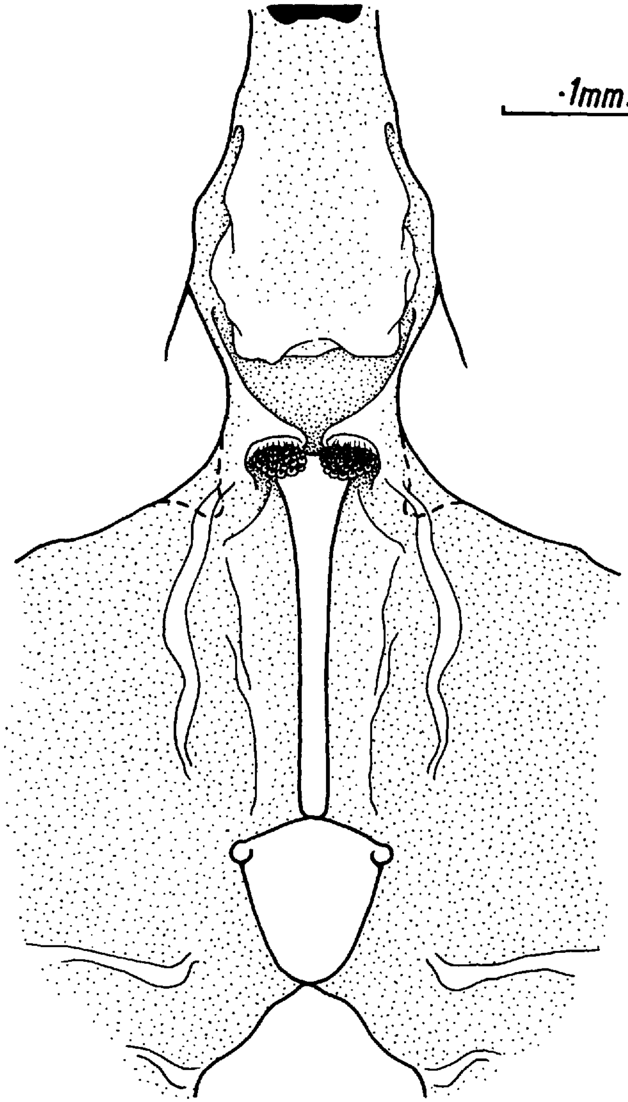
15 (contd.)



16

FIGS. 15-16

FIGS. 17-18



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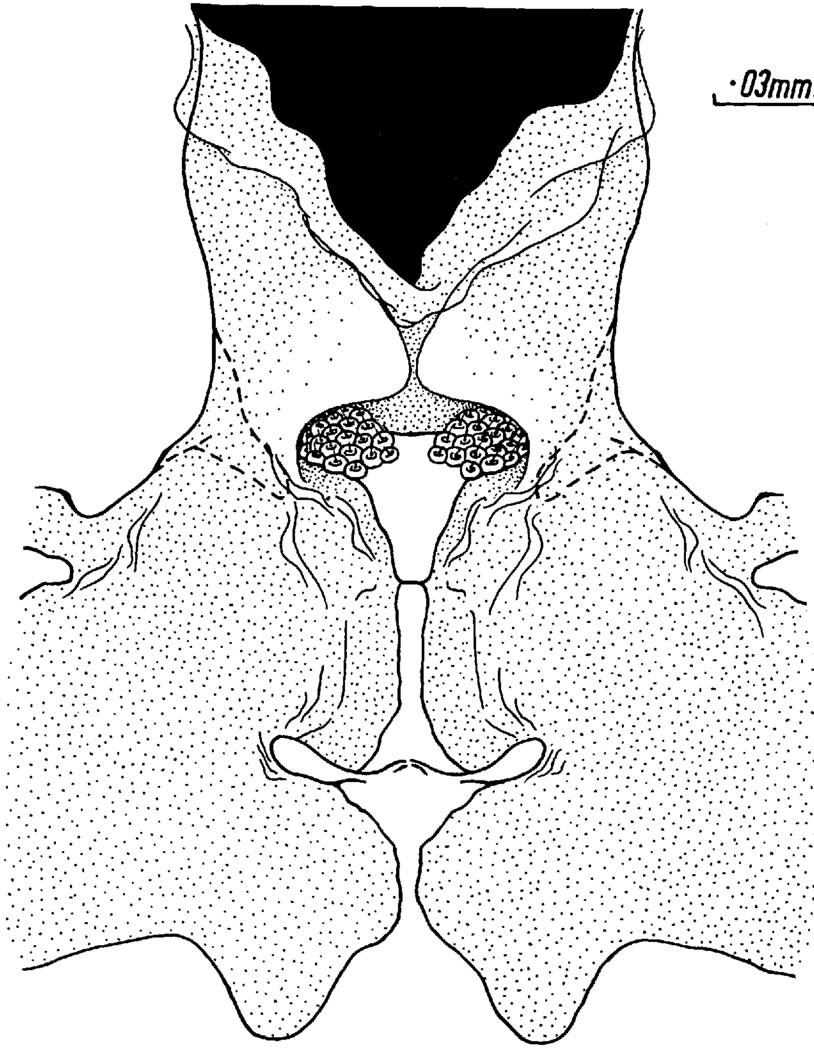

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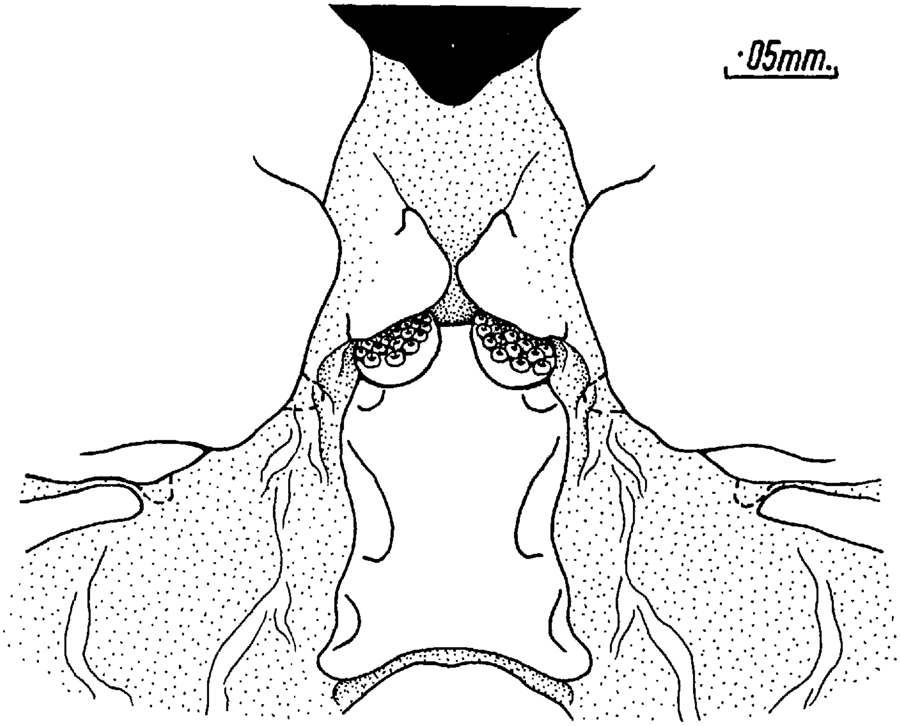

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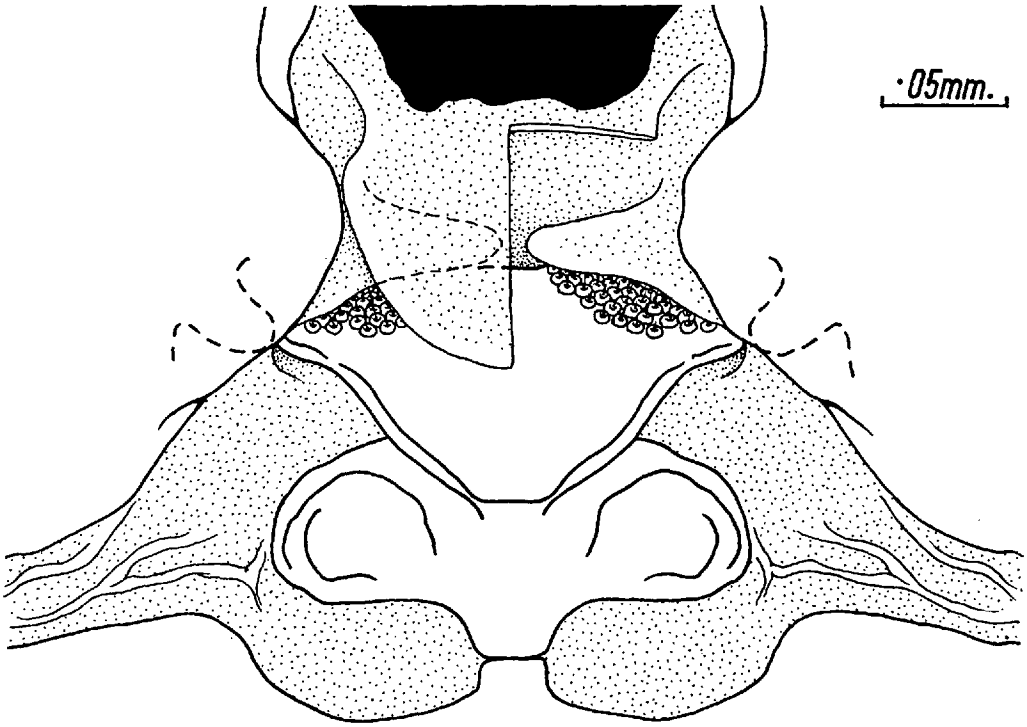


20

FIGS. 19-20

FIGS.21-30. Apodemes associated with the basisternum

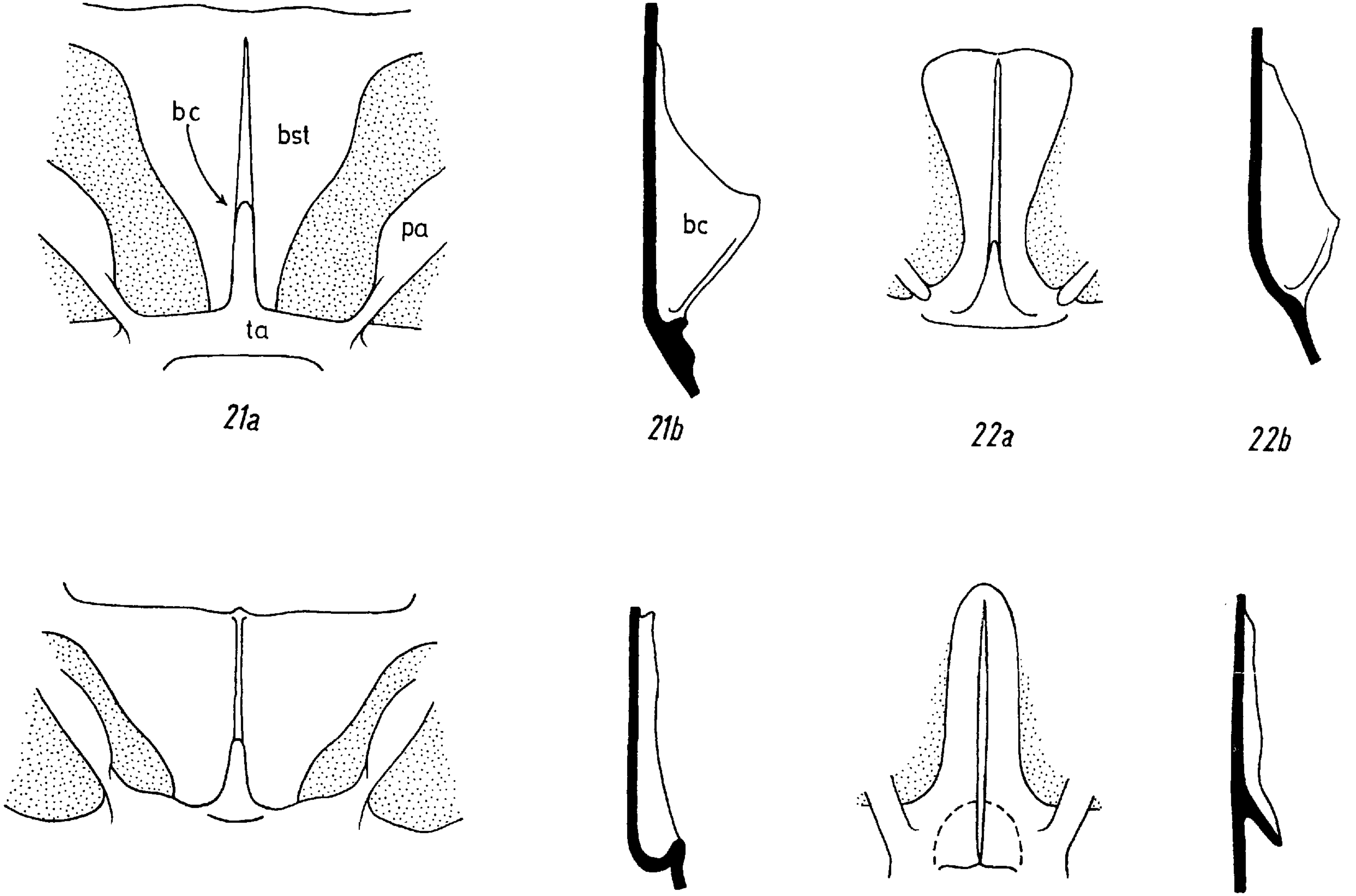
Internal (i.e. dorsal) and side views of the basisternum.

21a, b.	Helcomyza (Helcomyzidae).
22a, b.	Coelopa (Coelopidae)
23a, b.	Ephydra (Ephydridae)
24a, b.	Grammicomyia (Micropezidae)
25a, b.	Calobata (Micropezidae)
26a, b.	Toxopoda (Sepsidae)
27	Plagiostenopterina (Platystomatidae)
28	Sepedon (Sciomyzidae)
29	Palloptera (Pallopteridae)
30	Sphyracephala (Diopsidae)

LABELLING OF FIG.21.

bc = basisternal carina
bst = basisternum
pa = pleurosternal apophysis
ta = transverse apodeme

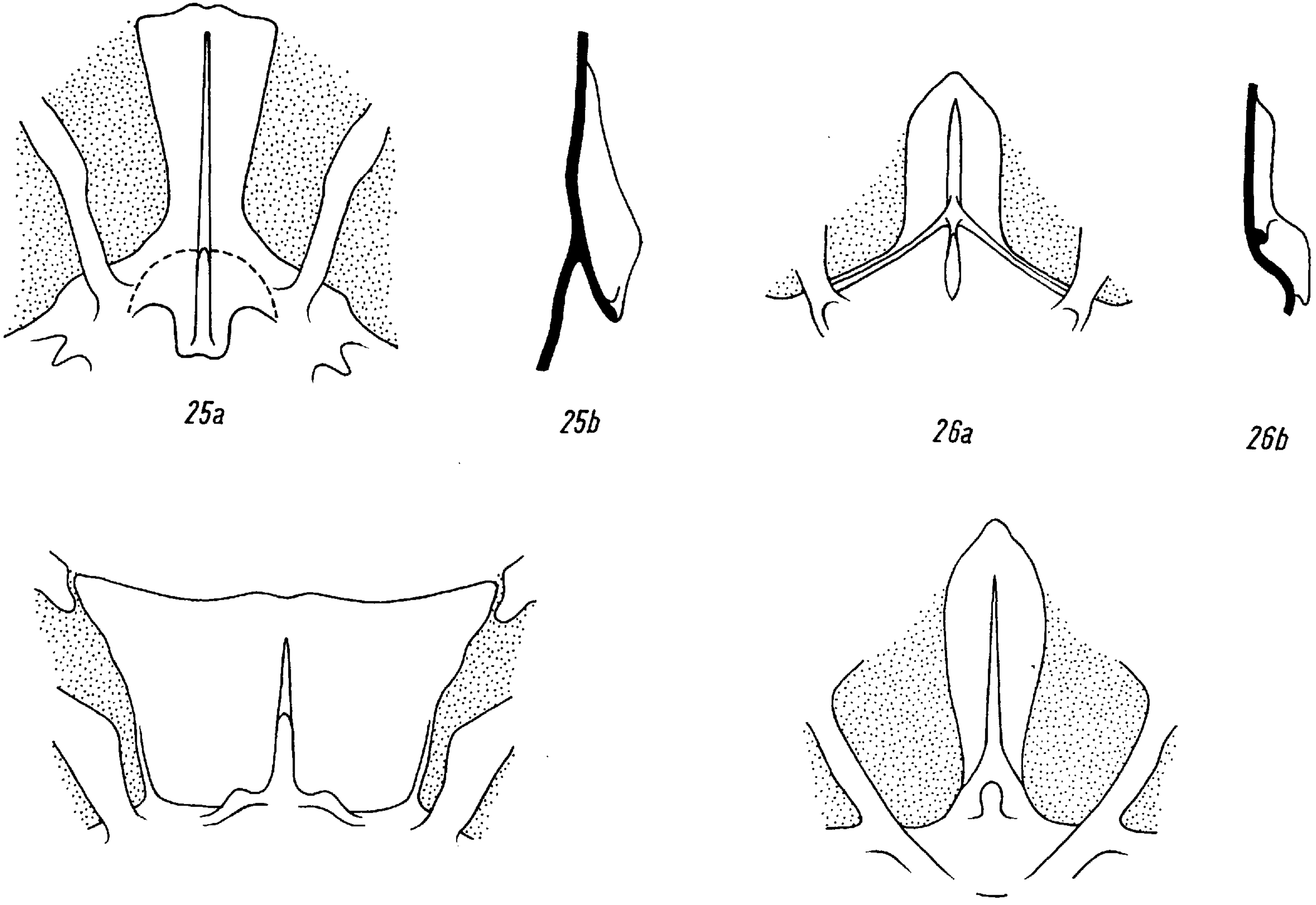
Note: The thickness of the cut edge of the basisternum has been exaggerated in 21b etc., to simplify the diagrams.



21a 21b 22a 22b

23a 23b 24a 24b

FIGS.21-24



25a

25b

26a

26b

27

28

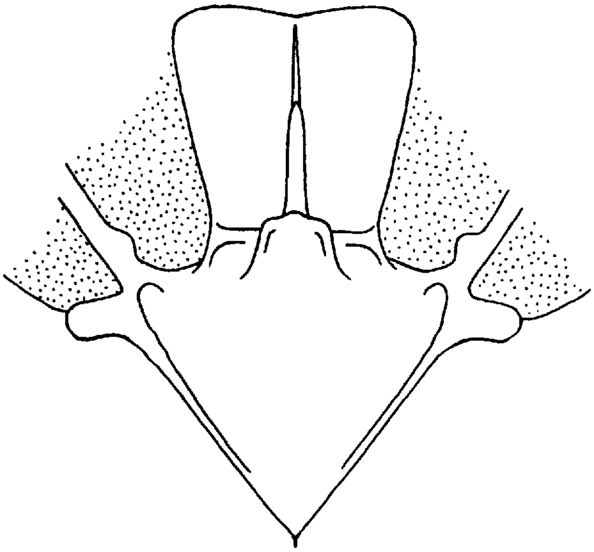
FIGS. 25-28

FIGS.31-36: Internal view of the basisternum, showing associated musculature.

31	Coelopa (Coelopidae)
32	Sepedon (Sciomyzidae)
33	Rivellia (Platystomatidae)
34	Lauxania (Lauxaniidae)
35	Curtonotum (Curtonotidae)
36	Sphyracephala (Diopsidae)

LABELLING:

a = sternal adductor
cr = coxal rim
p = sternal promotor
p_1 = strand of the sternal promotor
p_2 = " " " " ,"



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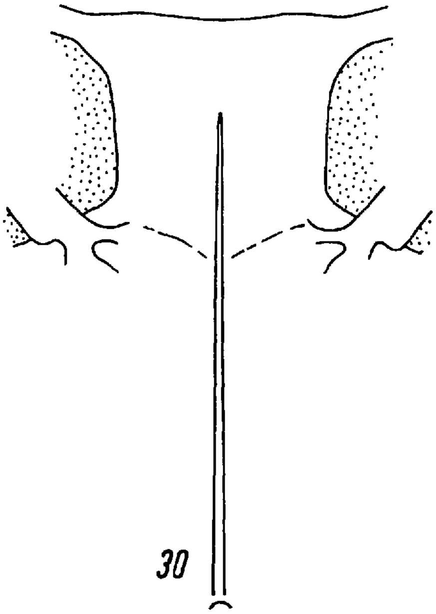

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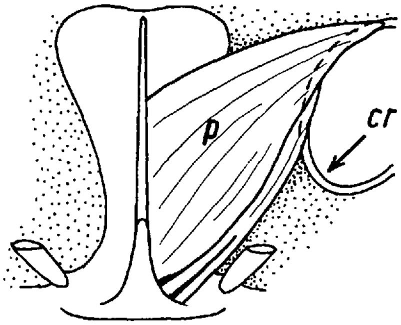

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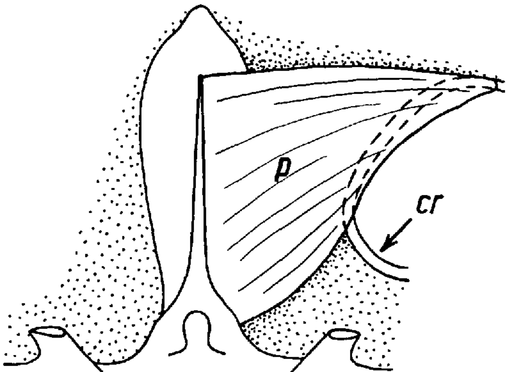

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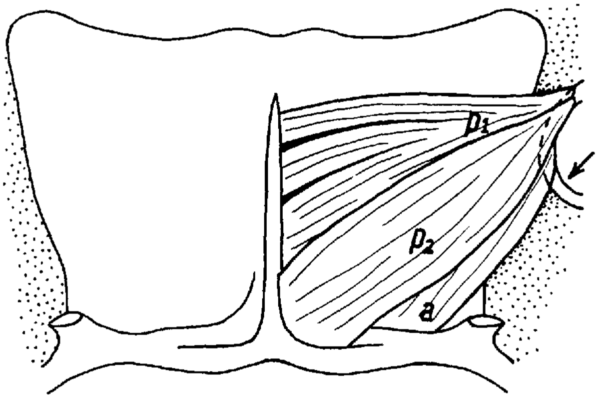


33

FIGS. 29-33

FIG.37: Diagrams showing the combinations of sternal variants found in individual genera.

The lettering scheme used to denote the different variants is the same as that used in figs. 13-15.

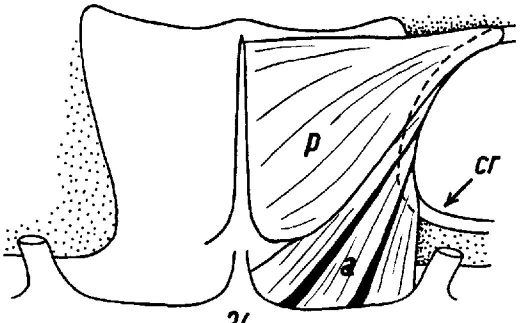
37a. Set of combinations found in genera in which more than one species possesses each sternal variant.

37b (i-iii) Set of combinations found in genera where at least one of the sternal variants is represented in only a single species, but the combination concerned is found in at least two genera (but see note 1 below). This set has been broken into three parts for ease of representation.

37c. Set of combinations common to both 37a and 37b (see notes 1-3 below).

Notes:

1. A single line joining two variants indicates a combination found in only one genus in figs.37a and 37b, and in only one genus of each of the other two sets in fig. 37c.
2. A double line indicates a combination found in more than one genus in figs. 37a and 37b, and in more than one genus in each of the other two sets in fig. 37c.
3. The dotted line between H and Y in fig. 37c indicates that this combination has only occurred in one of the other two sets.
4. Variant H has been given greater prominence because it acts as the link between all sets of combinations.
5. The actual placing of variants and the distances between them have not been arranged to have any particular significance.



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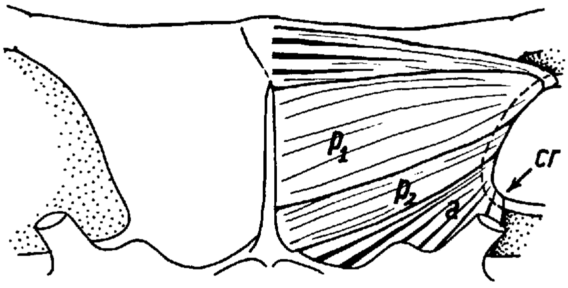

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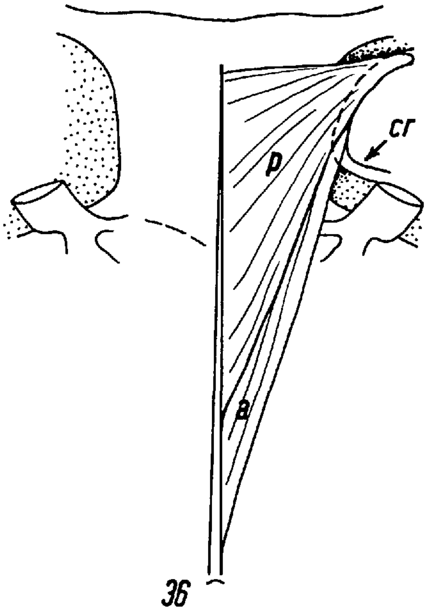

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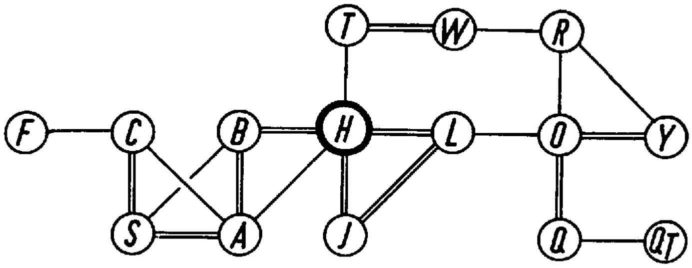
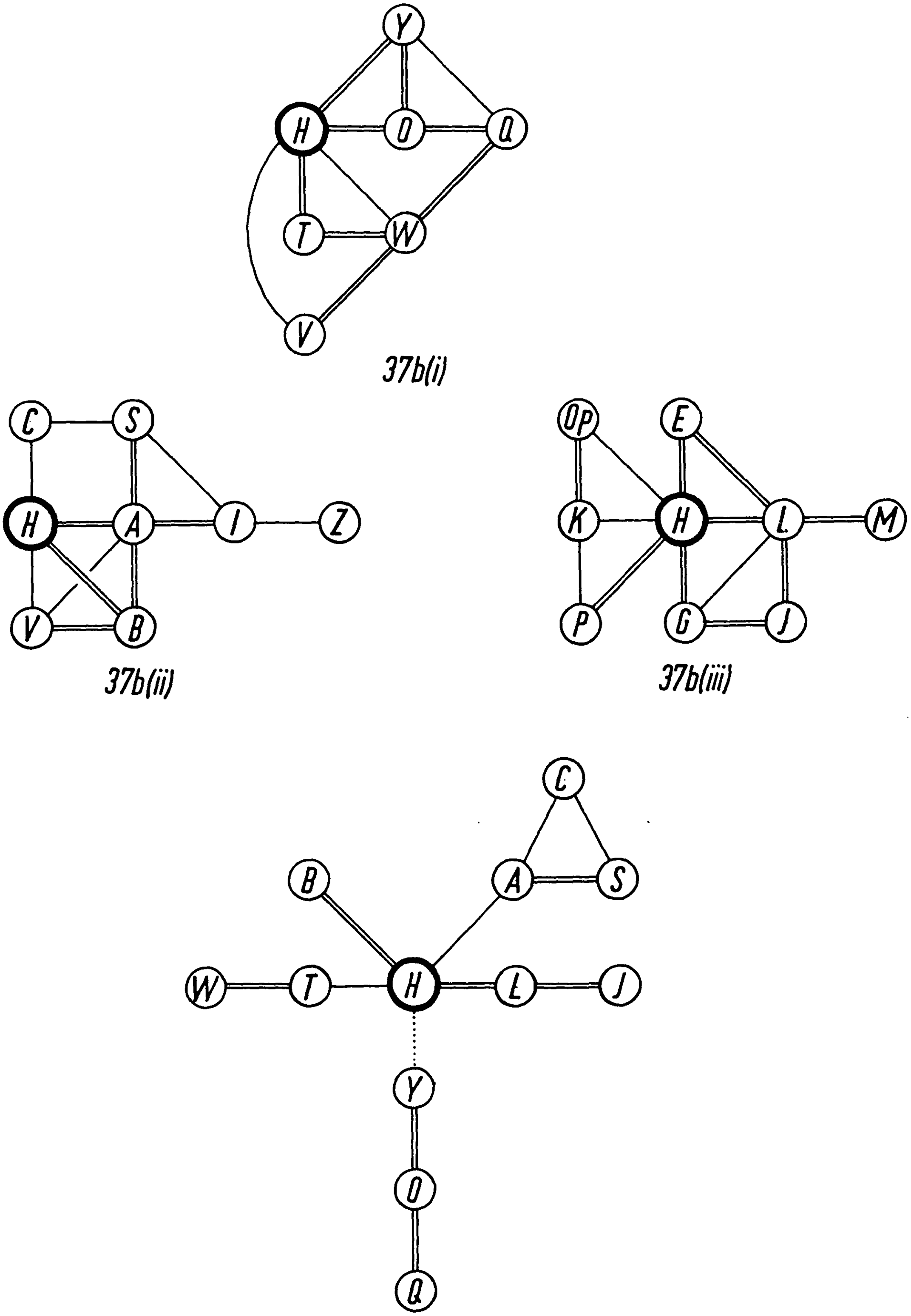


37a

FIGS. 34-37(part)



37b(i)

37b(ii)

37b(iii)

37c

FIG. 37(cont'd)

FIGS.38-39: Range of prosternal variation at different taxonomic levels.

38 Histograms showing the frequency with which different numbers of sternal variants occur within a genus.

39 Scatter diagram showing the frequency with which different numbers of sternal variants occur within a family.
Each family currently recognised as well-established is represented by an open circle.
Each family currently regarded as doubtfully established is represented by a cross.

Note:

In fig.38, only those genera for which five or more species have been examined are used.

In fig. 39, families for which only one genus has been examined, are excluded.

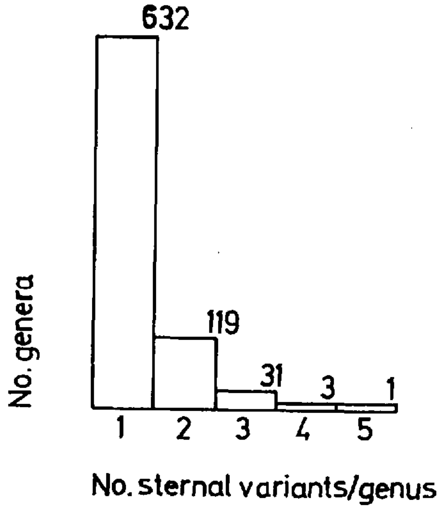

632
119
31
3
1
No. genera
1
2
3
4
5
No. sternal variants/genus

Fig. 38

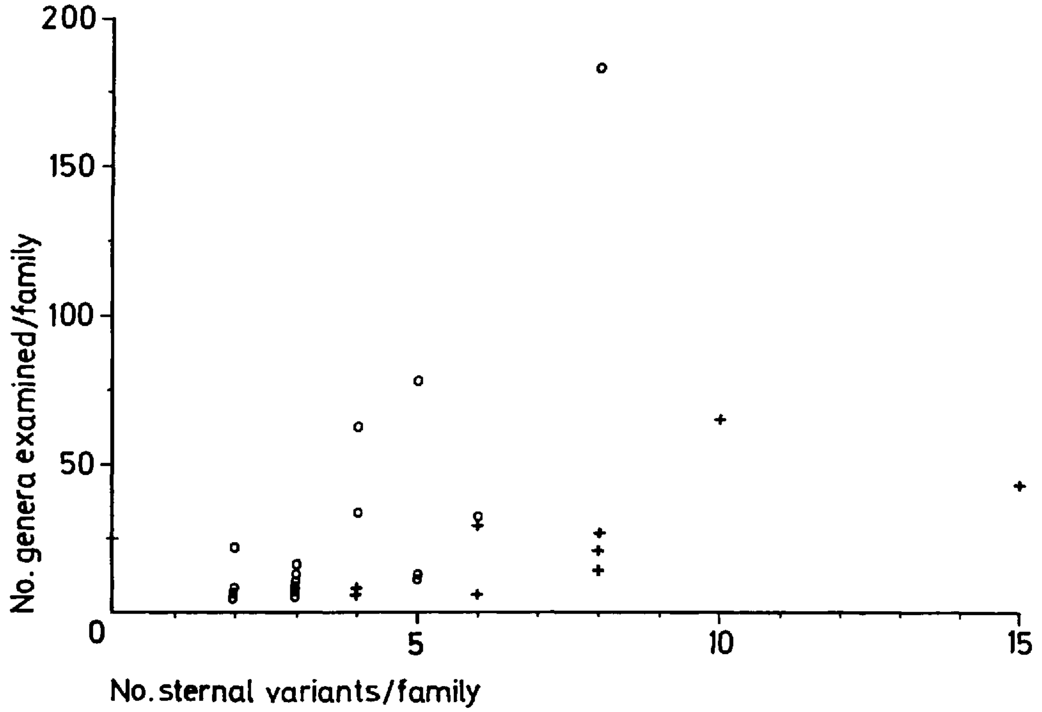

200
150
100
50
0
5
10
15
No. genera examined/family
No. sternal variants/family

Fig. 39

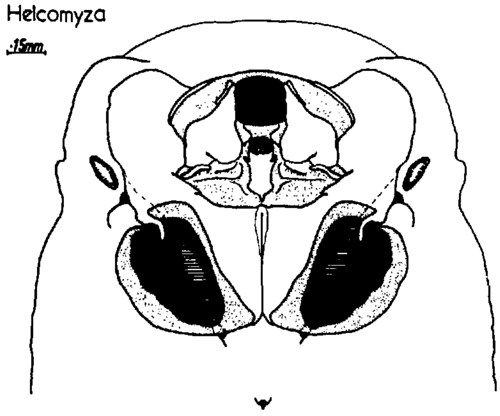
FIGS.40-56: Ventral view of the prothoracic region of some Acalypterates.

40	Helcomyza (Helcomyzidae)
41	Coelopa (Coelopidae)
42	Nemopoda (Sepsidae)
43	Dryomyza (Dryomyzidae)
44	Piophila s.g. Allopiophila (Piophilidae)
45	Lonchaea (Lonchaeidae)
46	Neottiophilum (Neottiophilidae)
47	Canace (Canaceidae)
48	Madiza (Milichiidae)
49	Desmometopa (Milichiidae).
50	Copromyza s.g. Stratioborborus (Sphaeroceridae)
51	Drosophila (Drosophilidae).
52	Curtonotum (Curtonotidae).
53	Diastata (Diastatidae).
54	Ephydra (Ephydridae)
55	Parydra (Ephydridae)
56	Lipara (Chloropidae)

Note:

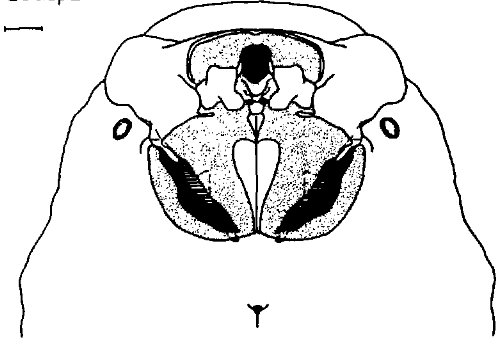
For labelling consult fig. 12.

Helcomyza



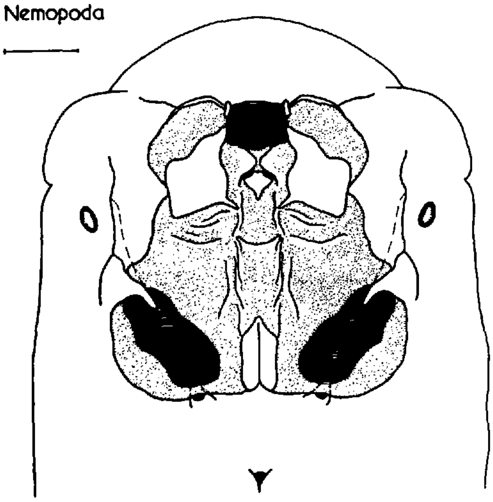
40

Coelopa



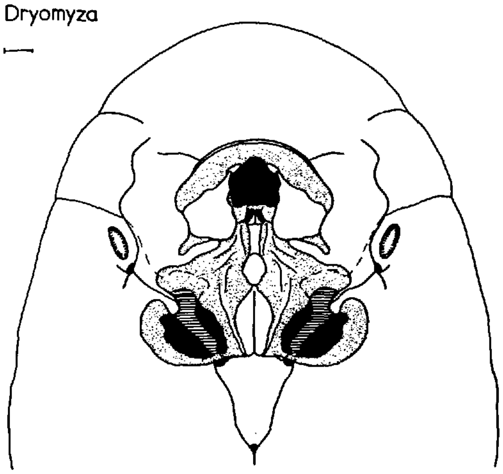
41

Nemopoda



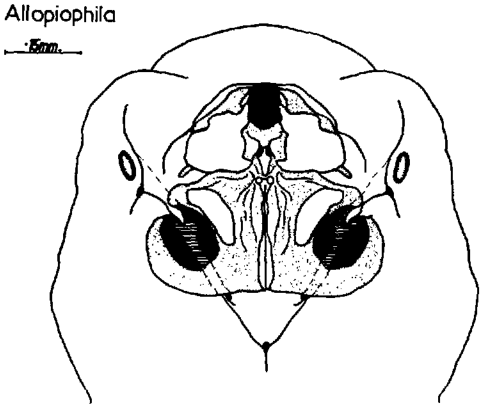
42

Dryomyza

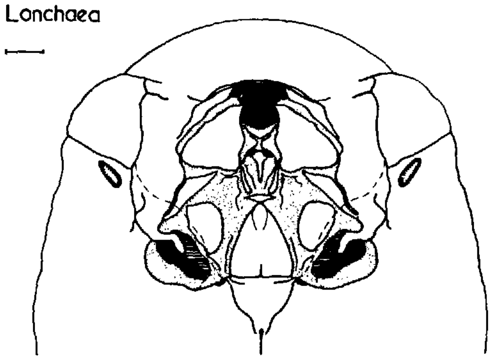


43

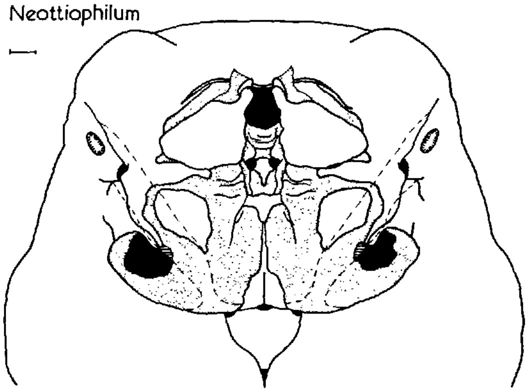
FIGS.40-43



44

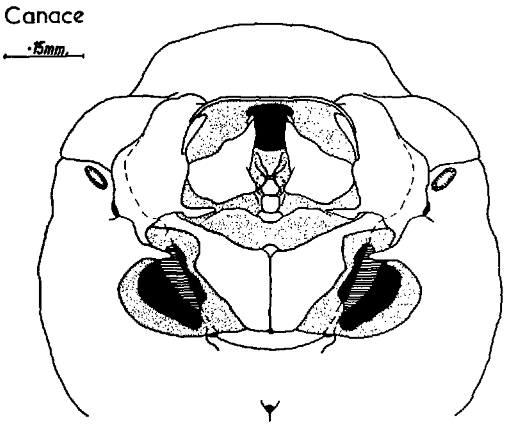


45



46

FIGS. 44-46



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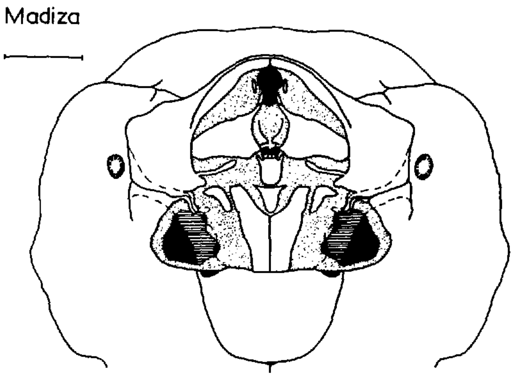

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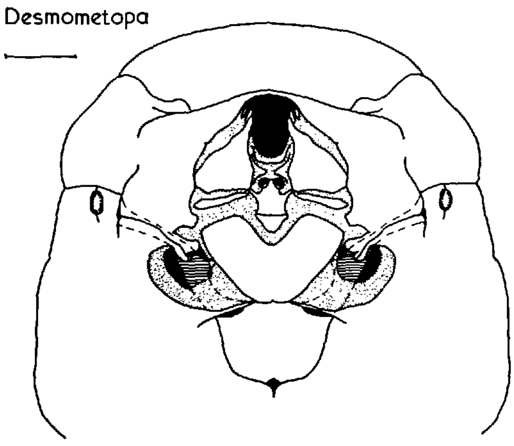
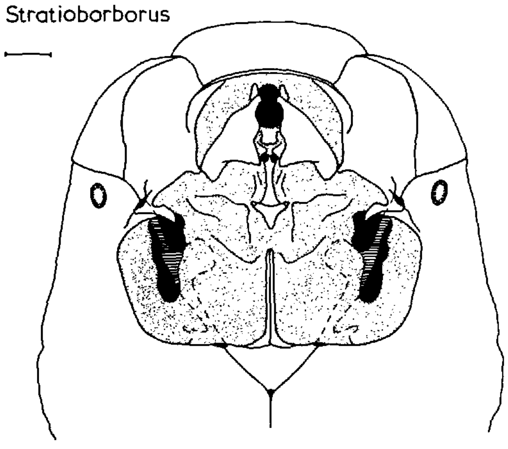
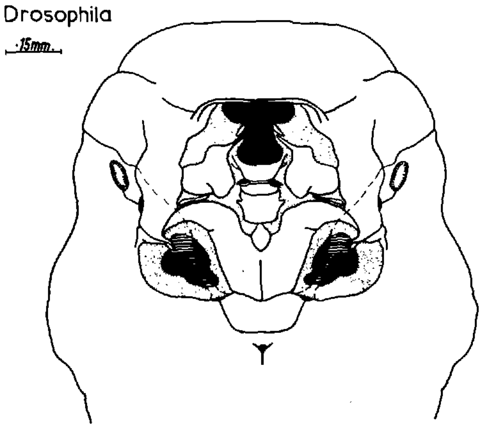


49

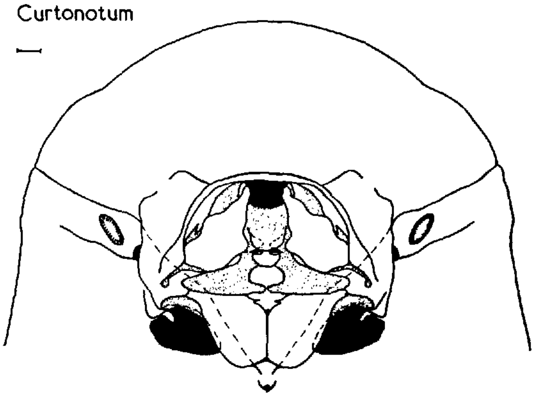


50

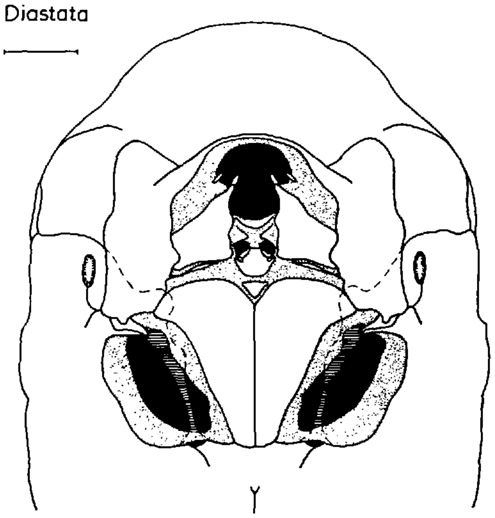
FIGS. 47-50



51

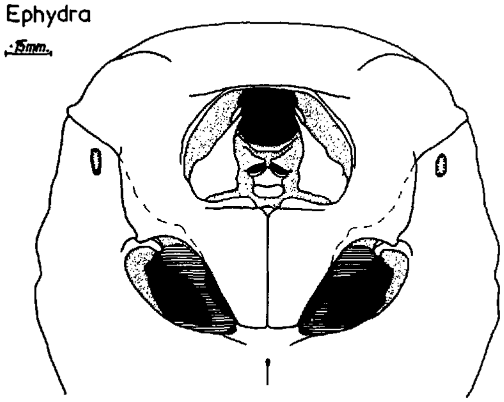


52

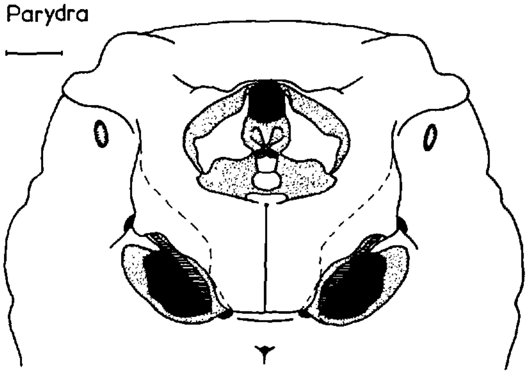


53

FIGS. 51-53



54



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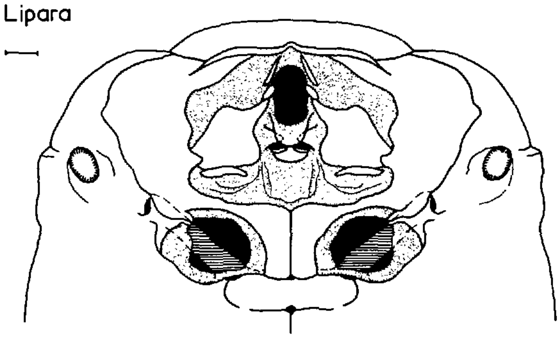


56

FIGS. 54-56

FIGS. 57-59: Acalypterate prosterna: Conopidae, Sciomyzoidea, Pallopteroidea, Milichioidea.

		STERNAL VARIANT
57a	Stylogaster (Conopidae)	C
b	Physocephala (")	H/C
c	Parazodion (")	A
d	Thecophora (")	I
e	Sciomyza (Sciomyzidae)	B
f	Rhopalomera (Rhopalomeridae)	W
g	Sepedon (Sciomyzidae)	A
h	Coelopa (Coelopidae)	A
i	Themira (Sepsidae)	H
j	PPherbellia (Sciomyzidae)	V
k	Sepsis (Sepsidae)	S
58a	Neomaorina (Pallopteridae)	H
b	Piophila (Piophilidae)	C
c	Piophila (Piophilidae)	A
d	Actenoptera (Neottiophilidae)	
e	Aenigmatomyia (Pallopteridae)	C
f	Pseudopyrgota (Pallopteridae)	A
g	Lamprolonchaea (Lonchaeidae)	C
h	Dasiops (Lonchaeidae)	S
59a	Australimyza (Milichiidae)	C
b	Canaceiodes (Canaceidae)	N
c	Phyllomyza (Milichiidae)	B
d	Archileptocera (Sphaeroceridae)	S
e	Leptometopa (Milichiidae)	Gb
f	Pareccoptomma (Milichiidae)	Gt
g	Braula (Braulidae)	W
h	Tethina (Tethinidae)	T

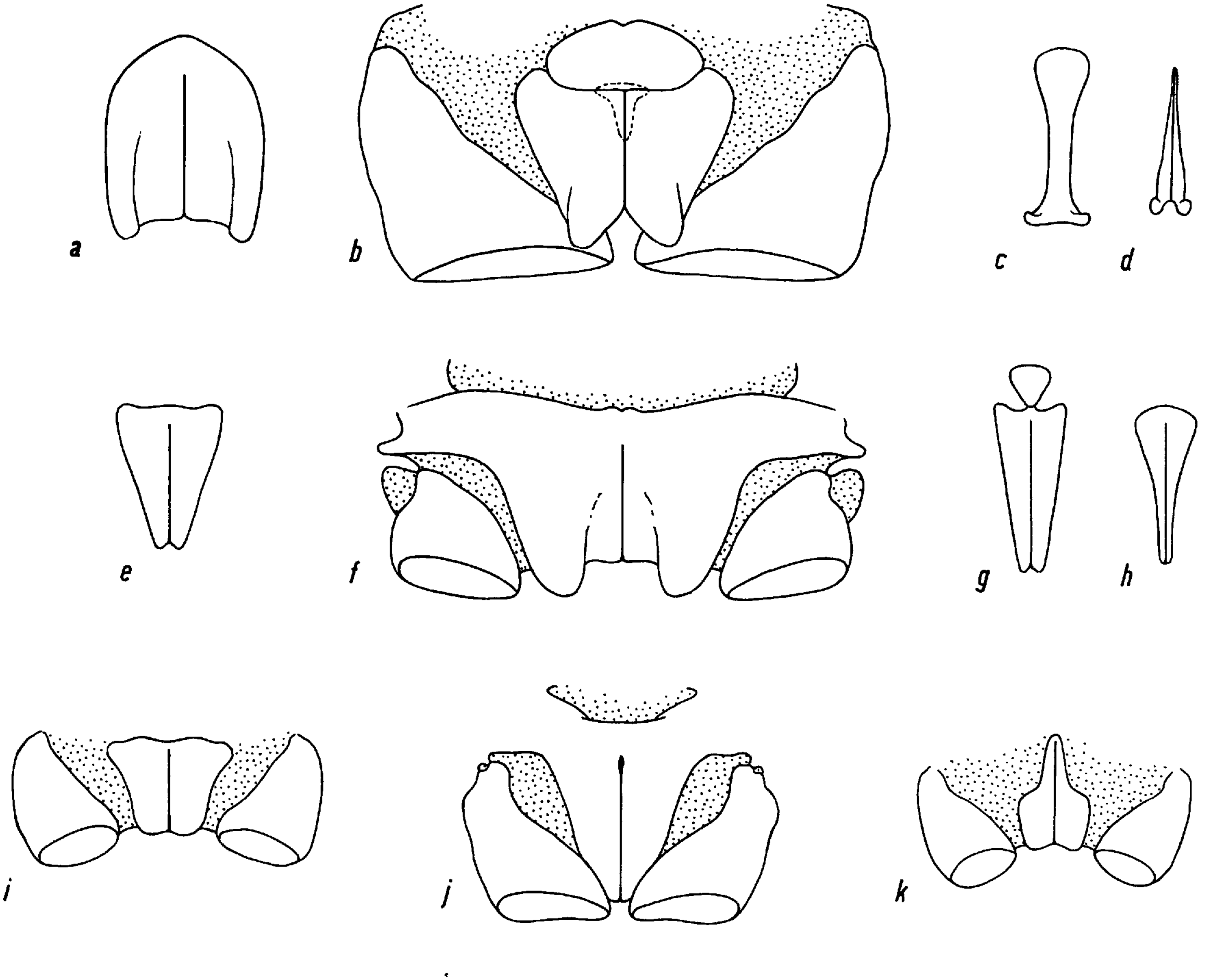


FIG.57

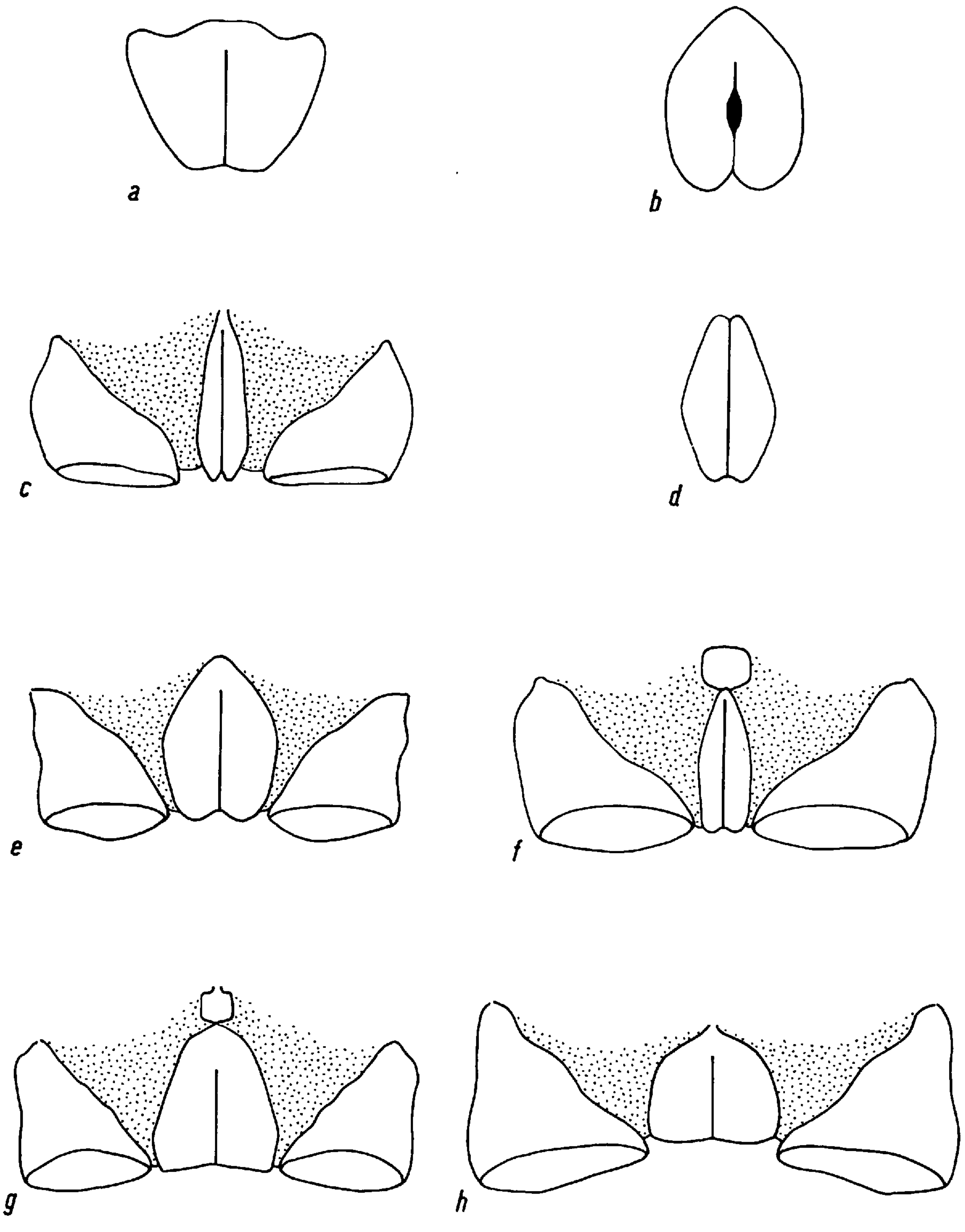


FIG. 58

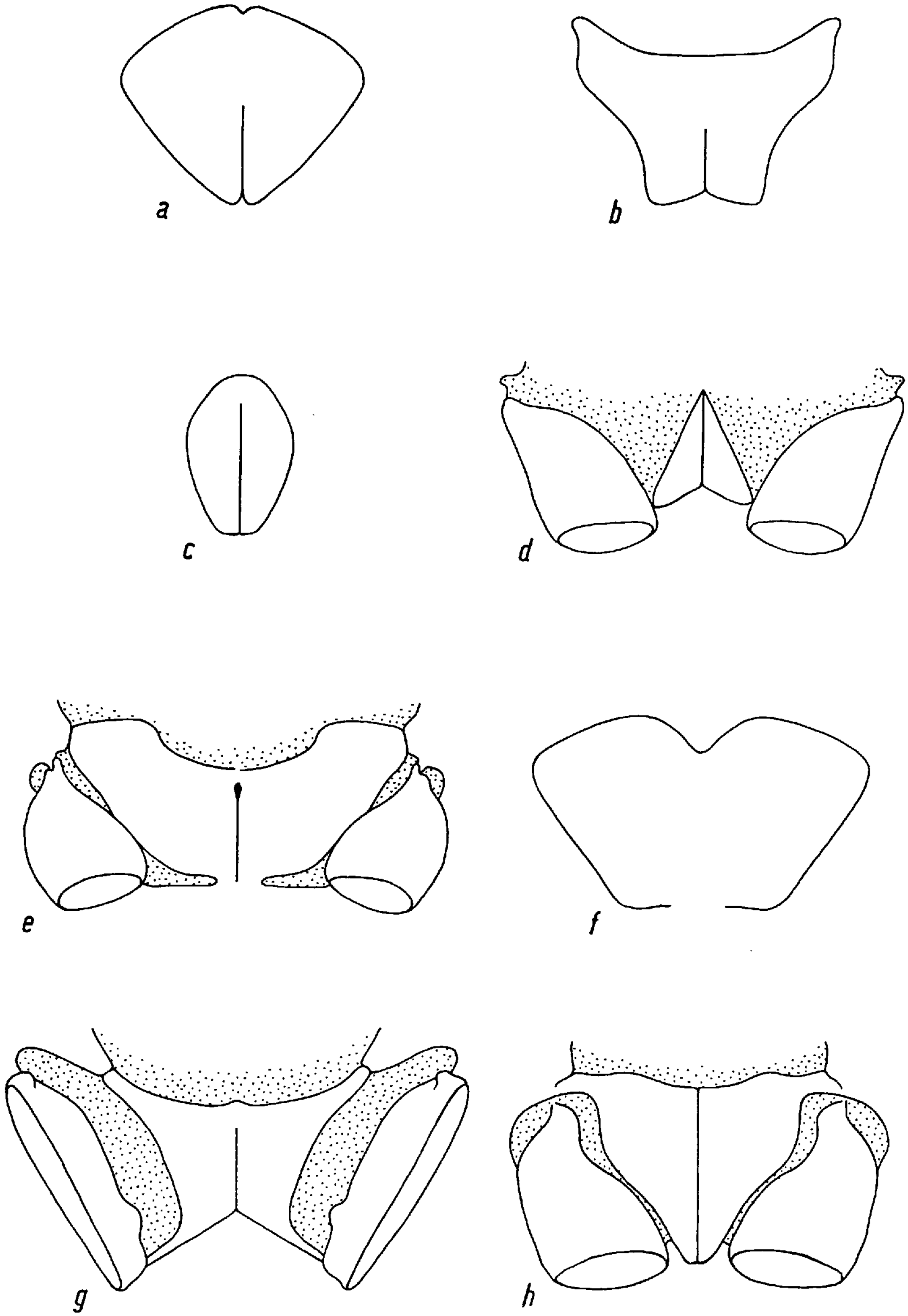


FIG. 59

FIGS.60-61: Acalypterate prosterna: Drosophiloidea, Chloropidae.

		STERNAL VARIANT
60a	Cacoxenus (Drosophilidae)	L
b	Paraleucophenga (")	N
c	Chymomyza (")	T
d	Chymomyza (")	F
e	Ditrichophora (Ephydridae)	T
f	Anasaeiomyia (Curtonotidae)	Q
g	Dimecoenia (Ephydridae)	T
h	Leptopsilopa (")	Q
61a	Camilla (Camillidae)	T
b	Oscinosoma (Chloropidae)	T
c	Alombus (")	T
d	Meromyza (")	Q/T
e	Meromyza (")	V
f	Epimadiza (")	V
g	Cetema (")	W
h	Gaurax (")	W

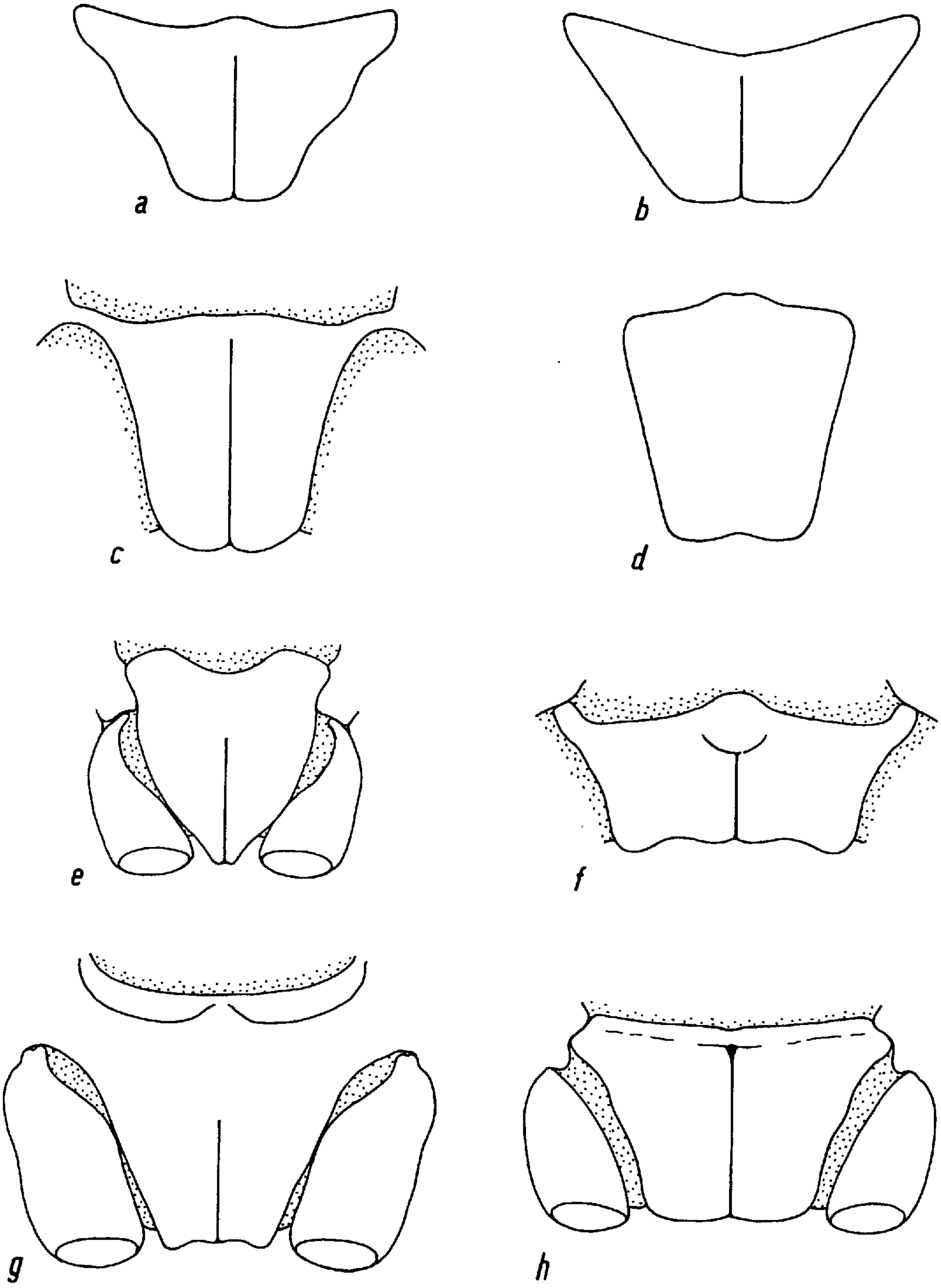


FIG. 60

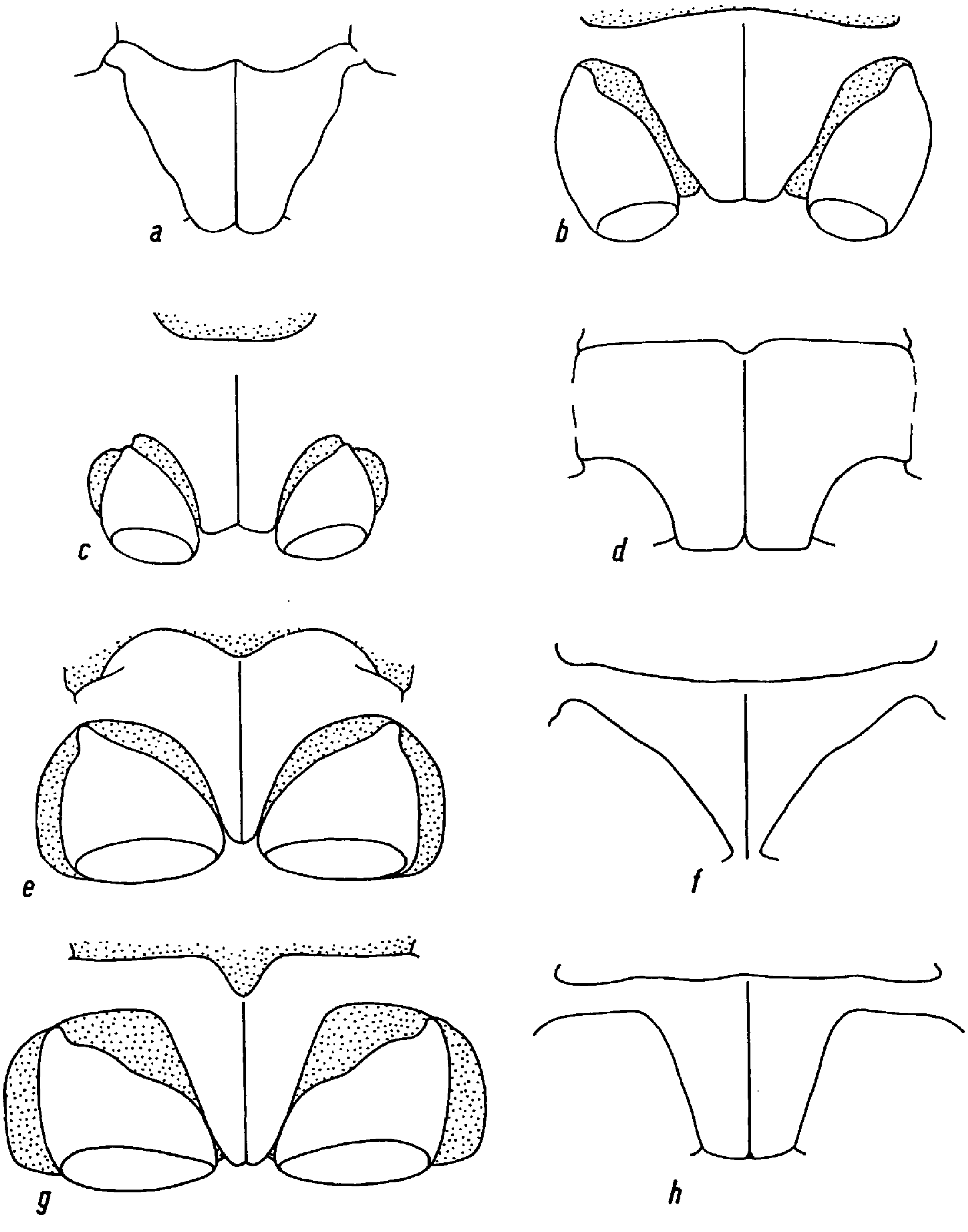


FIG. 61

GS.62-68: Polar Diagrams.

62 The sternal variants are each represented by a code letter and arranged on the diagram according to their degree of physical similarity to one another. Dotted lines are used between pairs of variants which occur together in the same genus (see fig. 37).

63 - 68 Exactly the same arrangements of sternal variants is used here, as in fig. 62. Each diagram demonstrates the range of sternal variation found in a particular superfamily; the variants represented are left blank, the rest of the diagram is blacked out. Each family is represented by a symbol and the symbols have been used to plot in on the polar diagram the positions belonging to the sternal variants occurring in each family.

"POLAR DIAGRAM"

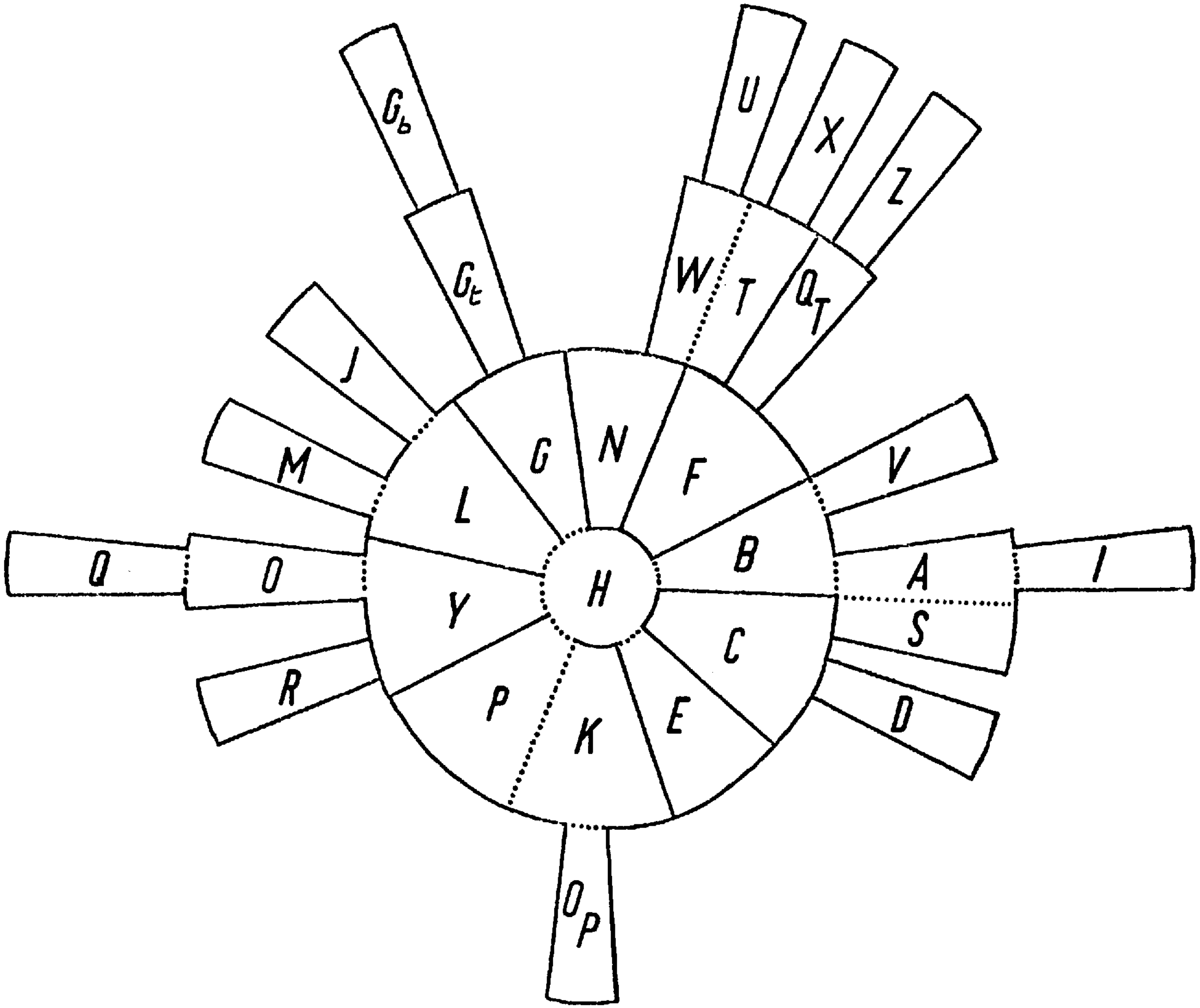
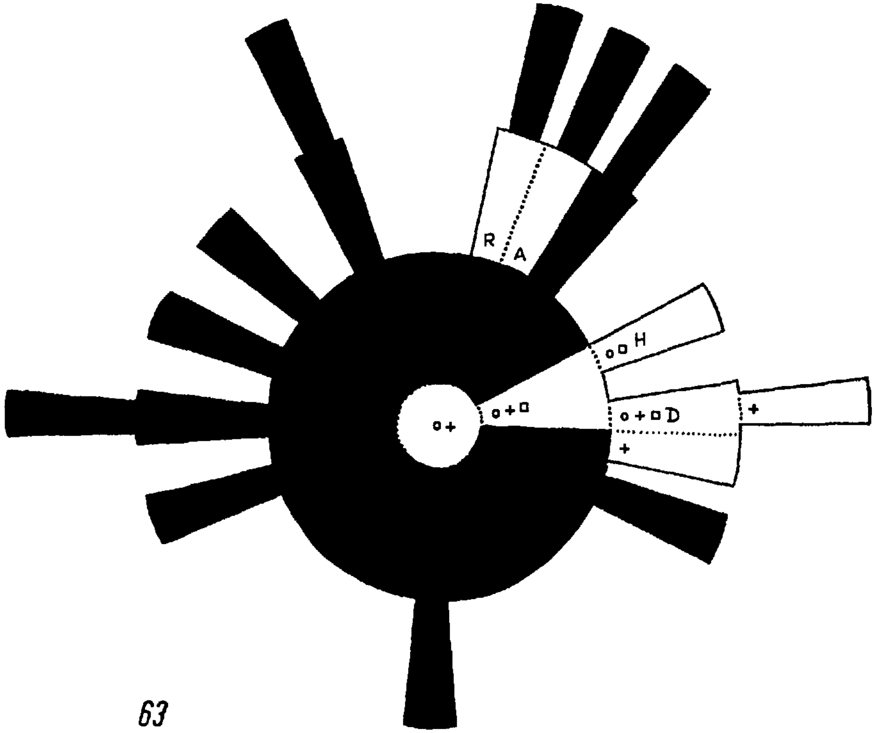


FIG. 62

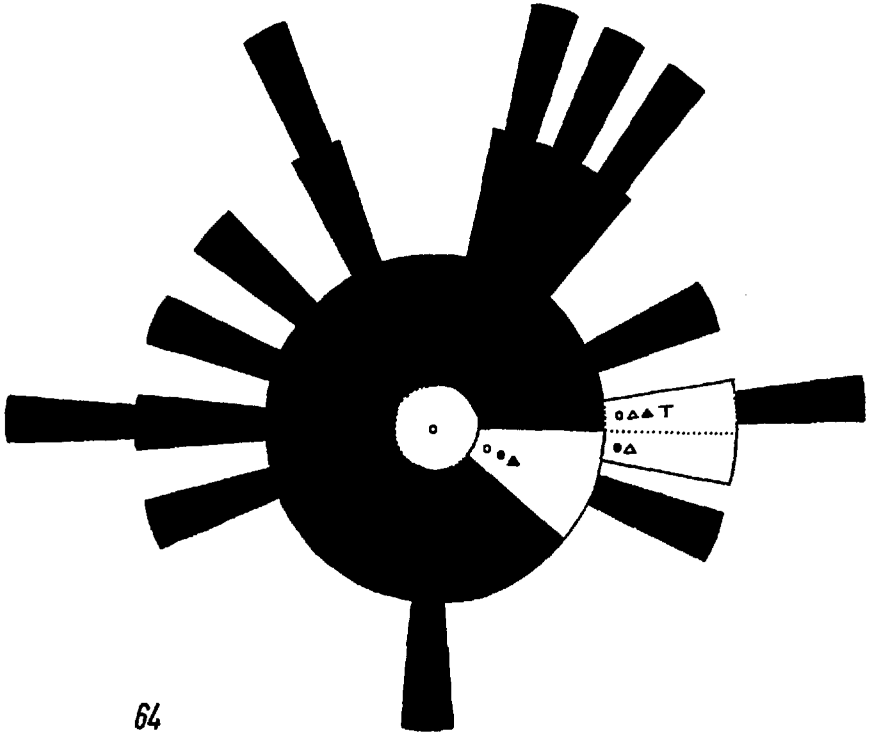
FIGS. 63-64



63

SCIOMYZOIDEA: Polar Diagram

Apterosepsis=A
Coelopidae=□
Dryomyzidae=D
Helcomyzidae=H
Rhopalomeridae=R
Sciomyzidae=○
Sepsidae=+

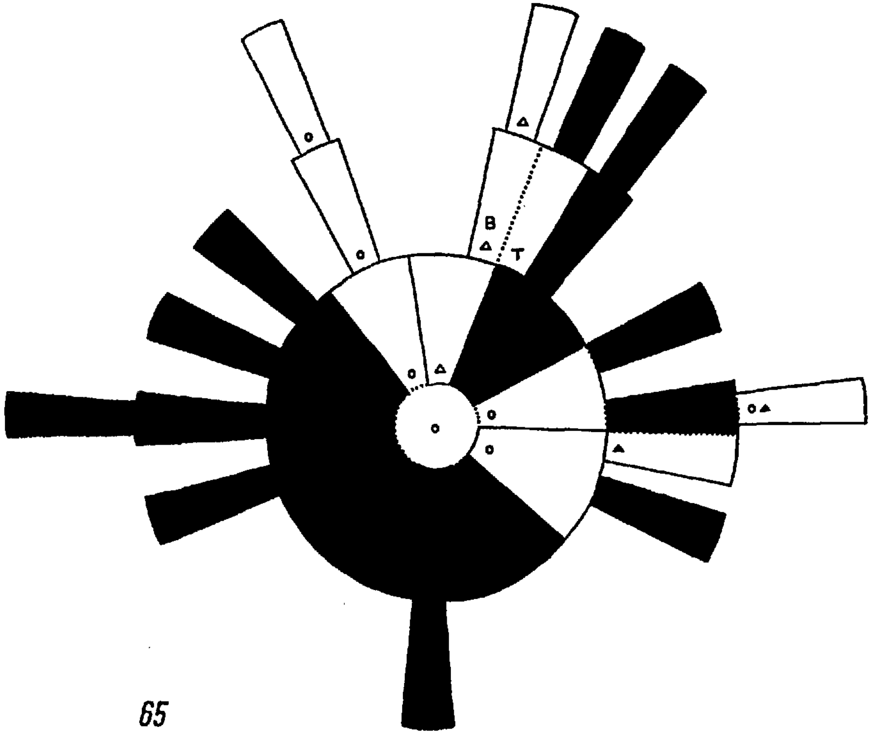


64

PALLOPTEROIDEA: Polar Diagram

Lonchaeidae=●
Neottiophilidae=△
Pallopteridae=○
Piophilidae=▲
Thyreophoridae=T

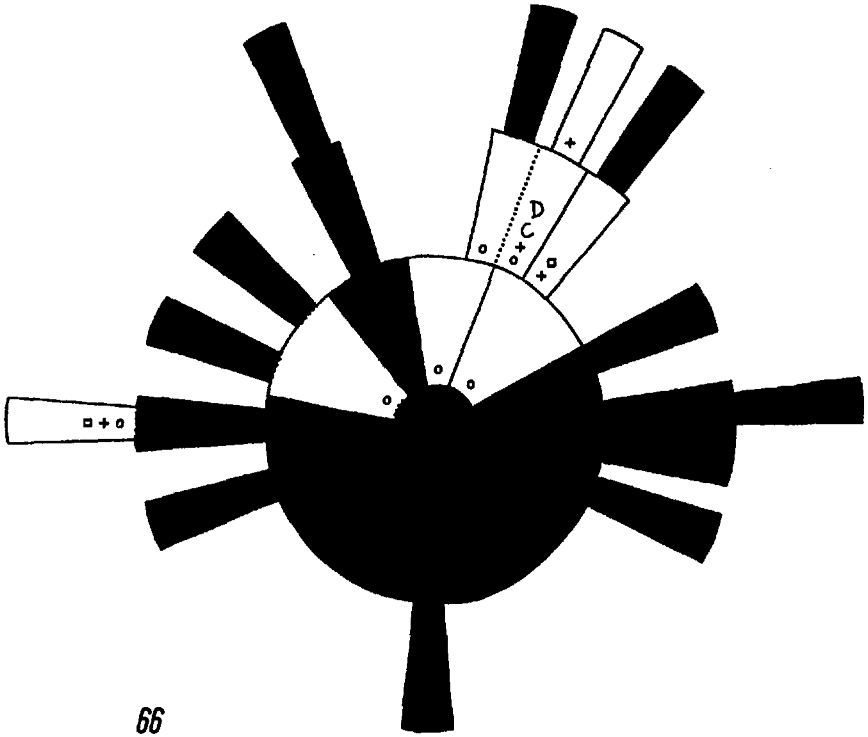
FIGS.65-66



65

MILICHIOIDEA: Polar Diagram

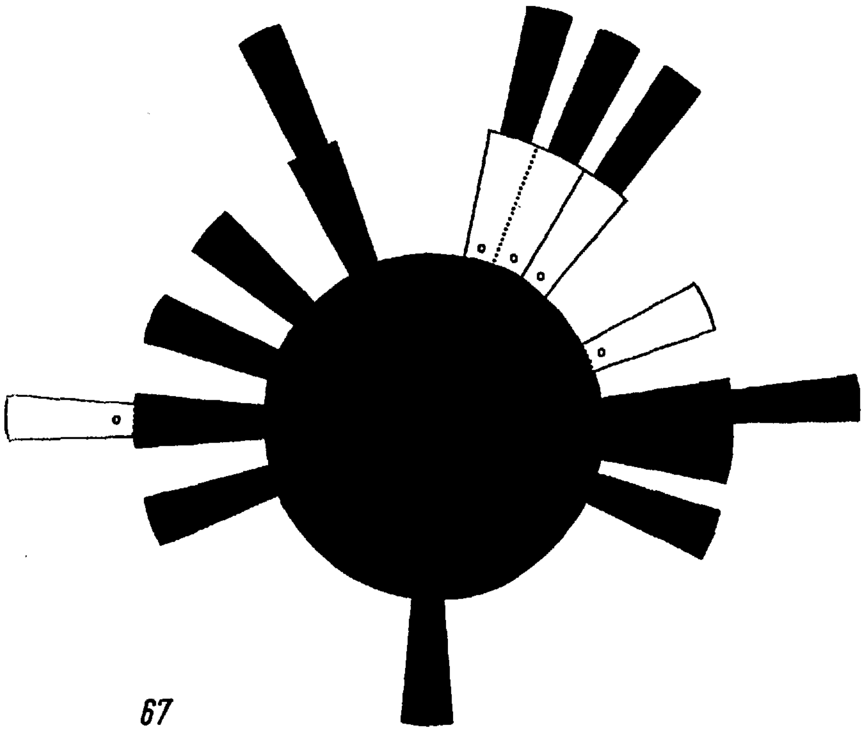
Braulidae=B
Canaceidae=△
Milichiidae=○
Sphaeroceridae=▲
Tethinidae=T



66

DROSOPHILOIDEA: Polar Diagram

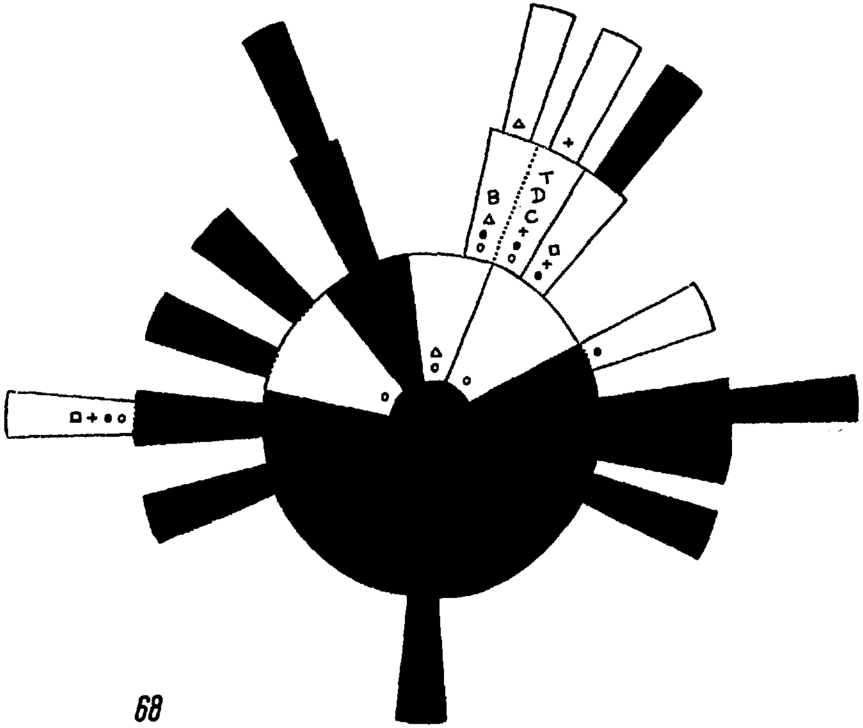
Camillidae=C
Curtonotidae=□
Diastatidae=D
Drosophilidae=○
Ephydridae=+



67

CHLOROPOIDEA: Polar Diagram

Chloropidae=○



68

"NEW GROUP" DROSOPHILOIDEA: Polar Diagram

Braulidae=B
Camillidae=C
Canaceidae=△
Chloropidae=●
Curtonotidae=□
Diastatidae=D
Drosophilidae=○
Ephydridae=+
Tethinidae=T

FIGS.67-68